Lycopsids from the *Glossopteris* flora: contributions to poorly understood Permian Gondwanan plants

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“The earth is not a mere fragment of dead history, stratum upon stratum like the leaves of a book, to be studied by geologists and antiquaries chiefly, but living poetry like the leaves of a tree, which precede flowers and fruit, – not a fossil earth, but a living earth”

H. D. Thoreau in Walden (1854)

This cumulative thesis is based on the following publications:

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Spiekermann, R., Jasper, A., Bamford, M.K., Uhl, D., 2022. A fresh look on the morphology of *Azaniadendron* Rayner: a ligulate lycopsid from the Permian of Gondwana. Review of Palaeobotany and Palynology 307, 104780. https://doi.org/10.1016/j.revpalbo.2022.104780.

Spiekermann, R., Jasper, A., Pozzebon-Silva, Â., Carniere, J.S., Benício, J.R.W., Guerra-Sommer, M., Uhl, D., 2023. Small but not trivial: *Nothostigma sepeensis* sp. nov., a lycopsid from the Cisuralian (early Permian) of the Paraná Basin, Brazil. Journal of South American Earth Sciences 122, 104188. https://doi.org/10.1016/j.jsames.2022.104188.

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Abstract

The Permian witnessed a transition from an icehouse to a greenhouse world. Elucidating the vegetation response to that transition is a remarkable goal, but only achievable if we have a sound understanding of the plants that thrived during those times. Here, I focus on the problematics of the lycopsids from the Permian *Glossopteris* flora of Gondwana. The fossil record of these lycopsids comprises mainly fragmented remains of sub- to arborescent forms, and little is known about them. This thesis includes four papers on these plants. *Publication 1* deals with late Palaeozoic lycopsid fossils from the Paraná Basin in South America. It delimits their updated stratigraphical distribution in the basin and provides a baseline for future research on these lycopsids. *Publication 2* deals with *Azaniadendron* Rayner from the Guadalupian of South Africa. Its reproductive structures are re-interpreted as arranged in fertile zones, and evidence for a ligule is reported, solving, at least for this genus, a dilemma about the presence of this feature in lycopsids from *Glossopteris* flora. Also, its leaf cushion variations are described, using an approach that may help to overcome the challenges in reliably identifying and circumscribing lycopsid fossil-taxa represented by fragmented axes. *Publication* 3 describes lycopsid axes from the Cisuralian of Brazil, using methods that include a vinyl polysiloxane casting technique, which revealed their epidermal features. Based on these fossils, we proposed the new fossil-species *Nothostigma sepeensis* Spiekermann et al. This paper reveals how the lack of studies of long-ignored remains, has been obscuring the lycopsid diversity of the *Glossopteris* flora. *Publication* 4 re-examines an anatomically preserved axis from the Kungurian of Brazil first interpreted as an Euramerican Sigillariaceae. The characters of this specimen indicate that it is not a lycopsid but a member of Cycadales. Based on its set of characters, we proposed the new-fossil genus and species *Iratinia australis* Spiekermann et al. It is the oldest known anatomically preserved cycad axis. There remains no evidence of sigillarians or any other typical Euramerican arborescent lycopsid in the *Glossopteris* flora. Together, these papers bring important novelties on the lycopsids from the *Glossopteris* flora and push the research on these plants forward. However, we are still far from understanding these

plants. Unknowns, such as their growth architecture and systematic position, can be solved only with the discovery of more complete specimens.

Zusammenfassung

Während des Perms fand ein globaler Klimawandel von Eishaus zu Treibhaus statt. Die Reaktion der Paläovegetation auf diesen vergangenen Klimawandel aufzuklären, ist ein bedeutendes Ziel, das nur erreichbar ist, wenn wir ein fundiertes Verständnis der Pflanzen haben, die während dieser Zeit gewachsen sind. Hier konzentriere ich mich auf die Problematik der Lycopsiden aus der *Glossopteris* Flora, Perm von Gondwana. Über diese Gondwana-Pflanzen, die hauptsächlich durch fragmentierte Fossilien von sub- bis baumartigen Formen repräsentiert werden, ist wenig bekannt. Meine Dissertation umfasst vier Publikationen über diese Pflanzen. *Publikation 1* befasst sich mit den spätpaläozoischen Lycopsiden-Fossilien aus dem Paraná-Becken in Südamerika, grenzt ihre aktualisierte stratigrafische Verteilung im Becken ab und bietet eine Grundlage für zukünftige Forschungen über diese Pflanzen. *Publikation 2* befasst sich mit *Azaniadendron* Rayner aus dem Guadalupium von Südafrika. Die reproduktiven Strukturen dieses Taxons werden als in fertile Zonen angeordnet (nicht Zapfen) neu interpretiert, und Ligula-Beweise werden beschrieben, was zumindest für diese Gattung ein Dilemma über das Vorhandensein dieses Merkmals in Lycopsiden aus der *Glossopteris* Flora löst. Auch die morphologischen Variationen seiner Blattpolster werden beschrieben, wobei ein Ansatz verwendet wird, der helfen kann, die Herausforderungen bei der zuverlässigen Identifizierung und Umschreibung anderer Lycopsiden-Gattungen und -Arten, die durch fragmentierte Achsen dargestellt werden, zu überwinden. *Publikation 3* beschreibt Lycopsiden-Achsen aus dem Cisuralium von Brasilien unter Verwendung von Methoden, die eine Vinylpolysiloxan Abgüsse-Technik beinhalten, die die epidermalen Merkmale der Fossilien offenbart. Basierend auf diesen Fossilien beschrieben wir die neue Art *Nothostigma sepeensis* Spiekermann et al. Diese Studie zeigt, wie der Mangel an Studien lange ignorierter Überreste die morphologische Vielfalt der Lycopsiden der *Glossopteris* Flora verdeckt hat. *Publikation 4* untersucht eine anatomisch erhaltene Achse aus dem Kungurium Brasiliens, die bisher als ein Sigillariaceae interpretiert wurde. Die Merkmale dieser Achse weisen darauf hin, dass sie überhaupt kein Lycopsid ist, sondern zu den Cycadales gehört. Basierend auf ihren Merkmalen beschreiben wir die neue Gattung und Art *Iratinia australis*

Spiekermann et al. Es ist der älteste bekannte anatomisch erhaltene Palmfarn. Es gibt keine Hinweise auf Sigillarien oder andere typische baumartige Lycopsiden Euramericas in der *Glossopteris* Flora. Zusammen liefern diese Publikationen wichtige Neuerungen über die Lycopsiden aus der *Glossopteris* Flora, und treiben die Forschung an diesen Pflanzen voran. Allerdings, sind wir noch weit davon entfernt, diese Lycopsiden zu verstehen. Die Rekonstruktion ihres Bauplans sowie der systematischen Position der meisten Lycopsiden-Taxa dieser Flora, können nur durch die Entdeckung vollständigerer Exemplare gelöst werden.

Table of contents

Acknowledgements……………………………………………………………………...v

Abstract…………………………………………………………………………………vi

Zusammenfassung………..…………………………………….…………………….viii

Introduction………………………………………………………………………………1

What are lycopsids?…………………………………………………………….…6

Origin of lycopsids………………………………………………………………...…9

Lycopodiales………………………………………………………..………………..9

Protolepidodendrales…………………………………………………………….…..10

Selaginellales…………………………………………………………………………10

Isoetaleans…………………………..………………………………………………...13

Permian lycopsid macrofossils from the *Glossopteris* flora……………………...15

Herbaceous macrofossils……………………………...……………………………17

Sub- to arborescent macrofossils…………………………………………….………..18

Objectives and overview of publications……………………………………………..20

Publication 1…………………………………………………………………….………23

Publication 2……………………………………………………………………………..55

Publication 3……………………………………………………………………….…….79

Publication 4……………………………………………………………………………92

Outlook……………………………………………………………………………………107

References……………………………………………………………………….….114

Introduction

Plant fossils provide indispensable information on ancient ecosystems and the unique opportunity to disclose the biodiversity and evolution of past floras (e.g., Willis and McElwain, 2002; Cleal and Thomas, 2009). Besides and unlike extant floras, the plant fossil record also allows long-term observations of vegetation responses to past climate/environmental changes (e.g., DiMichele et al., 2001; McElwain, 2018). During Earth's geological history, the late Palaeozoic (Fig. 1) has been considered a singular interval to study such long-term dynamics between vegetation and global changes (Gastaldo et al., 1996; DiMichele et al., 2001; Montañez, 2016). It was the only time that vegetated ecosystems experienced a complete icehouse–greenhouse transition (Gastaldo et al., 1996; Montañez et al., 2007; Isbell et al., 2008).

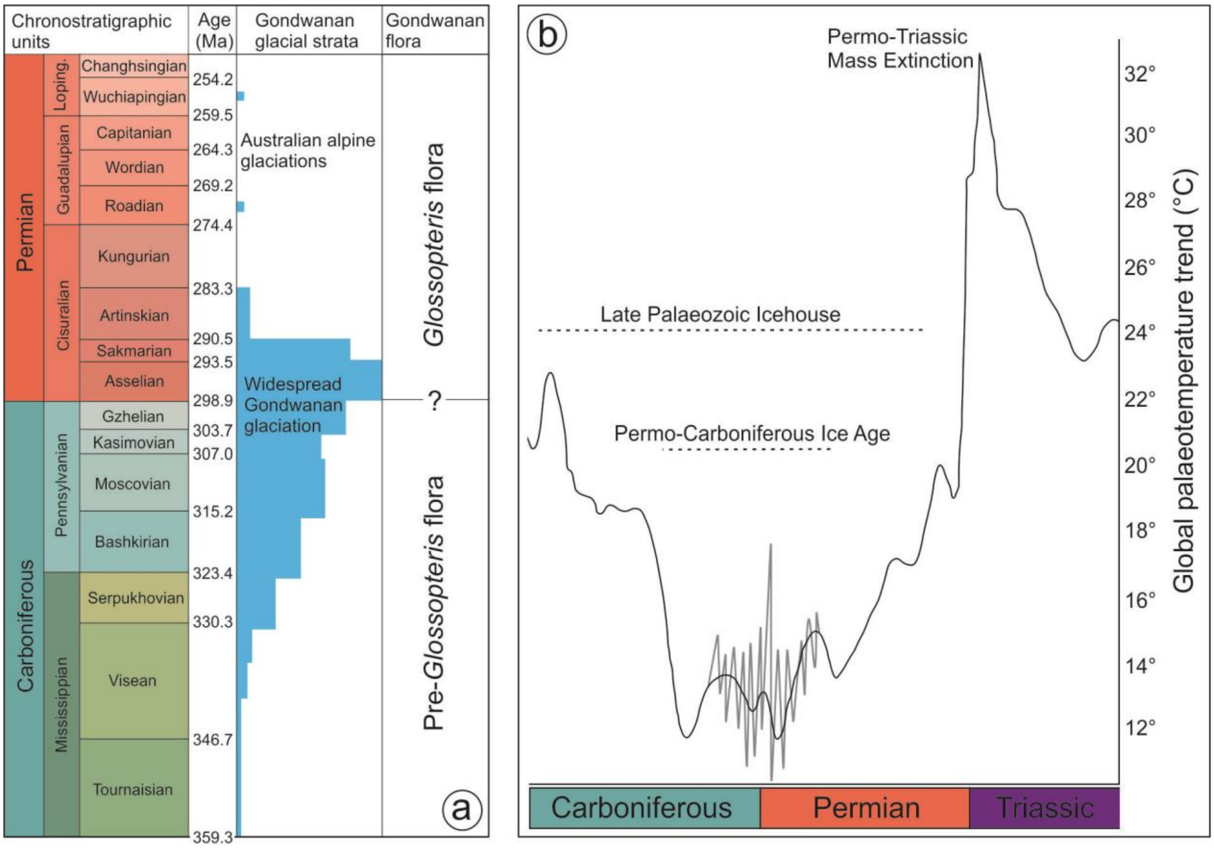

Figure 1. Overview of the late Palaeozoic. (a) Chronostratigraphic chart of the late Palaeozoic (Carboniferous and Permian) showing the temporal distribution of glacial strata in Gondwana. Adapted from Montañez (2022). (b) Global paleotemperature trend throughout the late Palaeozoic and early Mesozoic. Adapted from Scotese et al. (2021).

The onset of the late Palaeozoic major icehouse stage happened in the middle to the latest early Carboniferous (Gastaldo et al., 1996; Montañez, 2022). Thereafter, ice sheets arising from many ice centres, and a complex dynamic of glacial and interglacial intervals, occurred throughout the Southern Hemisphere middle and high latitudes (e.g., Isbell et al., 2012; Limarino et al., 2014; Montañez, 2022). In Euramerica, largely situated in the warmer tropical belt during the late Palaeozoic, evidence of the waxing and waning of those southern ice sheets has been identified through Permo-Carboniferous cyclothems (Montañez, 2022). These have been interpreted as resulting from glacioeustatic variations of the sea level (e.g., Heckel, 2008; Fielding, 2021; Montañez, 2022).

The major vanishing of the late Palaeozoic southern ice sheets took place in the early Permian (e.g., Isbell et al., 2012; Griffis et al., 2018, 2019; López-Gamundí et al., 2021; Montañez, 2022). However, an exception is eastern Australia, where glacial evidence has been reported from the middle and late Permian (Fielding et al., 2008, 2023), when even polar regions of the Southern Hemisphere were already deglaciated (Isbell et al., 2012). Such Australian glacial deposits have been interpreted as alpine glaciations (e.g., Isbell et al., 2012; Montañez, 2022). Recently, middle and late Permian glacial deposits have also been discovered in Siberia (Davydov et al., 2022).

Except for those younger Australian and Siberian glacial events, multiple lines of evidence coming from different parts of the world indicate a progressive transition from icehouse to greenhouse conditions towards the late Permian (e.g., Gastaldo et al., 1996; Rees et al., 2002; Montañez et al., 2007; Grossman et al., 2008; Retallack, 2013; Montañez and Poulsen, 2013; Limarino et al., 2014; Montañez, 2022). The end of the Permian is marked by the largest mass extinction ever reported (e.g., Erwin et al., 2002; Benton, 2003). What caused this biotic crisis is not fully understood. One of the most accepted hypotheses is that the extinction was linked to large amounts of greenhouse gases, released by volcanic activity and igneous intrusion into coal measures (e.g., Ogden and Sleep, 2011; Payne and Clapham, 2012; Benton and Newell, 2014; Burgess et al., 2017). That would have caused fast global warming and a chain of events, leading to the destabilisation and collapse of marine and terrestrial palaeo-ecosystems (e.g., Benton and Newell, 2014; Corso et al., 2022).

Elucidating the responses of the vegetation to such environmental changes remains a remarkable goal, especially during the Permian that witnessed the transition from an icehouse to a greenhouse. However, this can only be achieved if we have a robust taxonomical background and understanding of all plant groups that thrived during those times. Plant fossils from Permian strata of Europe and North America, for instance, have been studied in detail using a large set of methodological approaches, as summarised in several palaeobotanical books (e.g., Steward and Rothwell, 1993; Taylor et al., 2009; Cleal and Thomas, 2009, 2019). In contrast, the plant fossil biodiversity from coeval deposits of the Southern Hemisphere is far less understood, and detailed studies of particular groups (e.g., lycopsids) that were significant elements of the southern Permian floras are still missing.

Glossopteris Brongniart is undoubtedly the most iconic plant fossil from the Permian southern flora (Fig. 2). This fossil-genus comprises tongue-shaped gymnospermous leaves with midrib and reticulate venation (e.g., Brongniart, 1828; Pigg and Trivett, 1994). This type of leaf has been reported from Permian deposits situated in modern-day Antarctica, Australia, New Zealand, New Guinea, Madagascar, and the Indian subcontinent (e.g., Brongniart, 1828; Seward, 1914; Mildenhall, 1976; Appert, 1977; Rigby, 1996; McLoughlin, 1994, 2011). It also occurs in coeval strata lying in parts of what is now the Arabian Peninsula, Africa, South America, and the Falkland Islands (e.g., Lundqvist, 1919; Anderson and Anderson, 1985; Berthelin et al., 2006; Simões et al., 2012).

The occurrence of *Glossopteris* fossils in India as well as all the now widely separated Southern Hemisphere continents played a historically significant role in helping to shape our modern geological knowledge (McLoughlin, 2011). It served as a supporting argument for the continental drift theory, as well as the existence of the former Southern Hemisphere supercontinent Gondwana (Wegener, 1920; Du Toit, 1937), before the advent of the modern plate tectonic concept in the 1960s (Torsvik and Cocks, 2012). Today, the geological history of Gondwana since its formation during the Neoproterozoic, collision with Laurussia in the Carboniferous resulting in

Pangaea, and progressive fragmentation during Mesozoic times, is well understood based on multiple data from different geoscientific fields (Veevers, 2004; Torsvik and Cocks, 2013).

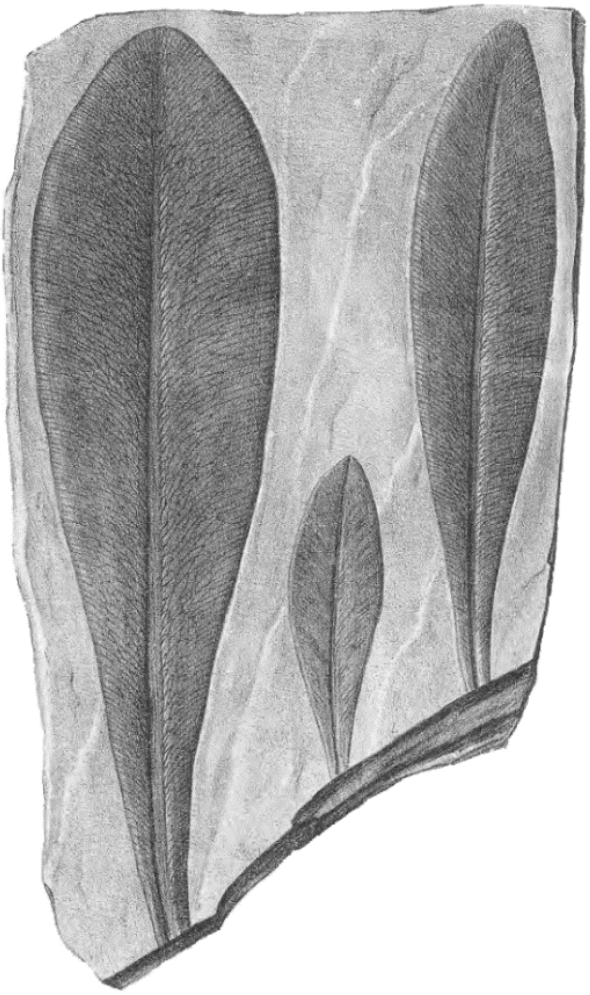

Figure 2. *Glossopteris browniana* Brongniart. From Brongniart (1828, pl. 62, fig. 1).

After that type of fossil leaf, the Permian Gondwanan floristic realm has been traditionally called *Glossopteris* flora (e.g., Seward, 1897; Arber, 1905; McLoughlin, 2011). As the southern glaciers contracted during the Permo-Carboniferous, this vegetation developed and successfully flourished between the middle to high latitudes of Gondwana (Fig. 3) throughout the Permian (e.g., Pant, 1987; McLoughlin, 2001, 2011; Tewari et al., 2015). In short, early elements of this flora seems to have grown in periglacial settings and cold temperate climates, which became gradually warmer towards the end of the Permian (Pant, 1987). During humid stages, this flora thrived in peat-forming systems, constituting most of the biomass that resulted in the economically important Permian coals from the Southern Hemisphere and India (e.g., Hunt, 1989; Mishra et al., 1990; Iannuzzi, 2010; Hancox and Götz, 2014). These coals also contain a large amount of charcoalified plant remains (i.e. pyrogenic inertinites), indicating that this vegetation frequently experienced wildfires as a major source of disturbance, most likely promoted by the high palaeoatmospheric oxygen levels during the Permian (e.g., Scott and Glasspool, 2006; Jasper et al., 2013). The collapse of the *Glossopteris* flora occurred in the late Permian at the onset of the end-Permian mass extinction event (Mays et al., 2020; Vajda et al., 2020).

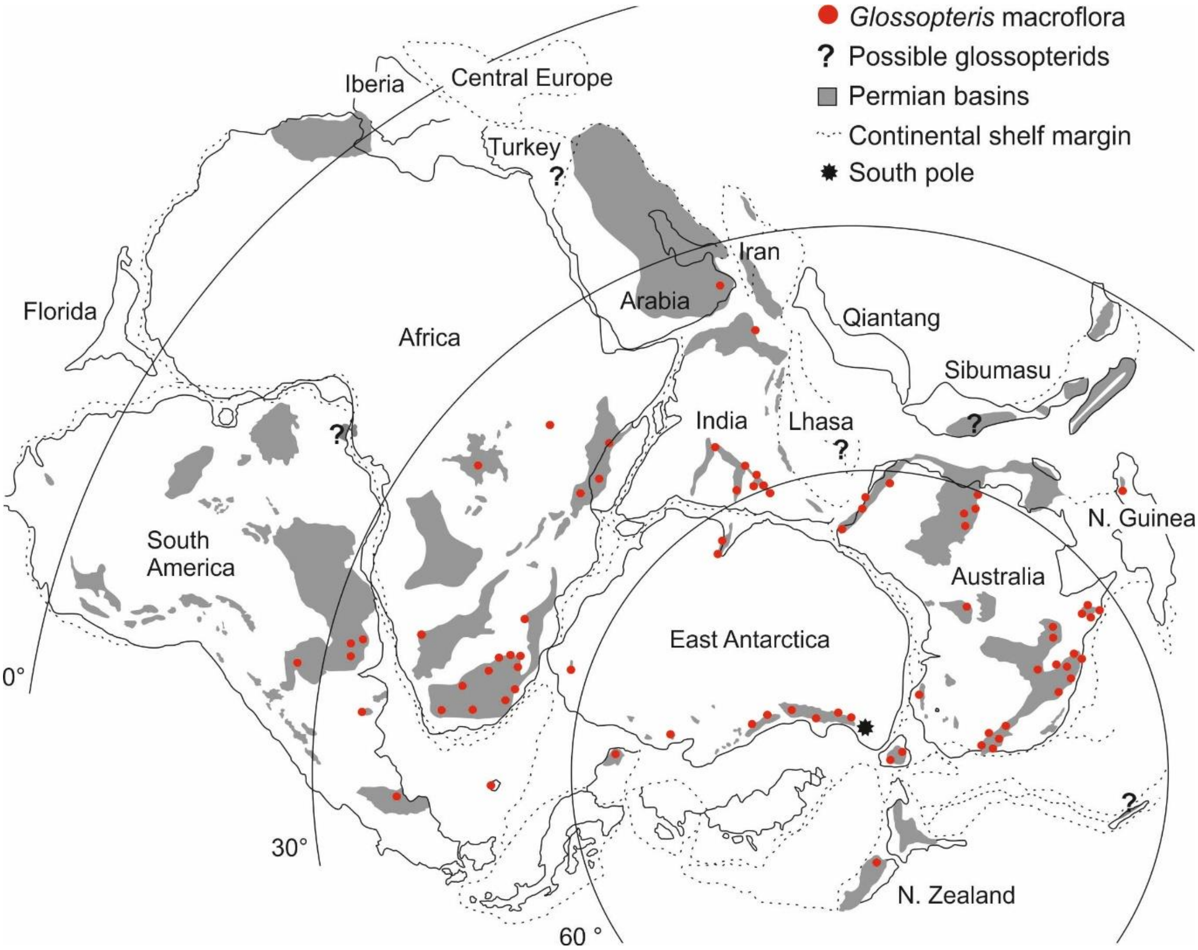

Figure 3. Sketch map of Gondwana showing the general distribution of the *Glossopteris* flora during the Permian based on selected fossil assemblages. Adapted from McLoughlin (2001).

At first glance, the name “*Glossopteris* flora” may give the impression of a homogeneous phytogeographic unit composed almost exclusively of glossopterid plants. Indeed, glossopterid remains are the most typical plant fossils found in Permian Gondwanan strata (e.g., Pant, 1999; McLoughlin, 2011; Bernardes-de-Oliveira et al., 2016). However, the whole flora was far more diverse, and other groups of plants, such as lycopsids, sphenophytes, ferns, cycads, cordaitaleans, conifers, and ginkgophytes, thrived in those southern terrains during that time as well (e.g., Anderson and Anderson, 1985; Cúneo, 1996; Jasper et al., 2006; Iannuzzi, 2010; Goswami et al., 2018; Spiekermann et al., 2021; **Publications 1** and **4**). Among these groups, lycopsids are one of the least studied plants, despite being significant and even dominant components of some fossil assemblages from western Gondwana (e.g., **Publication 1**). This scientific hiatus does not allow reliable palaeobiogeographical, evolutive and palaeoecological inferences about those plants. Consequently, our knowledge of the palaeobiodiversity and palaeoenvironmental dynamics during the Permian icehouse to greenhouse climate transition remains incomplete. In this cumulative dissertation, I focus on selected lycopsid macrofossils from the *Glossopteris* flora and on what was once interpreted as a lycopsid but can no longer be considered one, aiming to contribute to the understanding of these plants.

What are lycopsids?

Lycopsids constitute a well-supported monophyletic clade of spore-producing vascular plants (Kenrick and Crane, 1997; Taylor et al., 2009). A typical feature of the group is the presence of helically borne (Fig. 4a) microphyllous leaves (= microphylls; Taylor et al., 2009). Confusion concerning the term microphyll might arise because it also has been used to describe leaves of other vascular plants, such as the horsetail *Equisetum* L. (Corvez et al., 2012). Lycopsid microphylls, however, have a different evolutionary origin, and there is convincing evidence that they evolved independently and are not homologous to the leaves of other plant groups (e.g., Kenrick and Crane, 1997; Schneider et al., 2002; Harrison and Morris, 2017). For that reason, some authors have been calling them lycophylls (e.g., Corvez et al., 2012; Schneider, 2013), but this term has not been habitually used in palaeobotany. Lycopsid microphylls are unique in having vascular bundles that arise from a protostele without ever forming leaf gaps (Steward and Rothwell, 1993; Taylor et al., 2009). They typically exhibit a single undivided vascular bundle, but some exceptions exist (Steward and Rothwell, 1993; Wagner et al., 1982).

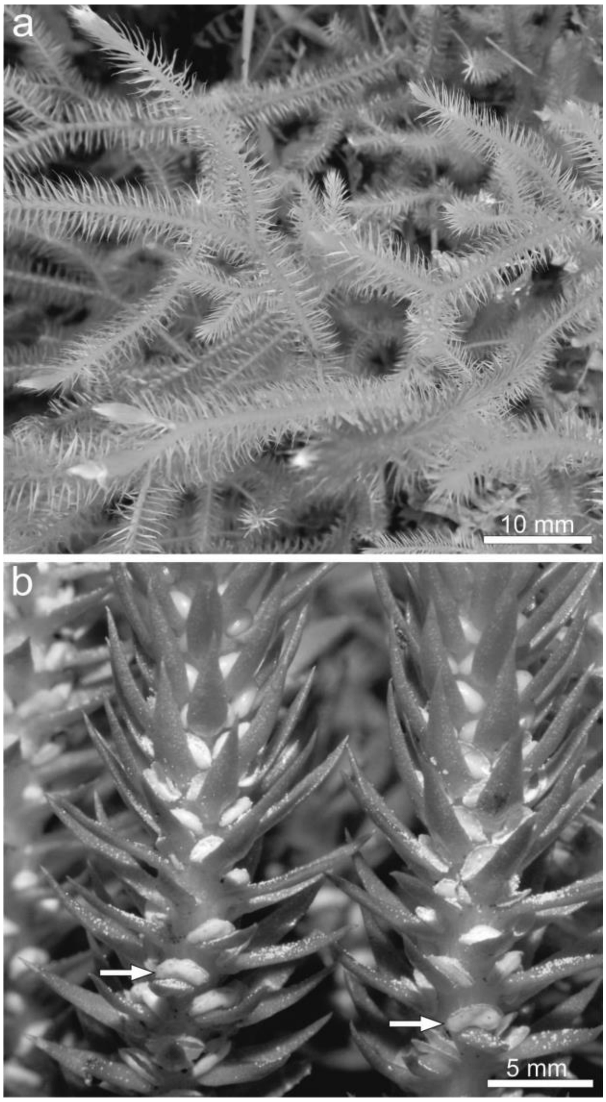

Figure 4. Examples of living lycopsids. (a) Detail of *Lycopodium* L. covered in helically arranged microphylls. Photo: Rafael Spiekermann. (b) Detail of *Huperzia selago* (L.) Bernh. ex Schrank & Mart showing eusporangia (arrows) borne in the axil on the adaxial side of the sporophyll. Photo: Hermann Schachner. https://commons.wikimedia.org/wiki/File:Huperzia_selago_(Teufelsklaue)_IMG_8967.JPG. Creative Commons CC0 1.0.

A synapomorphy of lycopsids is the position of their reproductive structures (Taylor et al., 2009). Their eusporangia are borne in the axil or on the adaxial side of a modified microphyll (Fig. 4b) known as sporophyll (Steward and Rothwell, 1993; Kenrick and Crane, 1997; Taylor et al., 2009). Together with their microphylls, the axillary and/or adaxially borne eusporangia have been used to readily separate them from other spore-bearing plant groups (e.g., Steward and Rothwell, 1993; Taylor et al., 2009). Another common characteristic of lycopsids is that their vascular cylinder generally has exarch protoxylem maturation (Gensel and Berry, 2001). Their metaxylem tracheids typically exhibit vertical fimbrils connecting the horizontal bars of the pits, known as “Williamson’s striations” (Taylor et al., 2009).

The lycopsid clade is widely accepted as a class called Lycopsida (e.g., Scott, 1909; Kenrick and Crane, 1997; Taylor et al., 2009) or Lycopodiopsida (e.g., Bartling, 1830; PPG I, 2016). Its fossil record extends back into the early Devonian or perhaps even late Silurian (e.g., Kenrick and Crane, 1997; Cleal and Thomas, 2009; Taylor et al., 2009). During such an extensive evolutionary story, lycopsids split into several orders (Kenrick and Crane, 1997; Fig. 5), evolving distinct reproductive strategies and growth habits, ranging from small herbs to large arborescent forms (e.g., Kenrick and Crane, 1997; Taylor et al., 2009). Nowadays, lycopsids are represented only by small and mostly herbaceous plants (Taylor et al., 2009; PPG I, 2016).

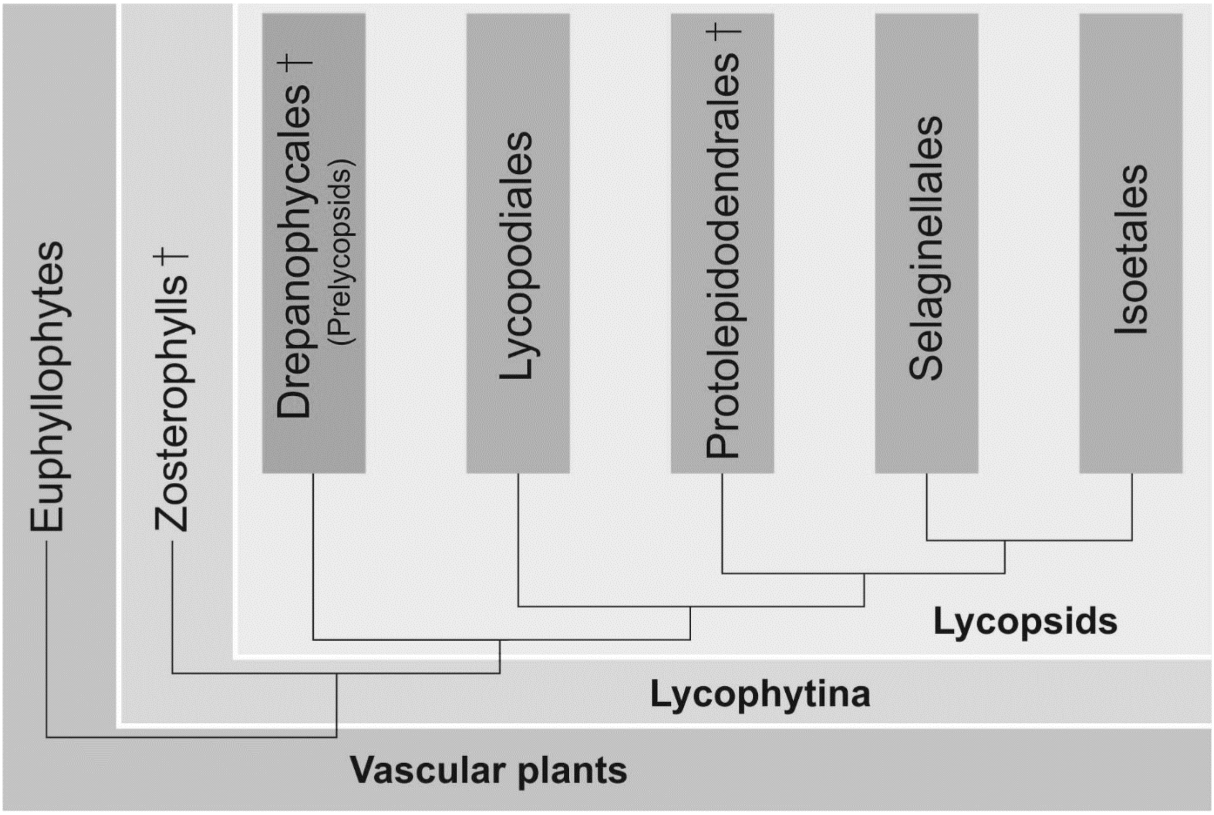

Figure 5. Simplified cladogram showing the distinct lycopsid orders and the relationship of the clade with other plant groups. † = extinct clades. Based on Kenrick and Crane (1997).

Origin of lycopsids

Fossil data indicates that lycopsids diverged from the extinct zosterophylls dur-ing early Devonian or possibly Silurian times (e.g., Kenrick and Crane, 1997; Gensel and Berry, 2001; Taylor et al., 2009). The most significant difference separating both is that zosterophylls lack leaves and thus leaf-borne eusporangia (Gensel and Berry, 2001). Together, lycopsid and zosterophylls form the division Lycophytina (Kenrick and Crane, 1997; Fig. 5) and have been routinely called lycophytes (e.g., Gensel and Berry, 2001; Taylor et al., 2009).

Early lycopsid-like plants include an array of homosporous (producing only one type of spores) and herbaceous plants assigned to the order Drepanophycales (e.g., Kenrick and Crane, 1997; Taylor et al., 2009). Although very similar to lycopsids, not all members of this order exhibit all distinctive characters of true lycopsids (e.g., *Drepanophycus* Göppert and *Asteroxylon* Kidston & Lang), such as fully vascularised microphylls and leaf-borne eusporangia (Gensel and Berry, 2001). Due to that, they have often been classified as prelycopsid or considered transitional forms between zosterophylls and true lycopsids (e.g., Taylor et al., 2009; Gensel and Berry, 2001). Nevertheless, Drepanophycales can be regarded as a sister clade of all other lycopsids (Kenrick and Crane, 1997).

Among fossil-taxa placed in Drepanophycales, the oldest known one is possibly *Baragwanathia* Lang & Cookson (Fig. 6a) from assumed Silurian deposits of Australia and the Czech Republic (Lang and Cookson, 1935; Rickards, 2000; Kraft and Kvaček, 2017). It is also the one that most resembles a true lycopsid in having vascularised microphylls and sporangia borne in the axil of those microphylls (e.g., Hueber, 1992). With exception of these specimens, the other known fossils assigned to this extinct order come from Devonian strata (e.g., Chaloner and Boureau, 1967).

Lycopodiales

This order occupies a basal position within Lycopsida, and its members show all characters of true lycopsids, such as fully vascularised microphylls and eusporangia borne in the axil of sporophylls (Kenrick and Crane, 1997). They have evolved from drepanophycalean plants and are ancestral to protolepidodendrids (Kenrick and Crane, 1997). The Lycopodiales comprises terrestrial and epiphytic herbaceous forms, generally showing dichotomous branching (Øllgaard, 1990). They are eligulate homosporous plants with reproductive structures arranged in compact cones or fertile zones (Øllgaard, 1992; Taylor et al., 2009).

Macrofossils potentially belonging to this order date back to the Devonian and have generally been lumped into the somewhat problematic fossil-genus *Lycopodites* Lindley & Hutton (e.g., Dolianiti, 1967; Thomas, 1992; Salvi et al., 2008). Living Lycopodiales (Fig. 6b) are included in the cosmopolitan family Lycopodiaceae and have been placed in 16 genera and around 388 species (PPG I, 2016). The earliest unequivocal macrofossil evidence of crown Lycopodiaceae dates back to the early Cretaceous (Herrera et al., 2022).

Protolepidodendrales

Protolepidodendrids were spread worldwide and thrived during the middle and late Devonian (Berry, 1996; Gensel and Berry, 2001). They lacked secondary tissues and had branched, mostly creeping-like growth habits (e.g., Chaloner and Boureau, 1967; Gensel and Berry, 2001; Taylor et al., 2009). Their sporophylls were arranged in fertile zones rather than specialised cones (Chaloner and Boureau, 1967; Meyen, 1987). Known fertile fossil-taxa are homosporous (e.g., Wellman et al., 2009).

One of the most distinctive features of the protolepidodendrids (Fig. 6c) is their forked or even multi-forked microphylls (e.g., Bonamo et al., 1988; Gensel and Berry, 2001; Taylor et al., 2009). The most well-known component of the order is probably *Leclercqia complexa* Banks et al. This lycopsid is unusual since it was homosporous but also ligulate (e.g., Grierson and Bonamo, 1979), as the occurrence of a ligule is otherwise a typical characteristic of heterosporous lycopsids (Meyen, 1987).

Selaginellales

Selaginellales are heterosporous (producing micro and megaspores) herbaceous plants exhibiting ligules (Kenrick and Crane, 1997). The known taxa are small, generally dichotomously branched, and exhibit creeping-like to erect habits (Taylor et al., 2009). Their microphylls are isophyllous or anisophyllous (Banks, 2009). Unlike other lycopsids, a few living members of the order have microphylls with a relatively complex multi-branched venation pattern, interpreted as derived directly from the single vein of the microphyll (Wagner et al., 1982). Their heterosporous eusporangia are generally aggregated in cones (Taylor et al., 2009).

Fossils convincingly belonging to Selaginellales are known from the lower Carboniferous (e.g., Rowe, 1988). The Palaeozoic specimens have often been placed in *Selaginellites* Zeiller (e.g., Rowe, 1988; Thomas, 1992; Konijnenburg-van Cittert et al., 2014), but recently the new fossil-genus *Thomasites* Bek et al. (2023) has been proposed. It has been considered that the lineage dates back to the Devonian, based on cladistic studies and DNA-based divergence time estimates (e.g., Kenrick and Crane, 1997; Morris et al., 2018). Cladistic studies also have been indicating that the Selaginellales are either ancestral or a sister clade of the Isoetales (e.g., Kenrick and Crane, 1997; Rydin and Wikström, 2002; Sessa, 2018).

Today, Selaginellales are represented by the single but worldwide distributed genus *Selaginella* Beauvoir (Banks, 2009; Fig. 6d). The genus, placed in the family Selaginellaceae, encompasses around 700 living species, being the most diversified taxon among the extant lycopsids (PPG I, 2016). Available fossil data, coming especially from specimens preserved within Burmese amber, provide sound evidence that *Selaginella* was already well-diversified during the middle Cretaceous (Schmidt et al., 2020, 2022).

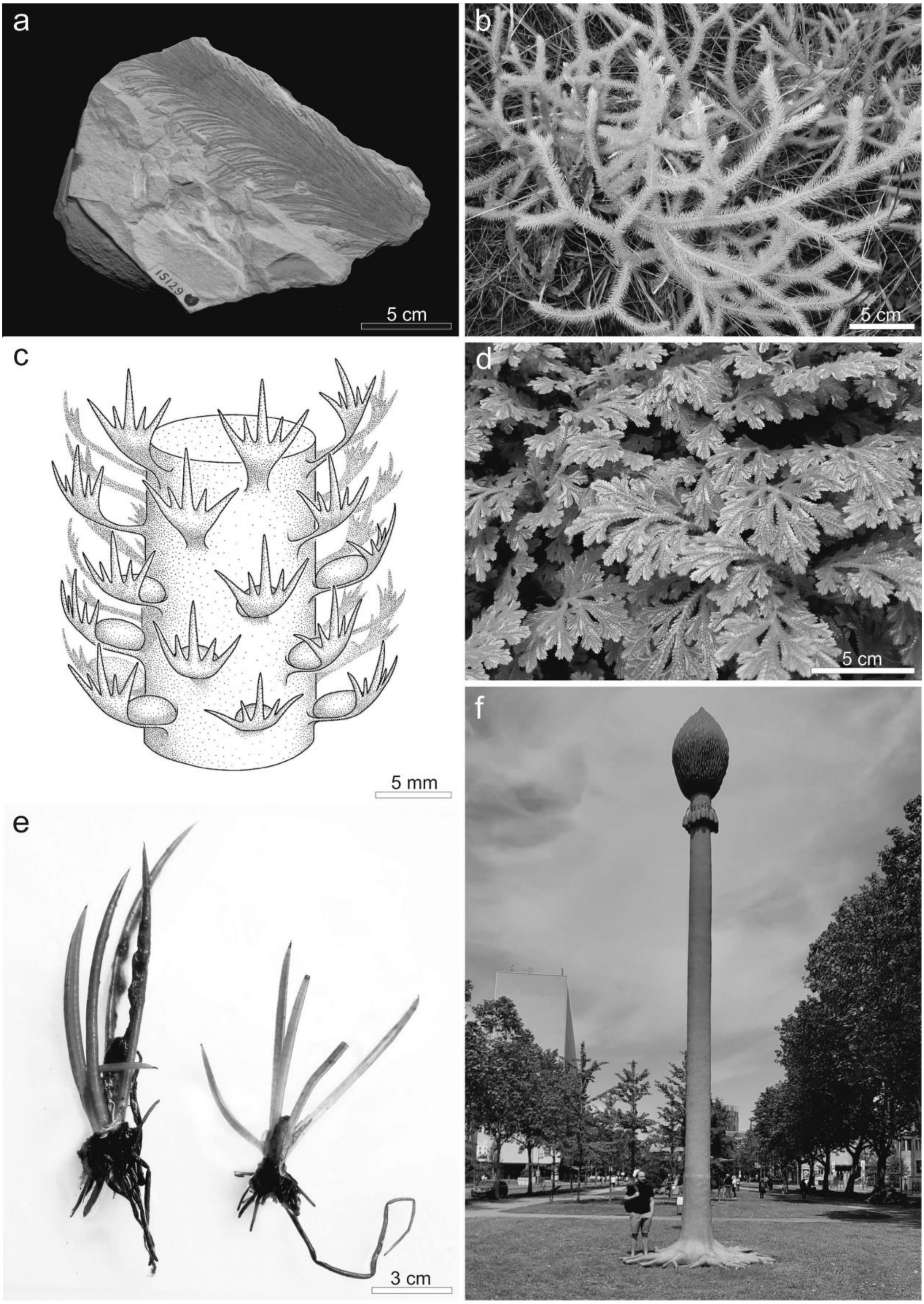

Figure 6; see caption on next page.

Figure 6. Examples of living and fossil lycopsids. (a) Fossil of *Baragwanathia longifolia* Lang & Cookson from the Devonian of Australia. Photo: Rodney Start, Museums Victoria; https://collections.museumsvictoria.com.au/specimens/1063492. Modified to include an approximate scale bar. Reproduced according to CC BY 4.0 terms. (b) Living Lycopodiales (*Lycopodium* L.) growing in the subtropical highlands of the Rio Grande do Sul State, Brazil. Photo: Dieter Uhl. (c) Partial reconstruction of *Leclercqia andrewsii* Kasper & Gensel from the Devonian of Canada. Reproduced and reprinted from Review of Palaeobotany and Palynology, 137, 3–4, Gensel, P.G., Kasper, A.E.J., A new species of the Devonian lycopod genus, *Leclercqia*, from the Emsian of New Brunswick, Canada, pp. 105–123, 2005, with permission from Elsevier. (d) Living *Selaginella* Beauvoir photographed at the Botanical Garden of the University of Tübingen, Germany. Photo: Dieter Uhl. (e) Living *Isoetes* L. from Denmark. Photo: https://commons.wikimedia.org/wiki/File:IsoetesLacustris.jpg. Creative Commons CC0 1.0. (f) Reconstruction of an arborescent isoetalean (*Sigillaria* Brongniart) from the Carboniferous. Photographed in front of the Senckenberg Naturmuseum Frankfurt. Photo: Bianca Spiekermann.

Isoetaleans

The Isoetales (Fig. 6e–f) is the most diverse and derived lycopsid order (e.g., Kenrick and Crane, 1997; DiMichele and Bateman, 1996). The key characters of the order include bipolar growth from a shoot-like rootstock and the presence of secondary tissues, including the formation of periderm and at least some amount of wood (DiMichele and Bateman, 1996). They are heterosporous and ligulate plants and generally have aerenchymatous tissues (known as foliar parichnos) in their leaves (e.g., Meyen, 1987; Bateman et al., 1992; Pigg, 2001). Some arborescent fossil-genera, such as *Lepidodendron* Sternberg and *Lepidophloios* Sternberg, exhibited two additional infrafoliar parichnos strands (DiMichele and Bateman, 1996).

The eusporangia in isoetaleans are arranged in compact cones or fertile zones (e.g., DiMichele and Bateman, 1996; Pigg and Rothwell, 1983; Bonacorsi and Leslie, 2019). The cones and fertile zones can be either monosporangiate (micro and mega-sporangia occurring in separated fertile zones or cones) or bisporangiate (micro and megasporangia arranged in the same fertile zone or cone). The bisporangiate forms are considered the most derived isoetaleans (e.g., Bateman et al., 1992; DiMichele and Bateman, 1996).

The origin of isoetaleans dates back to Devonian times (e.g., Pigg, 2001; Xue, 2011). Extinct members of the order are notable for having evolved sub-arborescent[1] to large arborescent growth habits (e.g., Pigg and Rothwell, 1983; DiMichele and Bateman, 1996; Taylor et al., 2009). The acme of the isoetaleans occurred during the Pennsylvanian when arborescent forms, such as the widely known *Lepidodendron* and *Sigillaria* Brongniart (Fig. 6f), constituted extensive peat-forming forests across the Euramerican palaeotropical belt (Taylor et al., 2009). These arborescent forms were one of the most important components of the biomass that resulted in the extensive Carboniferous coals from the Northern Hemisphere (DiMichele and Phillips, 1985; Taylor et al., 2009).

Some sub-arborescent isoetaleans had a corm-like rooting system (e.g., Pigg and Rothwell, 1983). In contrast, the giant isoetalean trees exhibited a large and branched stigmarian rooting system (e.g., Steward and Rothwell, 1993; Taylor et al., 2009). It has been hypothesised that these large arborescent forms had a determinate growth pattern (Eggert, 1961; Bateman, 1994; Thomas and Cleal, 2018). Well-understood sub-arborescent isoetalean forms, such as *Chaloneria* Pigg & Rothwell from Carboniferous and *Pleuromeia* Corda from Triassic, developed an unbranched growth architecture (e.g., Pigg and Rothwell, 1983; Looy et al., 2021). In contrast, the large "*Lepidodendron* tree" exhibited an extensively branched crown (e.g., Eggert, 1961; Taylor et al., 2009).

The stems and branches of sub- and arborescent isoetaleans were clothed in leaf cushions (Fig. 7a). One of the most common types of fossils belonging to those plants are fragmented impressions and compressions of such stems and branches, and the morphology and characters of the leaf cushions (Fig. 7b) preserved on them have been useful to identify fossil-taxa (e.g., Chaloner and Boureau, 1967; Thomas and Meyen, 1984; **Publications 2** and **3**). Today, the isoetalean clade is represented only by the small *Isoetes* L. (PPG I, 2016; Fig. 6e). Despite being small, the latter still

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[1] Following Bek et al. (2008), the term sub-arborescent is used throughout this text to refer to lycopsids that are considerably smaller than the large lepidodendrids but much taller and far more robust than *Selaginella* and *Isoetes*-like forms.

produces a limited amount of secondary tissues (Scott and Hill, 1900; Stokey, 1909), such as the extinct tree-like forms.

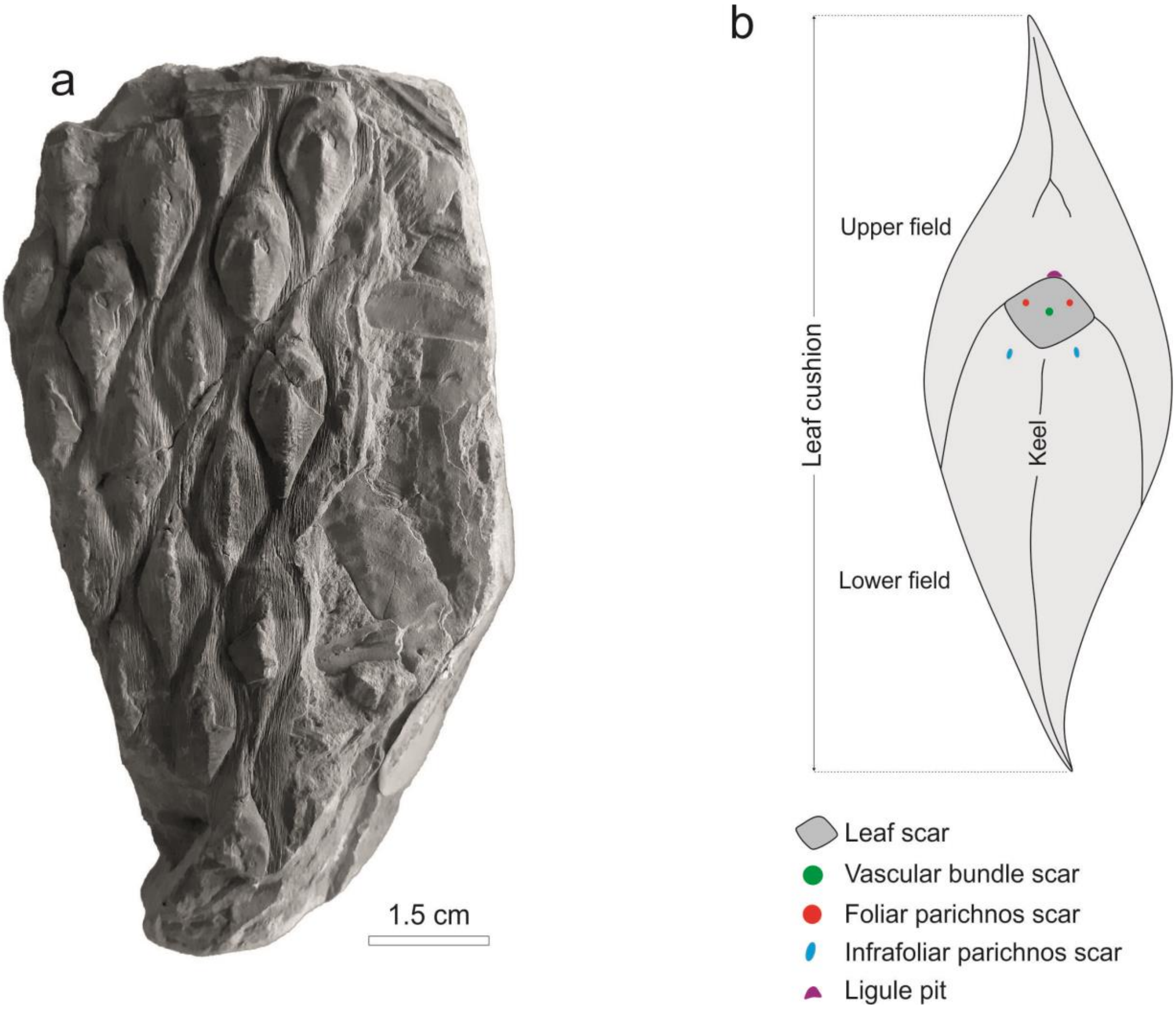

Figure 7. Example of isoetalean leaf cushions. (a) Impression of *Lepidodendron* sp. covered in leaf cushions. Photo: Rafael Spiekermann. (b) Schematic drawing of *Lepidodendron*-like leaf cushion showing important taxonomic characters. Based on Bateman et al. (1992).

Permian lycopsid macrofossils from the *Glossopteris* flora

Reports of lycopsid macrofossils in strata from the *Glossopteris* flora date back to the late 19th century (e.g., Carruthers, 1869; Zeiller, 1895). From that time onwards, many other specimens have been discovered and described/mentioned in the literature (e.g., Anderson and Anderson, 1985; Kräusel, 1961; Cariglino et al., 2012; McLoughlin et al., 2015; Spiekermann et al., 2018; Carvalho et al., 2022; **Publication 1**). These fossils include some specimens interpreted as herbaceous, plus numerous remains belonging to assumedly sub-arborescent to arborescent forms (Fig. 8).

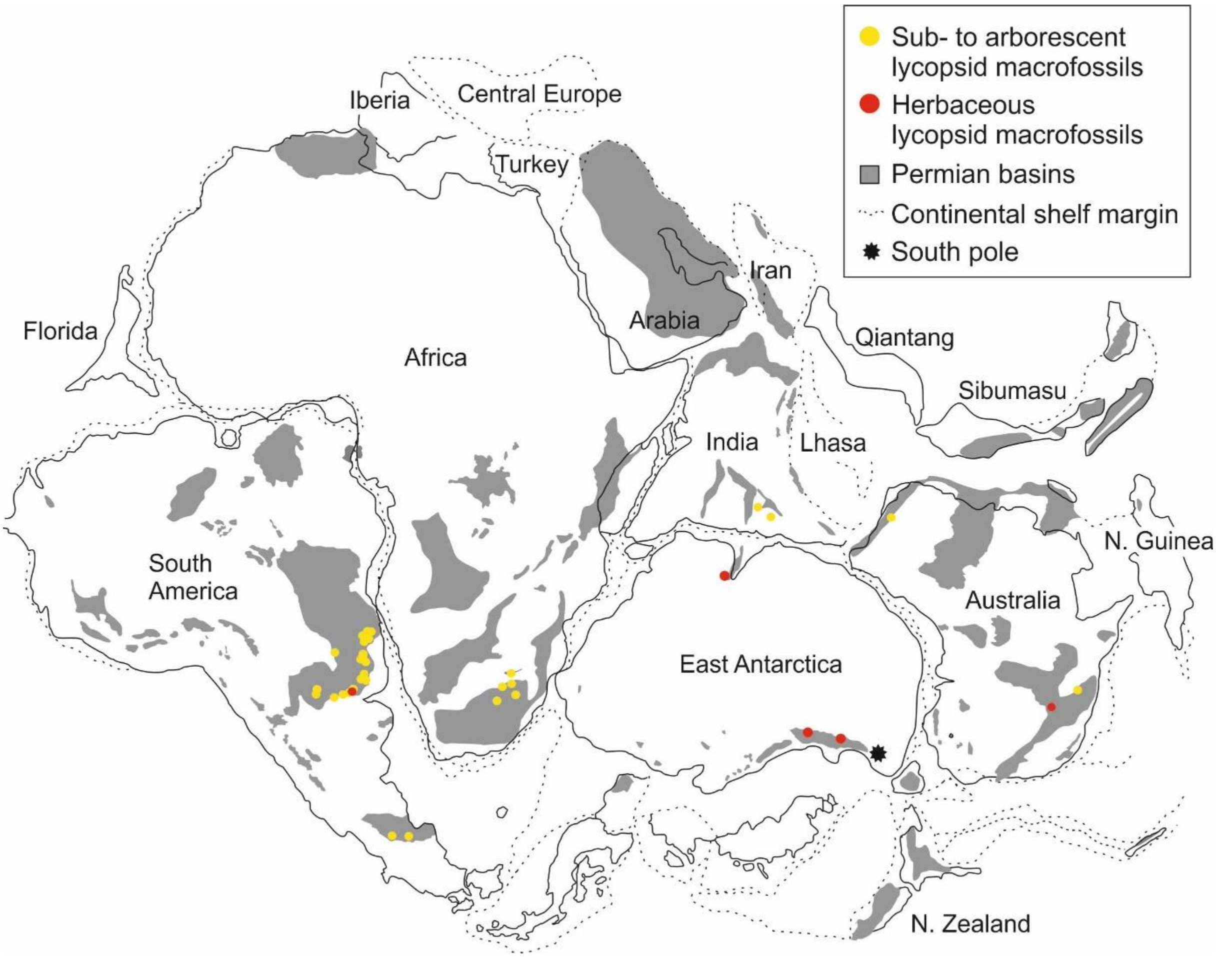

Figure 8. Overview of the distribution of main herbaceous and sub- to arborescent lycopsid macrofossil-bearing areas in the Permian of Gondwana. Based on information from **Publication 1**, Rigby (1966), Townrow (1968), Chandra and Rigby (1981), Cúneo and Andreis (1983), Anderson and Anderson (1985), Beeston (1990), Schwendemann et al. (2010), Ryberg et al. (2012), Cariglino et al. (2012), McLoughlin et al. (2015), Goswami et al. (2018), and Mottin et al. (2022). Map adapted from McLoughlin (2001).

Herbaceous macrofossils

The oldest herbaceous lycopsid macroremains from the *Glossopteris* flora are specimens from Asselian deposits of the Quitéria outcrop in southern Brazil (Fig. 9a). These consist of adpressions of fertile shoots lumped in *Lycopodites* and named *L. riograndensis* Salvi et al. (2008). Additionally, presumed Kungurian deposits from New South Wales in Australia yielded a set of impressions/compressions, including aerial vegetative axes, rhizomes, and fertile shoots containing *in situ* micro and megaspores (Townrow, 1968). These fossils were vigorously lumped in the living genus *Selaginella* and are the basis of the almost entirely reconstructed *Selaginella harrisiana* Townrow (1968). Bek et al. (2023), however, suggest that *S. harrisiana* should possibly be included in the new fossil-genus *Thomasites*.

The meagre herbaceous lycopsid macrofossil record from the flora was slightly but importantly expanded after detailed descriptions of a few herbaceous remains from Antarctica. McLoughlin et al. (2015) described anatomically preserved axes found in Guadalupian strata from the Bainmedart Coal Measures, East Antarctica. These fossils were assigned to the ligulate *Paurodendron* Fry and placed in the new fossil-species *P. stellatum* McLoughlin et al. (2015). The presence of *Paurodendron* in those Antarctic strata extended considerably the spatiotemporal range of this fossil-genus, previously known only from Carboniferous deposits of Euramerica (McLoughlin et al., 2015). The late Permian strata of Mount Achernar in the central Transantarctic Mountains yielded many impressions/compressions of herbaceous vegetative axes (Schwendemann et al., 2010). These exhibit eligulate microphylls and are known as *Collinsonites schopfii* Schwendemann et al. (2010). Moreover, in late Permian strata from the central Transantarctic Mountains, but at the locality of Skaar Ridge, Ryberg et al. (2012) documented permineralised sporophylls bearing eusporangia containing *in situ* spores. It was considered that such sporophylls could represent fertile parts of *Collinsonites schopfii*, but due to the lack of hard data to connect both, Ryberg et al. (2012) consequently placed them in a new fossil-taxon named *Collinsonostrobus eggertii* Ryberg et al.

Sub- to arborescent macrofossils

Sub- to arborescent lycopsid macrofossils are rare in *Glossopteris* flora strata from the eastern part of Gondwana (McLoughlin et al., 2015). However, they are common in Cisuralian and Guadalupian deposits from the western part of the supercontinent (e.g., Anderson and Anderson, 1985; Cariglino et al., 2012; Carvalho et al., 2022; **Publications 1** and **2**). In South America, for instance, some Cisuralian fossil assemblages are dominated by relatively large *in situ* lycopsid stumps (Cúneo and Andreis, 1983; Jasper and Guerra-Sommer, 1998; Mottin et al., 2022; Fig. 9b). These assemblages provided significant palaeoecological information on the post-glacial lycopsid-dominated groves of the *Glossopteris* flora (e.g., Cúneo and Andreis, 1983; Jasper et al., 2006; Mottin et al., 2022; **Publication 1**). Unfortunately, the incomplete and poor preservation of the so far available *in situ* specimens precludes sound taxonomic and systematic interpretations.

Except for those *in situ* stumps, the sub- to arborescent lycopsid macrofossil record from the *Glossopteris* flora includes mainly non-autochthonous fragments of axes (e.g., Kräusel, 1961; Chaloner et al., 1979; Spiekermann et al., 2018; **Publications 1**, **2** and **3**). Most are preserved as impressions and compressions (Fig. 9c–e). These constitute the basis of fossil-genera such as *Cyclodendron* Kräusel (1928), *Brasilodendron* Chaloner et al. (1979), and *Azaniadendron* Rayner (1986). The only exception is *Lycopodiopsis* Renault (1890), which is based on anatomically preserved axes from Guadalupian deposits of Brazil (Fig. 9f). Another anatomically preserved axis from the Permian of Brazil, formerly interpreted as a lycopsid (Guerra-Sommer, 1981), does not belong to this lineage of plants at all (**Publication 4**). Among such fossil-genera, reproductive structures are up to date only known for *Cyclodendron* and *Azaniadendron* (Rayner, 1985, 1986).

Little is known about these Gondwanan plants, especially when comparing them with the enormous amount of data published on the late Palaeozoic arborescent lycopsids from the Northern Hemisphere (Spiekermann et al., 2021). They have been traditionally interpreted as lacking evidence of ligule; however, see **Publication 2**. Despite being common in Permian strata from western Gondwana, they are notoriously difficult to identify taxonomically and tricky to deal with, mainly due to the fragmented state of their fossils. This fragmented state also may have left them out of the main research focus of most palaeobotanists for years. The lack of knowledge about these lycopsids, and their common occurrence in many Permian fossils assemblages from Gondwana, motivate this study.

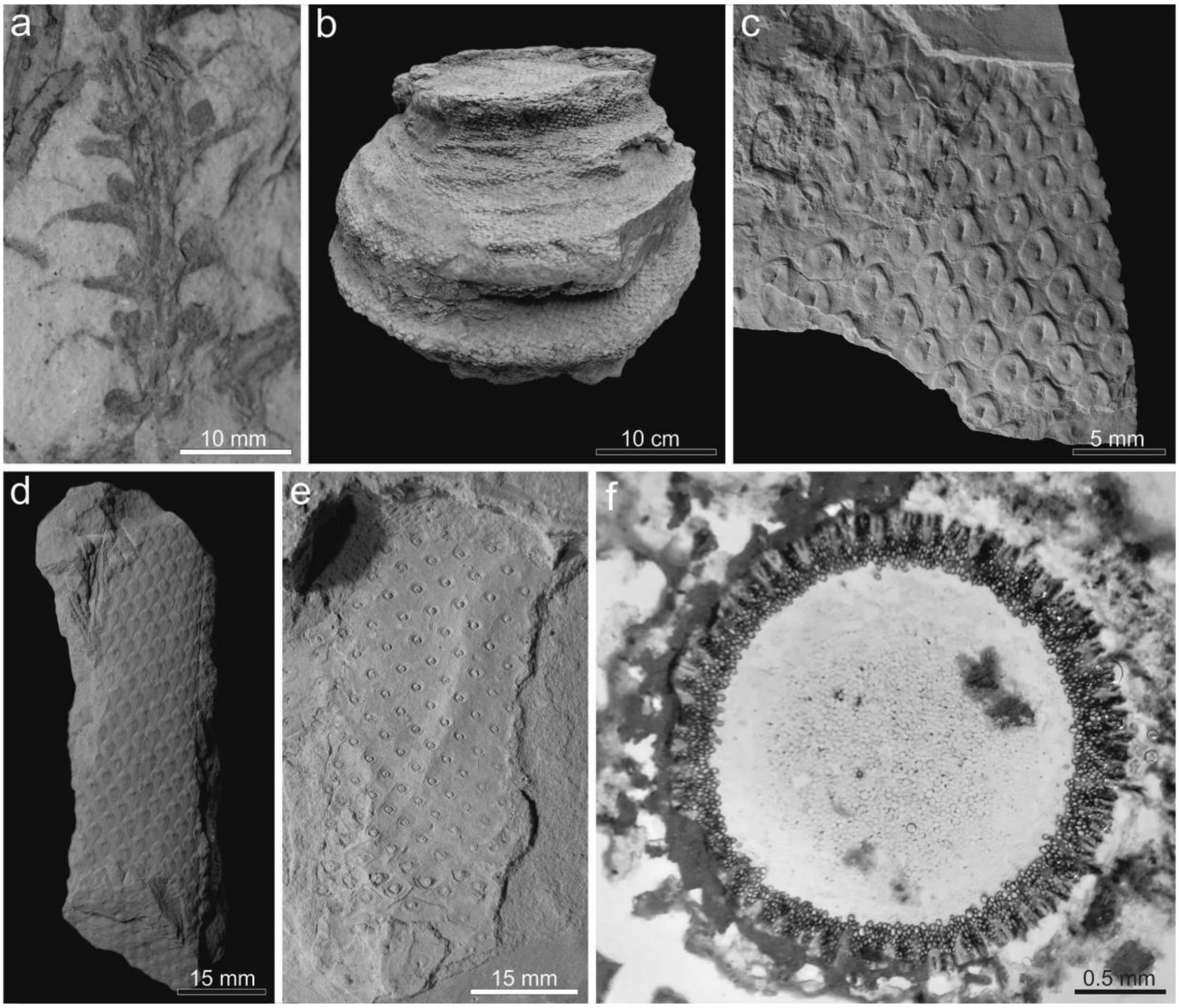

Figure 9. Lycopsid fossils from the *Glossopteris* flora. (a) *Lycopodites riograndensis* Salvi et al. from the Quitéria outcrop, Brazil. (b) Lycopsid stump from the Quitéria outcrop. This specimen was found in a growth position at the outcrop. (c) *Azaniadendron fertile* Rayner from the West Driefontein quarry, South Africa (d) *Brasilodendron pedroanum* Chaloner et al. from the Morro do Papaléo outcrop, Brazil. (e) *Cyclodendron leslii* (Seward) Kräusel from the Leeukuil quarries, South Africa. (f) Anatomically preserved axis of *Lycopodiopsis derbyi* Renault from Brazil. Photos: Rafael Spiekermann.

Objectives and overview of publications

This cumulative thesis comprises four original publications on selected problematic issues regarding lycopsids from the *Glossopteris* flora. The studies deal mainly with the sub- to arborescent lycopsids from the flora, which are one of the least understood plant groups from Gondwana due to the fragmented and incompletely preserved nature of their fossil remains. Together, the general scope of these publications include: (i) develop and demonstrate an approach to deal with numerous fragmentary impressions/compressions of lycopsids axes to achieve robust taxonomical circumscriptions, using *Azaniadendron fertile* as a case study; (ii) determine if all lycopsid fossil-taxa from *Glossopteris* flora really lacked ligules as traditionally assumed; (iii) describe a new fossil-taxon applying a set of techniques, showing that the lycopsid morphological diversity from the *Glossopteris* flora might be underrepresented due to lack of detailed investigations on long ignored specimens; (iv) evaluate if there is evidence of typical Euramerican late Palaeozoic arborescent lycopsids in the *Glossopteris* flora, reinvestigating an anatomically preserved axis previously interpreted as a Sigillariaceae; (v) summarise the state of the art and construct a strong background for future research on lycopsids from the *Glossopteris* flora, highlighting the needs to solve the unknowns concerning these plants. An overview of the studies covering these aims is presented below; they are organised thematically in this document.

Publication 1. This investigation provides a review of the late Palaeozoic lycopsid macrofossil record from the entire Paraná Basin in South America. Strata of this basin yielded most of the lycopsid macrofossils from the *Glossopteris* flora but also remains preserved in late Carboniferous pre-*Glossopteris* deposits. This review was extended into those Carboniferous deposits as some typical lycopsids of the *Glossopteris* flora (e.g., *Brasilodendron*) already flourished during that time in interglacial stages. This publication also provides a complete historical account of the lycopsid research in the Paraná Basin. It also defines the updated spatiotemporal distribution of the lycopsids macrofossils in this basin and provides a robust baseline for future research on these plants, which applies not only to the Paraná Basin but also to the entire Gondwana.

Publication 2. This publication provides a fresh look on the morphology of the monotypic *Azaniadendron* Rayner from the Guadalupian of South Africa. Little was known about the morphological characters of this fossil-taxon before. In this study, the reproductive structures of *Azaniadendron* were re-interpreted as arranged in fertile zones rather than compact cones. Evidence for a ligule is presented for the first time, solving, at least for this genus, a historical dilemma about the presence of this structure in sub- to arborescent lycopsids from the Permian *Glossopteris* flora. Most importantly, the intraspecific/taphonomical variations of the leaf cushions of the genus are thoroughly described based on numerous fragmented axes that represent this fossil-taxon. The descriptive approach applied in this study is an example of how to overcome challenges in reliably identifying and circumscribing lycopsid fossil-taxa, such as those of the *Glossopteris* flora, which are mainly represented by fragmented remains of axes.

Publication 3. This publication investigates lycopsid axes from Cisuralian deposits of the São Sepé outcrop in southern Brazil. These fossils have been outside the scope of research for years. We described them in detail, using standard palaeobotanical techniques, and a vinyl polysiloxane casting technique, which revealed the imprints of their epidermal characters under the scanning electron microscope. We placed them in *Nothostigma* Doweld, a fossil-genus of lycopsids that thrived in Gondwana during a Mississippian pre-glacial stage but was so far unknown in the Permian post-glacial *Glossopteris* flora. Due to their unique set of morphological characters, we proposed *Nothostigma sepeensis* Spiekermann et al. sp. nov. This study reveals how the lack of detailed descriptions of long-ignored remains, especially because they are small and attract little attention, has been obscuring our knowledge of the lycopsid morphological diversity in the *Glossopteris* flora. Techniques used for the description of this new fossil-species may serve as a basis for future taxonomical studies of lycopsid axes from the Gondwana flora.

Publication 4: Sigillarians are typical arborescent lycopsids from the Euramerican late Palaeozoic ecossystems. However, an anatomically preserved axis from the Kungurian Irati Formation in Brazil was previously interpreted as a Sigillariaceae lycopsid and remained so in the literature. If correct, this would be the only evidence of this type of Northern hemispheric lycopsid in the *Glossopteris* flora. In this study, this particular axis is re-examined in detail. The morpho-anatomical characteristics of this axis indicate that it is not a lycopsid at all but belongs to Cycadales. Based on these morpho-anatomical features, the new fossil-genus and species *Iratinia australis* Spiekermann et al. has been proposed. This fossil is outstanding, as it represents the oldest known anatomically preserved cycad axis, indicating that during the Kungurian Cycadales or their direct ancestor were already well-established. Most important for this thesis, however, is that there remains no evidence of Euramerican sigillarians in the *Glossopteris* flora from Gondwana.

Publication 1

Late Palaeozoic lycopsid macrofossils from the Paraná Basin, South America – an overview of current knowledge

Spiekermann, R., Jasper, A., Benício, J.R.W., Guerra-Sommer, M., Ricardi-Branco, F.S. & Uhl, D., 2020.

Journal of South American Earth Sciences 101, 102615.
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Contribution statement

R. Spiekermann: author position, 1; scientific ideas, 80%; data generation 85%; analysis and interpretation, 80%; paper writing, 80%.
A. Jasper: author position, 2; scientific ideas, 5%; data generation 3%; analysis and interpretation, 5%; paper writing, 5%.
J.R.W. Benício: author position, 3; scientific ideas, 2%; data generation 2%; analysis and interpretation, 4%; paper writing, 2%.
M. Guerra-Sommer: author position, 4; scientific ideas, 4%; data generation 3%; analysis and interpretation, 3%; paper writing, 4%.
F.S. Ricardi-Branco: author position, 5; scientific ideas, 4%; data generation 4%; analysis and interpretation, 3%; paper writing, 4%.
D. Uhl: author position, 6; scientific ideas, 5%; data generation 3%; analysis and interpretation, 5%; paper writing, 5%.
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Late Palaeozoic lycopsid macrofossils from the Paraná Basin, South America – an overview of current knowledge

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ABSTRACT

Lycopsids evolved arborescent and sub-arborescent growth habits and played a major paleoecological role during the late Palaeozoic. Here we provide an overview of lycopsid macrofossils documented so far in the late Palaeozoic deposits of the South American Paraná Basin. Most of these lycopsid remains were reported from the Brazilian part of the basin, whereas only a few records have been documented from the Uruguayan and Paraguayan parts. The oldest well-documented macrofossil record of these plants in late Palaeozoic strata of this basin comes from Pennsylvanian interglacial deposits of the Itararé Group. As the late Palaeozoic ice retreated, arborescent and sub-arborescent lycopsids successfully colonized the Brazilian Cisuralian post-glacial palaeoenvironments represented by the Rio Bonito Formation, becoming important elements of the iconic *Glossopteris* flora. The late Palaeozoic transgression during the Artinskian coincided with the termination of the fluvio-deltaic and peat-forming systems of this formation in most areas of the basin, and this might have affected the lycopsids that grew in these peat-forming palaeoenvironments. Lycopsids again became significant components of the flora in the Brazilian part of the basin during the deposition of the Teresina and Corumbataí formations in the Guadalupian. After the increase of aridity in South America during the upper Permian, the group seems to have disappeared from the late Palaeozoic fossil record of the basin. The late Palaeozoic lycopsid macrofossil record of the Paraná Basin consists mainly of fragmented and incompletely preserved specimens, which lack crucial parts for systematics, such as reproductive structures. Therefore many aspects of these plants are still poorly known. The discovery of more completely preserved specimens and reproductive structures is required to provide a robust taxonomical and systematical classification, and reliable palaeobiogeographical and evolutionary hypotheses for the distribution and evolution of these particular lycopsids.

1. Introduction

Lycopsids are seedless vascular plants. Synapomorphies of the lineage include helically arranged microphyllous leaves and eusporangia located either in the axil or adaxial portion of the sporophyll (Taylor et al., 2009). The first lycopsids were herbaceous, and it has been suggested that they evolved from the extinct group of the zosterophylls during the early Devonian or even the late Silurian (Gensel, 1992; Gensel and Berry, 2001). However, already in the Devonian, the lineage had evolved sub-arborescent and arborescent growth habits, becoming significant components and even the dominant plant group within some of the first forests (e.g. Stein et al., 2012; Berry and Marshall, 2015; Wang et al., 2019).

Arborescent and sub-arborescent lycopsids flourished in both temperate and tropical regions during the Mississippian (e.g. Iannuzzi and Pfefferkorn, 2002; Falcon-Lang, 2004; Orlova et al., 2015). However, the arborescent taxa reached their zenith in the Lower and Middle Pennsylvanian, forming extensive swamp-forests across the Euramerican palaeotropical realm. They contributed significantly to large peat deposits in these swamps and were the most significant components of the biomass that resulted in the extensive palaeotropical coal measures (DiMichele and Phillips, 1985). Common arborescent

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lycopsid taxa found in these coal-bearing strata include, amongst others, *Lepidophloios*, *Synchysidendron*, *Diaphorodendron*, *Sigillaria*, and *Lepidodendron* (DiMichele and Phillips, 1994).

Due to massive climate and/or environmental changes during the Middle to Upper Pennsylvanian, the arborescent lycopsid swamp-forests collapsed, and a major extinction of these plants occurred in Euramerica (DiMichele and Phillips, 1996; Cleal and Thomas, 1999). However, in the Permian, arborescent and sub-arborescent lycopsids became significant components of the iconic *Glossopteris*-flora in Western Gondwana (e.g. Rayner, 1985; Spiekermann et al., 2018). Moreover, in Europe and Cathaysia *Sigillaria* persisted at least until the Cisuralian (e.g. Schindler et al., 2004; Pfefferkorn and Wang, 2009), and descendants of Pennsylvanian lepidodendrids continued to flourish in Cathaysia until the Lopingian (Wang and Chen, 2001).

The diversity of the lycopsids dropped significantly at the end of the Lopingian, and only herbaceous and sub-arborescent forms inhabited Mesozoic palaeoenvironments (e.g. Retallack, 1975; Skog and Hill, 1992). In the Triassic, the most conspicuous representative of the group was the sub-arborescent genus *Pleuromeia* (Retallack, 1975; Grauvogel-Stamm and Ash, 2005). By the Cretaceous, the lineage was represented by herbaceous forms, as well as small sub-arborescent lycopsids related mainly to the genus *Nathorstiana* (Richter, 1910; Mägdefrau, 1932). Currently, lycopsids compose a modest group of mostly herbaceous plants recently divided into 18 genera and approximately 1338 species (PPG I, 2016).

In the Paraná Basin, lycopsid fossils have been collected for more than a century. However, there are still many gaps in our knowledge about this group of plants in this particular basin. Here we present an overview of the lycopsid macrofossils reported so far from the late Palaeozoic deposits of the Paraná Basin. The current state of knowledge about these plant fossils is summarized (based on the fossil content of individual localities and stratigraphic units) and discussed, providing a base-line for future research on this topic.

2. Stratigraphical settings

The Paraná Basin is a vast intracratonic basin (Fig. 1), covering southern-central Brazil and parts of Uruguay, Paraguay and Argentina (Milani et al., 1998). In a broader sense, the Chaco-Paraná Basin in Argentina has been considered as an extension of the Paraná Basin. To date, no lycopsid macrofossils have been reported from the late Palaeozoic strata of this Argentinean basin, and here we deal only with the Paraná Basin *sensu stricto*.

According to Milani et al. (1998), the Paraná Basin comprises six depositional supersequences, ranging from the Ordovician up to the Cretaceous. All the late Palaeozoic lycopsid-bearing strata of the basin are included in the Gondwana I supersequence, which represents a major transgressive-regressive cycle of the Panthalassa Ocean (Milani et al., 2007).

2.1. Late Palaeozoic strata of the Paraná Basin in Brazil

In Brazil, the basal late Palaeozoic strata of the basin comprise the glacial and interglacial deposits of the Itararé Group (Holz et al., 2010; Bernardes-de-Oliveira et al., 2016). França and Potter (1988) divided this group into the Lagoa Azul, Campo Mourão, and Taciba formations (Fig. 2). Palynological studies have been suggesting that the Itararé was deposited between the Pennsylvanian and Cisuralian (Souza, 2006). However, recent U–Pb dating indicates that at least in the southern region of the basin, its deposition may have occurred only during the Pennsylvanian (Cagliari et al., 2016; Griffis et al., 2018).

The Guatá Group succeeds the glacial strata and is composed from the base to the top of the Rio Bonito and Palermo formations (Fig. 2). The Rio Bonito Formation contains fluvio-deltaic and estuarine facies as well as minor coal seams deposited in barrier-lagoon systems. This unit is divided into the Triunfo, Paraguaçu, and Siderópolis members. The latter does not occur in the southernmost part of the basin where the formation remains undivided (Holz et al., 2010). U–Pb dating indicates that the deposition of the Rio Bonito Formation began in the Asselian and extended up to the Artinskian (Griffis et al., 2018; Jurigan et al., 2019). Two distinct coal intervals occur in this formation. The oldest coals (Asselian) occur in the south-eastern margin of the basin (Griffis et al., 2018), while the youngest ones (Artinskian) in the central-eastern part (Jurigan et al., 2019). The Palermo Formation has been positioned in the middle Artinskian and was deposited in a shallow marine system (Holz et al., 2010). This unit overlies conformably the Rio Bonito Formation and represents the maximum flooding interval of the Paraná Basin in Brazil (Milani et al., 2007).

The Passa Dois Group overlies the Guatá units and its late Palaeozoic formations are named as Irati, Serra Alta, Teresina, Corumbataí, and Rio do Rasto (Fig. 2). The Irati Formation represents a vast inland sea (Holz et al., 2010), and U–Pb dating indicates an Artinskian-Kungurian age for this formation (Rocha-Campos et al., 2019). The Irati is succeeded by the Serra Alta Formation, which is interpreted as having formed in a marine system below storm wave base during the Kungurian (Schneider et al., 1974; Holz et al., 2010). The overlying Teresina Formation is interpreted as deposited in a storm-influenced offshore to coastal-plain system (Holz et al., 2010). In the northeastern part of the basin, the Corumbataí Formation has been considered as equivalent to the Teresina deposits (Milani et al., 2007).

Recently, Rocha-Campos et al. (2019) positioned the Teresina and Corumbataí formations in different chronostratigraphic intervals. The authors suggested a Wordian age for the Teresina and a Wuchiapingian age for the Corumbataí based on zircon U–Pb dating. This conflicts with the traditional interpretation that the units are of equivalent age. According to Rocha-Campos et al. (2019), these ages are not beyond doubt since U–Pb analyses for the Teresina are based only on a few samples, and zircons recovered from two putative ash-fall layers of the Corumbataí Formation could have been affected by the loss of radiogenic Pb.

The Rio do Rastro Formation is divided from the base to the top into the Serrinha and Morro Pelado members. The Serrinha Member is interpreted as a shallow lake system, whereas the Morro Pelado Member has many different interpretations such as meandering-fluvial to lacustrine, deltaic and aeolian, and fluvial plain (Holz et al., 2010 and citations therein). U–Pb dating indicates a maximum depositional age of Wuchiapingian for the Morro Pelado (Rocha-Campos et al., 2019). Sedimentation of the Gondwana I supersequence is completed by fluvial and aeolian deposits of the Sanga do Cabral and Pirambóia formations, which have been considered as Lopingian or Lower Triassic (Milani et al., 2007; Holz et al., 2010).

2.2. Late Palaeozoic strata of the Paraná Basin in Uruguay

The Uruguayan late Palaeozoic deposits of the basin are included in the Cerro Largo Group (Fig. 2). The basal portion of this group comprises glacially-influenced deposits of the Permo-Carboniferous San Gregorio Formation. This unit is succeeded by the Cerro Pelado, Tres Islas, Fraile Muerto, Mangrullo, Paso Aguiar, Yaguarí, and Buena Vista formations (de Santa Ana et al., 2006). Earlier, Bossi and Navarro (1991) interpreted Fraile Muerto, Mangrullo and Paso Aguiar as members of a unit named as Melo Formation. The latter was mentioned by Andreis et al. (1996) as a single unit with no members.

The Cerro Pelado Formation is interpreted as a transgressive event that covered the San Gregorio deposits (de Santa Ana et al., 2006). The overlaying Tres Islas Formation comprises clastic sediments and some minor coal-bearing layers deposited in fluvio-deltaic settings (Beri et al., 2015). It is divided into the Lower and Upper members and is interpreted as Sakmarian based on palynological correlations (Beri et al., 2011). The Frayle Muerto Formation was deposited in a marine platform environment, and a Sakmarian-Artinskian age is suggested for this unit based on its palynological content (de Santa Ana et al., 2006;

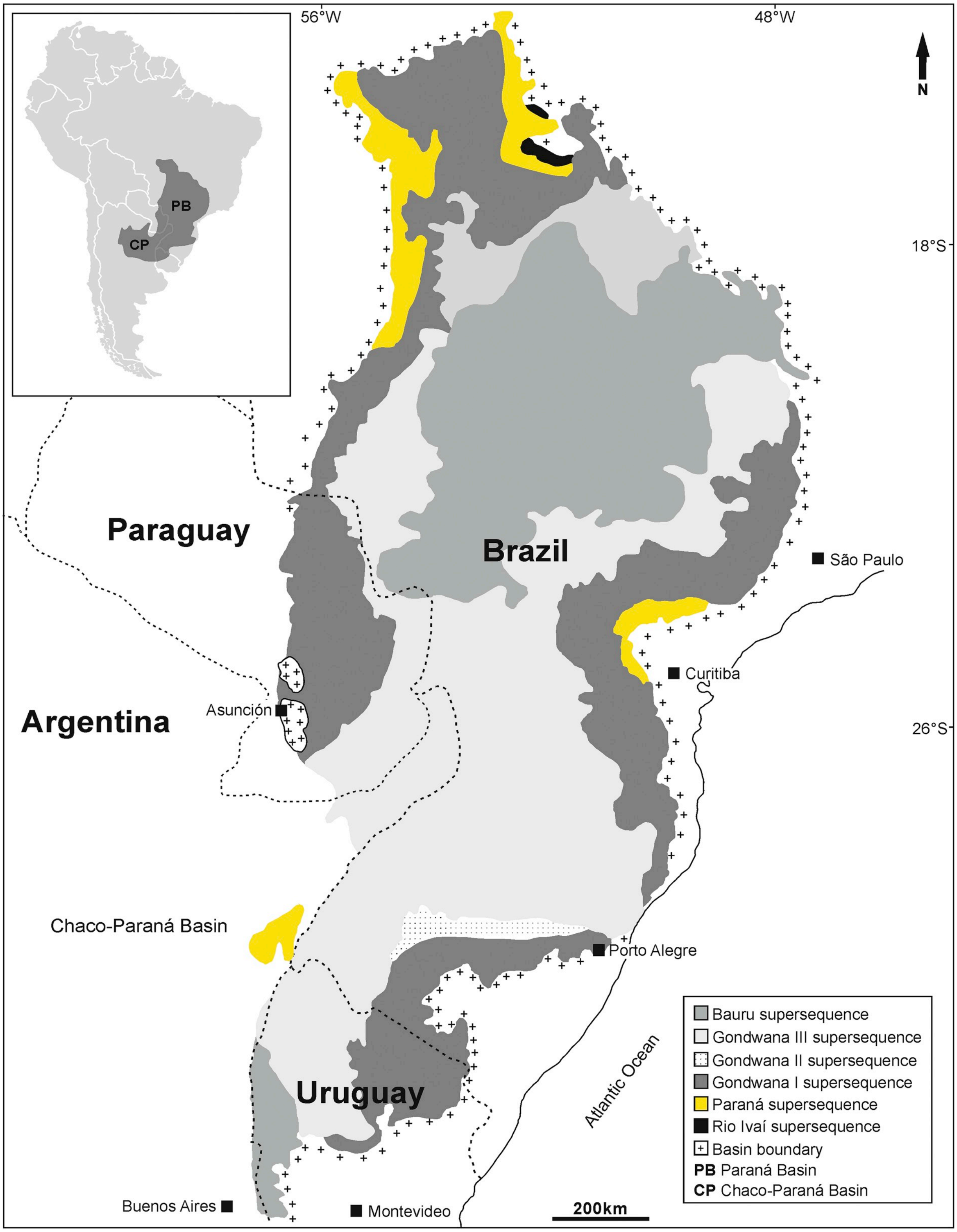

Fig. 1. Geological map of Paraná Basin. Adapted from Milani et al. (1998). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Beri et al., 2011). The Mangrullo Formation is interpreted as being formed under restricted subaqueous settings and is traditionally correlated with the Irati Formation in Brazil (de Santa Ana et al., 2006). U–Pb dating of an ash-fall layer that occurs directly below the overlaying Paso Aguiar Formation indicates a Kungurian age for the upper part of the Mangrullo Formation (Rocha-Campos et al., 2019).

The Paso Aguiar Formation was deposited in a marine platform (de Santa Ana et al., 2006), while the Yaguarí Formation is interpreted as formed in a prograding fluvial system (Bossi et al., 1998). The Yaguarí is divided into the Lower and Upper members (de Santa Ana et al., 2006). U–Pb dating of bentonite that occurs in the Upper Member indicates that the maximum depositional age of this formation is Roadian-

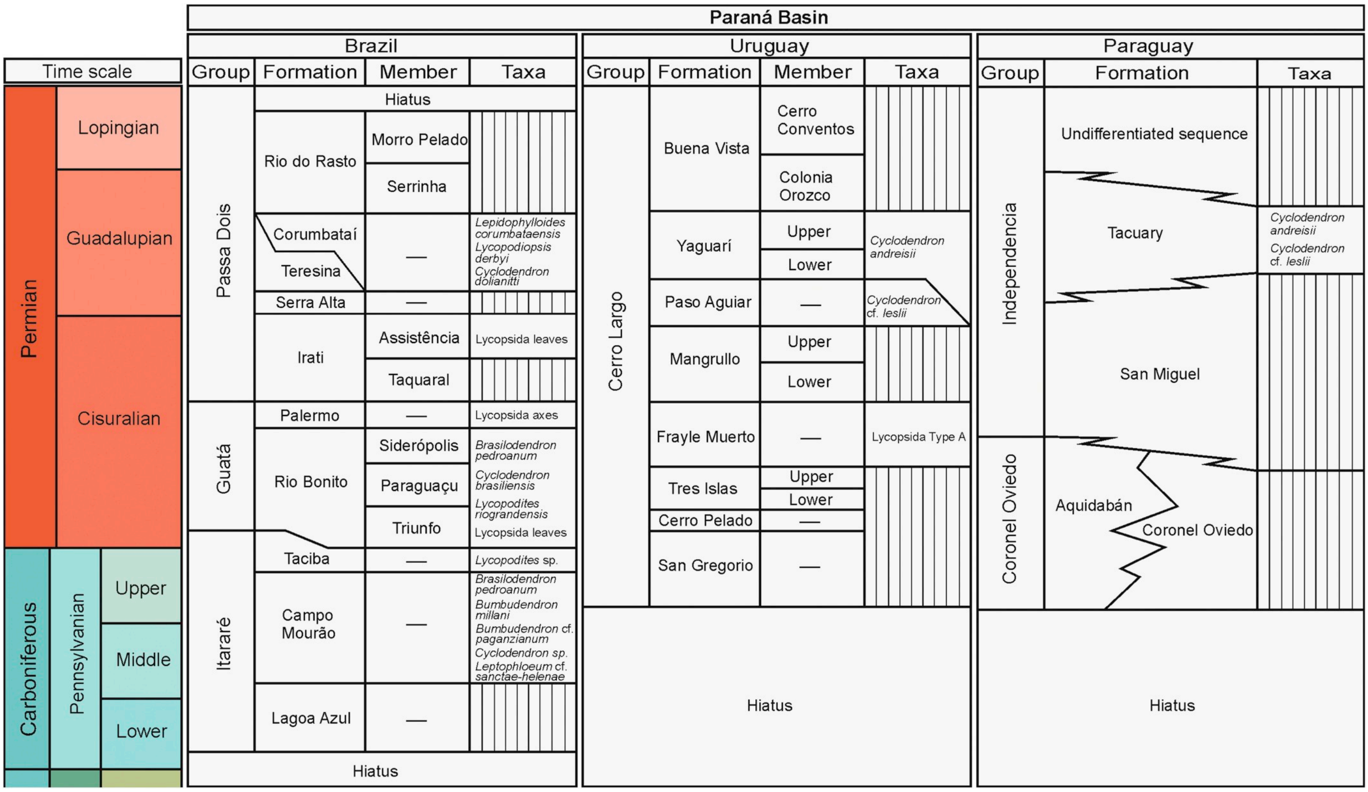

Fig. 2. Simplified chart of the late Palaeozoic of the Paraná Basin and stratigraphical distribution of the lycopsid taxa from the basin. Chart based on de Santa Ana et al. (2006), Milani et al. (2007), Holz et al. (2010), Beri et al. (2011), Rocha-Campos et al. (2019) and Muff et al. (1999). In this chart, the Teresina and Corumbataí formations are still maintained as equivalents.

Wordian (Rocha-Campos et al., 2019). The late Palaeozoic sedimentation of the basin in Uruguay ended with fluvial and aeolian sediments of the Buena Vista Formation, tentatively assigned to the upper Permian (de Santa Ana et al., 2006).

2.3. Late Palaeozoic strata of the Paraná Basin in Paraguay

The late Palaeozoic strata of the Paraguayan part of the basin are divided into only a few units (Fig. 2), and their ages are not satisfactorily known so far. The base of this sequence comprises the Permo-Carboniferous sediments of the Coronel Oviedo Group, which is composed of the Aquidabán and Coronel Oviedo formations. Both are overlain by the Permian deposits of the Independencia Group, divided from the base to the top into the San Miguel and Tacuary formations (Mapa Geológico del Paraguay, 1986). Earlier, Wiens (1982) included the Tapytá and Cabacuá formations at the top of the Independencia group. Muff et al. (1999) refer to both formations as “undifferentiated sequence” and positioned them from the Guadalupian up to the Lopingian. However, the authors considered that further investigations are necessary to elucidate whether such an undifferentiated sequence belongs to the late Palaeozoic sequence or are part of the overlying Mesozoic strata. Herbst and Amábili (2011) speculated that the Tapytá and Cabacuá formations could represent facies variations of the Tacuary Formation.

The San Miguel Formation is interpreted as deposited in a braided river system (Muff et al., 1999) and was considered as late Cisuralian-Guadalupian in age based on palynological correlations (Loinaze et al., 2010). The Tacuary Formation might represent a fluviolacustrine system or either a partially open or restricted estuarine-lagoonal system (Muff et al., 1999). An age ranging from the Kungurian up to the Roadian was suggested for this unit based on its palynological content (Muff et al., 1999). Considering palaeomagnetic data, Rapalini et al. (2006) proposed a late Guadalupian or early Lopingian age for this formation. According to Herbst and Amábili (2011), the Tacuary Formation may be an equivalent to the Brazilian Serra Alta and Teresina formations based on the presence of the *Pinzonella* fauna and plant fossils such as *Asterotheca*.

3. Overview of the current state of knowledge

The late Palaeozoic lycopsid macrofossil record of the basin comprises fertile and vegetative parts of herbaceous forms, vegetative axes and *in situ* corm-like stumps that belonged either to sub-arborescent or arborescent lycopsids, and isolated microphyllous leaves (Table 1). The lycopsid-bearing localities and taxa reported so far for the late Palaeozoic of the basin are listed in Appendix A.

3.1. Lycopsids from the Itararé Group (Pennsylvanian – Cisuralian, Brazil)

To date, lycopsid macrofossils have been reported only from two outcrops of the Itararé Group. They occur in the interglacial deposits of the Sítio Volpe (municipality of Monte Mor), and Sítio Toca do Índio (municipality of Cerquilho) outcrops. Both cities are situated in São Paulo state, at the northeastern margin of the Paraná Basin, Brazil.

3.1.1. The lycopsid axes from the Sítio Volpe outcrop

The Sítio Volpe outcrop contains a coal layer, mudstones, sandstones and diamictites. The coal-bearing layer and mudstones are interpreted as deltaic plain and floodplain deposits, whereas the diamictites represent a glacial phase (Bernardes-de-Oliveira et al., 2016). These deposits were tentatively assigned to the Campo Mourão Formation (Christiano-de-Souza and Ricardi-Branco, 2015) and a Pennsylvanian age has been suggested for them based on their plant macrofossils and palynomorphs (Bernardes-de-Oliveira et al., 2016).

The lycopsid macrofossils from this outcrop represent fragmented unbranched axes, preserved mainly as impressions and rarely as casts

Table 1
Summary of the lycopsid macrofossil types and taxa reported from the late Palaeozoic of the Paraná Basin. Taxa according to the last synonymy or taxonomical mention of the material in the scientific literature.

Country	Formation	Age	Type of fossil	Taxa
Brazil	Campo Mourão?	Pennsylvanian	Impressions, compressions and casts of vegetative axes	*Leptophloeum* cf. *sanctae*-helenae, *Brasilodendron* sp., *Brasilodendron pedroanum*, *Bumbudendron millani*, *Cyclodendron* sp., *Bumbudendron* cf. *paganzianum*,
Brazil	Taciba	Asselian- Sakmarian?	Fertile herbaceous lycopsid shoots	*Lycopodites* sp.
Brazil	Rio Bonito	Asselian-Artinskian	Impressions, compressions and casts of vegetative axes; *in situ* corm-like stumps	*Brasilodendron pedroanum*, *Brasilodendron* cf. *pedroanum*
			Impressions and casts of vegetative axes	*Cyclodendron brasiliensis*
			Fertile and vegetative herbaceous lycopsid shoots	*Lycopodites riograndensis*
			Impressions and compressions of isolated microphyllous	Not assigned to any taxon yet
Uruguay	Frayle Muerto	Sakmarian-Artinskian	Impressions and casts of vegetative axes	Lycopsida Type A
Brazil	Palermo?	Artinskian	Impressions and casts of vegetative axes	Lycopsida axes
Brazil	Irati Formation	Artinskian-Kungurian	Isolated microphyllous	Not assigned to any taxon yet
Uruguay	Paso Aguiar	Roadian	Impressions of vegetative axes	*Cyclodendron* cf. *leslii*
Uruguay	Yaguarí	Roadian-Wordian	Impressions and casts of vegetative axes	*Cyclodendron andreisii*
Paraguay	Tacuary	Guadalupian?	Impressions and casts of vegetative axes	*Cyclodendron* cf. *leslii*, *Cyclodendron andreisii*
Brazil	Teresina	Roadian-Wordian	Impressions and casts of vegetative axes	*Lycopodiopsis derbyi*, *Lycopodiopsis* sp., *Cyclodendron dolianitti*
			Isolated microphyllous	*Lepidophylloides corumbataensis*
Brazil	Corumbataí	Roadian-Wuchiapingian?	Impressions, compressions, casts and permineralizations of vegetative axes	*Lycopodiopsis derbyi*
			Isolated microphyllous	*Lepidophylloides corumbataensis*

and compressions. Based on their leaf cushion morphology, Millan (1972) assigned them to the taxa *Lycopodiopsis* sp., *Lycopodiopsis derbyi*, *Lycopodiopsis pedroanus* and, *Lepidodendron pedroanum*. The latter is a single specimen, and for its leaf cushions, the author mentioned the presence of parichnos and a putative ligule scar. Later, Millan (1980) reinterpreted the *Lycopodiopsis pedroanus* specimens as *Brasilodendondron pedroanum*.

Mune et al. (2012) revisited all lycopsid macrofossils from Sítio Volpe and classified them as *Brasilodendondron pedroanum*, *Brasilodendondron* sp., *Bumbudendron millani*, *Bumbudendron* cf. *paganzianum*, *Cyclodendron* sp., and *Leptophloeum* cf. *sanctae-helenae* (Fig. 3A–E). The latter corresponds to the single specimen previously interpreted as *Lepidodendron pedroanum*, and the authors pointed out that it lacks evidence of ligule and parichnos. Moreover, in a sample classified as *Brasilodendondron* sp., they reported a possible indication of a ligule scar, which is not a characteristic for this genus (see description of this taxon in 3.2.1). Unfortunately, Mune et al. (2012) did not provide images of such a putative ligule scar.

Hypautochthonous lycopsid axes are abundant at the foot-wall of the coal layer of this outcrop, composing almost a monotypic assemblage interpreted as hydro-hygrophilous and associated either with tidal plains or brackish environments (Mune et al., 2012). The lycopsids preserved in the hanging-wall are hypautochthonous-allochthonous and were deposited either in a flood plain or on the margins of river channels of a deltaic plain (Mune et al., 2012). This vegetated system flourished during a short Pennsylvanian interglacial stage and collapsed with the beginning of a new glacial stage (Bernardes-de-Oliveira et al., 2016).

3.1.2. *Herbaceous lycopsids from the Sítio Toca do Índio outcrop*

The Sítio Toca do Índio outcrop is comprised of carbonaceous mudstones, siltstones, and shales (Bernardes-de-Oliveira et al., 2007). These deposits are probably related to the Taciba Formation (Bernardes-de-Oliveira et al., 2016). An age ranging from Asselian to Sakmarian has been suggested for them, based on its palynological content (Souza, 2006; Bernardes-de-Oliveira et al., 2016).

To date, only a single herbaceous lycopsid impression was reported from this outcrop. According to Salvi et al. (2008), this specimen lacks evidence of parichnos and ligule and is covered by helically arranged microphyllous leaves that arise from the stem at an angle of 45°. This fossil is fertile and bears ovate pedicellate sporangia borne in the sporophyll axils. Based on this set of morphological characteristics, Salvi et al. (2008) classified the specimen as *Lycopodites* sp.

3.2. *Lycopsid from the Rio Bonito formation (Asselian – Artinskian, Brazil)*

Lycopsid macrofossils were described from the Rio Bonito Formation at the Brazilian meridional states of Paraná, Santa Catarina and Rio Grande do Sul. A formal definition for this formation was not available for the pioneering investigations in Brazil, and early studies did not indicate the lithostratigraphic unit from where the plant fossils were extracted. Based on the available data about lithology and geographical locality, we included all the Brazilian fossils considered here in this unit.

3.2.1. *Lycopsid axes from the Rio Bonito formation: the first 110 years of studies*

The first description of lycopsid macrofossils from the Rio Bonito Formation was provided by Carruthers (1869). The fossils were collected from the Candiota coalfield, Rio Grande do Sul state and correspond to unbranched axes preserved as compressions and impressions (Fig. 4A). These vegetative axes were incorrectly assigned by him to the genus *Flemingites*, which is the bisporangiate cone of *Paralycopodites* (Brack-Hanes and Thomas, 1983; Phillips and DiMichele, 1992). Based on their specific morphology, Carruthers erected the new species *Flemingites pedroanus*.

Szajnocha (1891) described lycopsid axes from the Carboniferous of Argentina and provided the new combination *Lepidodendron pedroanum*. According to him, *Flemingites pedroanus* should be considered as a synonym of this taxon. Zeiller (1895) was not convinced about this interpretation and thought that the Argentinean specimens differ from *F. pedroanus*. However, the author interpreted the latter as an authentic *Lepidodendron* and (also) reclassified the Brazilian taxon as *L. pedroanum*.

Additionally, Zeiller (1895) described lycopsid axes from the Arroio dos Ratos coalfield, Rio Grande do Sul state. Most of them were interpreted as *Lepidodendron pedroanum* and *Lepidophloios laricinus*. The latter was a component of the Euramerican Carboniferous peat-forming systems (DiMichele, 1979). Based on this, Zeiller (1895) claimed that the North Hemisphere Carboniferous flora was also present in Southern

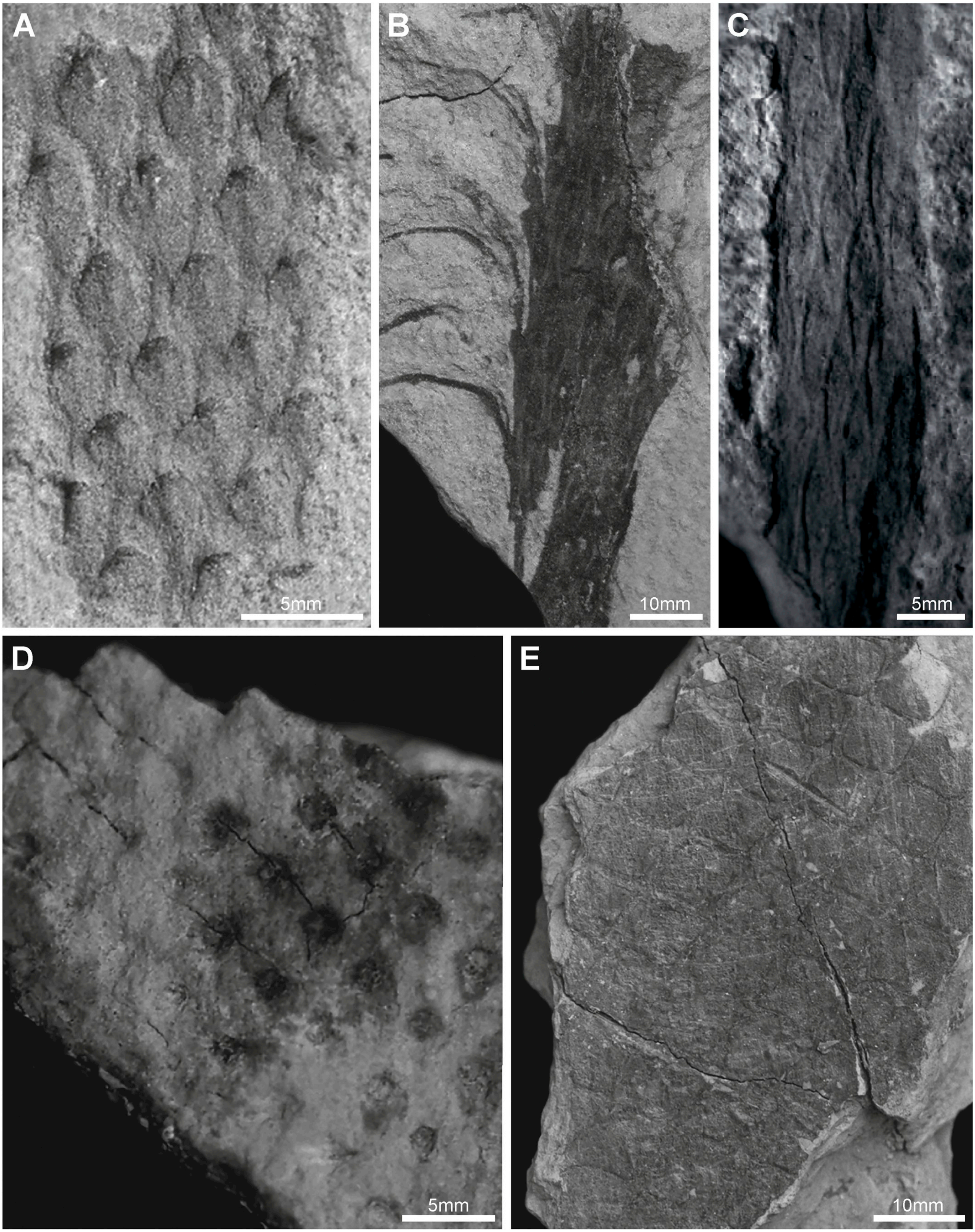

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Fig. 3. Lycopsid macrofossils from the Sítio Volpe outcrop. Taxonomical classification according to Mune et al. (2012). A) *Brasilodendondron pedroanum* (sample DGP MN 805 Pb). B) *Bumbudendron* cf. *paganzianum* (sample DGP MN 1088 Pb). C) *Bumbudendron millani* (sample DGP MN 803 Pb). D) *Cyclodendron* sp. (sample DGP MN 1093 Pb). E) *Leptophloeum* cf. *sanctae-helenae* (sample DGP MN 801 Pb). These specimens were deposited in the scientific collection of the *Museu Nacional* of the *Universidade do Rio de Janeiro*, Rio de Janeiro, Brazil. So far, it is unknown whether they survived the catastrophic fire that struck this museum in September 2018. Images courtesy of Mary E. C. Bernardes-de-Oliveira.

Brazil. Arber (1905) agreed with this interpretation and suggested that the Euramerican Carboniferous lycopsids migrated southward and colonized the Permian Gondwana environments.

According to White (1908), *Lepidodendron pedroanum* has parichnos, and this taxon, as well as *Lepidophloios laricinus*, also occur in the coals situated near the municipality of São Jerônimo, Rio Grande do Sul state. In the vicinity of this area, this author also discovered new remains and assigned them to the Euramerican taxon *Sigillaria brardii*. Moreover, White erected the new species *Sigillaria australis* based on a single axis collected at the municipality of Lauro Müller, Santa Catarina state. According to him, when the late Palaeozoic Ice Age (LPIA) ceased, the northern arborescent lycopsids migrated southward, becoming one of the most significant elements of the Cisuralian peat-forming vegetation of the Paraná Basin.

Seward (1910) claimed that “it is clear that Carruthers' species is a true *Lepidodendron*”, but considered that it could be specifically different from the Euramerican ones. Later, Lundqvist (1919) reported axes from the locality of Arroio dos Cachorros and classified them as *Sigillaria brardii* and *Sigillaria* sp. Oliveira (1927) mentioned the presence of *Sigillaria* and *Lepidodendron* for the Figueira coalfield, Paraná state. The fossils assigned by him to *Lepidodendron* are impressions of dichotomizing branches (Fig. 4B) and axes bearing spirally arranged leaf cushions (Fig. 4C). The author neither provided a morphological description of this material nor figured the specimens mentioned as *Sigillaria*.

Read (1941) interpreted fragments collected at the Rio Ferreira outcrop (Treviso, Santa Catarina state) as strobili and assigned them to *Lepidostrobus* sp. (Fig. 4D). According to him, these strobili could belong to *Lycopodiopsis*. For this same locality and the Figueira coalfield, the author reported lycopsid axes and assigned them to *Lepidodendron pedroanum* (Fig. 4E). Two of these remains were interpreted by him as strobili of *Lepidodendron pedroanum* (Fig. 4F), and the author suggested that this taxon could be heterosporous.

According to Read (1941), the *Lepidodendron pedroanum* axes are covered by large leaf cushions that are practically square in outline. The author mentioned the presence of ligule and parichnos for the leaf cushions of some specimens of this taxon. However, he did not provide detailed images of these characteristics, and it is impossible to verify whether ligule and parichnos are present or not.

According to Edwards (1952), a reliable establishment of species for the Permian Gondwanan lycopsid axes described up to that time was impossible, since they were extremely fragmented and poorly preserved. However, the author interpreted that they exhibit similar details (e.g. leaf cushions lacking parichnos) and assigned them all to *Lycopodiopsis pedroanus*. Based chiefly on the absence of parichnos, Edwards claimed that there was no evidence of Euramerican arborescent lycopsids in the Gondwana *Glossopteris* flora. According to him, this strengthens the hypothesis of Sahni (1926), who suggested that these plants could be either survivors or descendants of austral lycopsids from a pre-Gondwana period.

Kräusel (1961) formally synonymized most of the Brazilian fossils previously assigned to *Flemingites pedroanus* and *Lepidodendron pedroanum* with the species *Lycopodiopsis pedroanus*. Although not complying with Edwards's broad taxonomical interpretation, Kräusel also concluded that most of the Rio Bonito Formation material previously included in *Lepidophloios* and *Sigillaria* is similar to *Lycopodiopsis pedroanum*. According to him, the Permian Gondwana lycopsids lack parichnos and ligule and are different from the Euramerican Pennsylvanian arborescent ones.

Chaloner and Boureau (1967), included the Permian lycopsid taxa from Gondwana in the family Lycopodiopsidaceae. Rösler (1972) mentioned that lycopsid axes are abundant at the Figueira coalfield and also occur at the municipality of São João do Triunfo, Paraná state. He interpreted most of the specimens as *Lycopodiopsis pedroanus*. Later, Lejal-Nicol and Bernardes-de-Oliveira (1979) collected lycopsid axes at the Rio Ferreira outcrop and described the new species *Cyclodendron brasiliensis*. According to them, *C. brasiliensis* presents helically arranged leaf cushions with a shell-like shape, bearing reniform leaf scars, which lack parichnos and ligule.

Chaloner et al. (1979) revisited the original specimens of *Flemingites pedroanus* (Carruthers, 1869) and reclassified them as *Brasilodendron pedroanum*. The type material of this taxon is represented by small unbranched axes bearing persistent spirally arranged microphyllous leaves. The latter have long and narrow, longitudinally oriented epidermal cells, and two longitudinal bands of sunken stomata probably located abaxially. Its leaf cushions are fusiform (4 mm high and 2.5 mm wide), with sigmoidal extensions in their upper and lower parts. They lack evidence of leaf scar, parichnos and ligule and have a robust cuticle with short rectangular epidermal cells.

According to Chaloner et al. (1979), *Brasilodendron pedroanum* could have been an arborescent plant and the following material was considered as synonymous of this taxon: *Flemingites pedroanus* (Carruthers, 1869), *Lepidodendron pedroanum* (Zeiller, 1895), and specimens assigned to *Lycopodiopsis pedroanus* by Kräusel (1961). The authors also suggested that the axes assigned to *Lepidodendron pedroanum* by Read (1941) could belong to *B. pedroanum*. All the putative reproductive structures of Read were interpreted as vegetative parts by Chaloner and colleagues.

3.2.2. An in situ lycopsid assemblage from the Quitéria outcrop

The Quitéria outcrop is located in the municipality of Pantano Grande, Rio Grande do Sul state. The lower interval of the outcrop is composed of granule-grained conglomerates, siltstones and thin coal layers (Jasper et al., 2006). The upper interval comprises a primary volcanic ash-fall layer (Griffis et al., 2018), which is succeeded by siltstones, claystones, and sandstones (Jasper et al., 2006). The depositional settings of the lower interval are interpreted as parts of a peat-forming barrier-lagoon system, whereas the clastic sequence that succeeds the ash-fall layer might represent the rupture of this protective coastal barrier (Jasper et al., 2006). U–Pb dating indicates an Asselian age for the ash-fall layer preserved at this outcrop (Griffis et al., 2018). The Quitéria outcrop can be included in the first stage of coal formation of the Rio Bonito Formation (Griffis et al., 2018).

The plant fossil assemblage preserved in the Quitéria ash-fall layer is predominantly composed of large *in situ* lycopsid stump casts (Fig. 5), as well as by horizontally bedded impressions of lycopsid axes and isolated microphyllous leaves. According to Jasper and Guerra-Sommer (1998), the *in situ* lycopsid stumps present a corm-like root-system, bearing elongated acicular appendices. These stumps are vertically compressed (Fig. 6A), and most of them show poorly preserved morphological details. However, in some specimens, the authors reported rhomboidal and elliptical spirally arranged leaf cushions, which lack evidence of parichnos and ligule.

According to Jasper and Guerra-Sommer (1998), the horizontally bedded lycopsid impressions bear elliptical, fusiform and rhomboidal leaf cushions, which are spirally arranged and lack evidence of ligule, and foliar and infrafoliar parichnos (Fig. 6B–F). The fusiform ones exhibit a sigmoidal extension in their lower portion. All these lycopsid

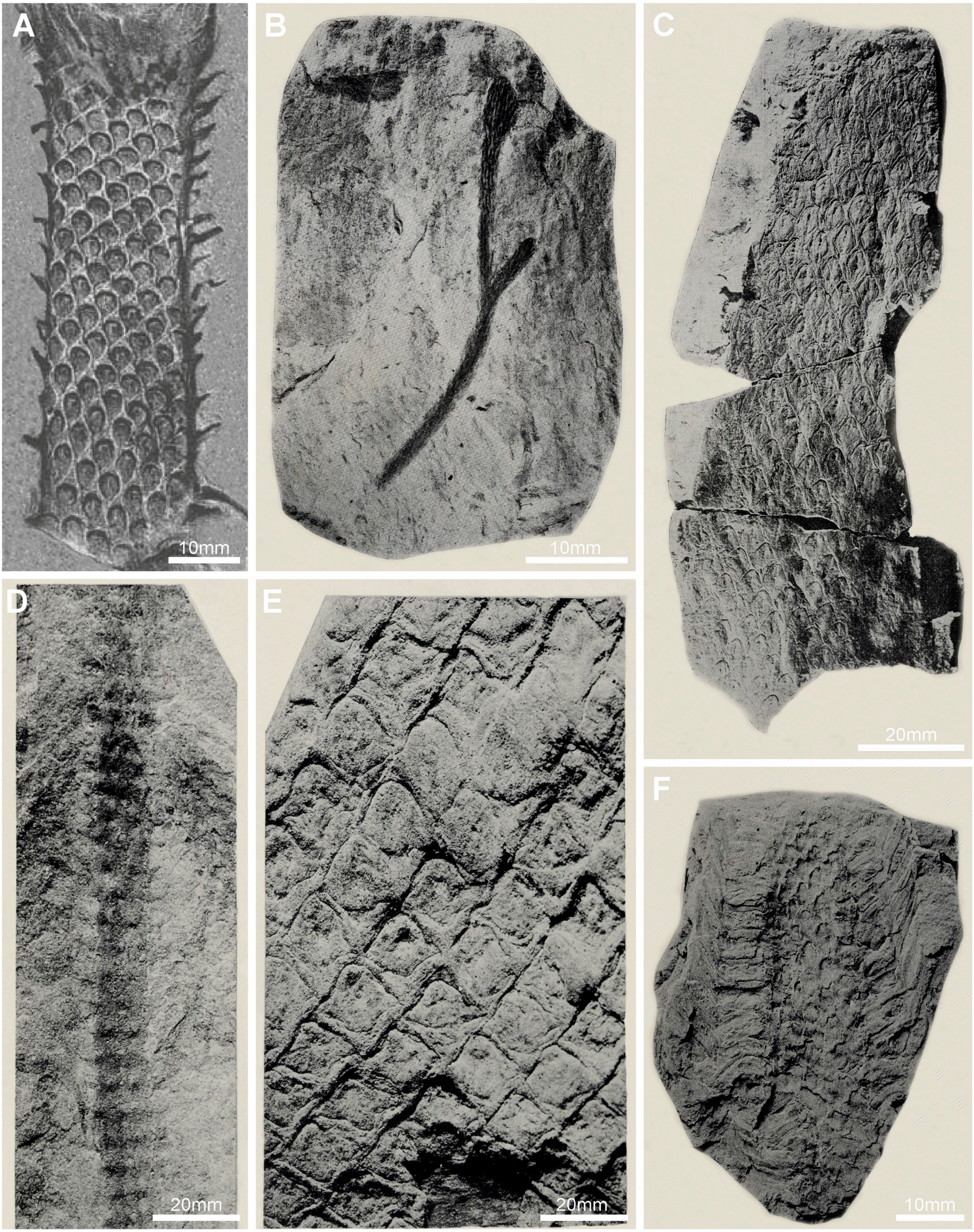

Fig. 4. Early records of lycopsid macrofossils from the Rio Bonito Formation. A) The original draft of *Flemingites pedroanus*. Later this specimen became the lectotype of *Brasilodendron pedroanum* (Chaloner et al., 1979). Image from Carruthers (1869). B) Dichotomizing fragment, originally interpreted as a *Lepidodendron*. C) Lycopsid axis first classified as *Lepidodendron*. Images B and C from Oliveira (1927). D) Impression first interpreted as *Lepidostrobus*. E) Lycopsid axis originally classified as *Lepidodendron pedroanum*. F) Impression first interpreted as a strobilus probably related to *Lepidodendron pedroanum*. Images D–F from Read (1941).

Fig. 5. *In situ* lycopsid stump preserved in the ash-fall layer at the Quitéria outcrop.

macrofossils were assigned to the genus *Brasilodendron*, and an arborescent growth habit was suggested for them (Jasper and Guerra-Sommer, 1998). Subsequently, these fossils were frequently mentioned as *Brasilodendron pedroanum* in the literature (Jasper et al., 2006; Guerra-Sommer et al., 2008; Boardman et al., 2012). These corm-like lycopsids and their leaf cushions are much larger than the type material of *B. pedroanum* (Chaloner et al., 1979). However, in the most well-known arborescent lycopsid taxa growth was determinate (Bateman, 1994), and size itself may not be a reliable taxonomic for these plants. For example, in the Carboniferous arborescent lepidodendrids from Euramerica, leaf cushion size depends on shoot size rather than shoot age (Eggert, 1961). In these Euramerican lycopsids, the most likely source for small leaf cushion covered axes is in the distal portions of the tree, in the final phases of determinate growth (e.g. Eggert, 1961; Opluštil, 2010). Hypothetically, a similar development may have occurred in *Brasilodendron*, and this could explain differences in leaf cushion size between small and large axes related to this taxon.

The short distance between the *in situ* stumps probably indicates that these lycopsids had a reduced crown (Jasper and Guerra-Sommer, 1999). The presence of hypautochthonous charcoal in the lower and upper interval of the outcrop indicates that the vegetation that grew in the vicinity of the area frequently experienced wildfires (Jasper et al., 2008; Costa et al., 2016). Most of these charcoal fragments have a gymnosperm anatomy, and only a few of them belong to lycopsids (Jasper et al., 2008).

3.2.3. *Lycopsid macrofossils from the Figueira coalfield*

The Figueira coalfield is situated near the municipality of Figueira (Paraná state) and comprises thin coal layers associated with carbonaceous shales and siltstones. The depositional system of the area is interpreted as a deltaic plain with peat-forming wetlands protected by sandy barriers (Morrone and Daemon, 1985; Della Favera et al., 1993). U–Pb dating of an ash-fall associated with the coal-bearing interval indicates an Artinskian age for this coalfield (Jurigan et al., 2019). This coalfield was deposited during a second coal-forming stage of the Rio Bonito Formation (Jurigan et al., 2019).

Early descriptions of the lycopsid axes from this coalfield include the studies of Oliveira (1927), Read (1941) and Rösler (1972). However, a more recent and detailed description of these macrofossils was conducted by Ricardi-Branco and Ricardi (2003). According to them, the Figueira lycopsids axes are preserved as impressions and compressions and are covered by fusiform leaf cushions, which are spirally arranged and lack parichnos and ligule (Fig. 7A–C). The authors considered that four different decortication levels occur in these axes, and from the outermost to the innermost level, a progressive loss of the morphological characteristics of the leaf cushions occurs (see Fig. 3 of Ricardi-Branco and Ricardi, 2003).

Ricardi-Branco and Ricardi (2003) classified the Figueira lycopsid axes as *Brasilodendron* cf. *pedroanum* and suggested an arborescent growth habit for them. However, these axes and its leaf cushions are much larger than the type material of *Brasilodendron pedroanum*. According to Ricardi-Branco and Ricardi (2003), this size difference might indicate that the fragments studied by Chaloner et al. (1979) are either smaller or younger specimens than those preserved in Figueira. As already mentioned above, in the Carboniferous arborescent lepidodendrids from Euramerica, the most likely source for small leaf cushion covered axes is somewhere up on the tree in the final phases of determinate growth (e.g. Eggert, 1961; Opluštil, 2010).

Isolated microphylls are abundant in the siltstones that overlie the Figueira coal layer (Fig. 7D). They have a linear-lanceolate lamina, which tapers in the direction of the apex and presents a prominent central vascular bundle on its abaxial face (Fig. 7E). In cross-section, they present lateral extensions on the adaxial face and a thin epidermis (Fig. 8A, D). The abaxial face has papillae (Fig. 8A), and the adaxial face bears sunken stomata (Fig. 8B). The specimens have hypodermis and mesophyll preserved (Fig. 8A, C) and in the central portion, they have a vascular bundle surrounded by a bundle sheath (Fig. 8D and E). All these microphyllous leaves share a similar anatomical pattern, and it has been suggested that they could originate from a single lycopsid species (Ricardi-Branco and Ricardi, 2003; Marchetti, 2013).

According to Ricardi-Branco and Rösler (2004), *Brasilodendron* cf. *pedroanum* was the dominant component of the Figueira peat-forming

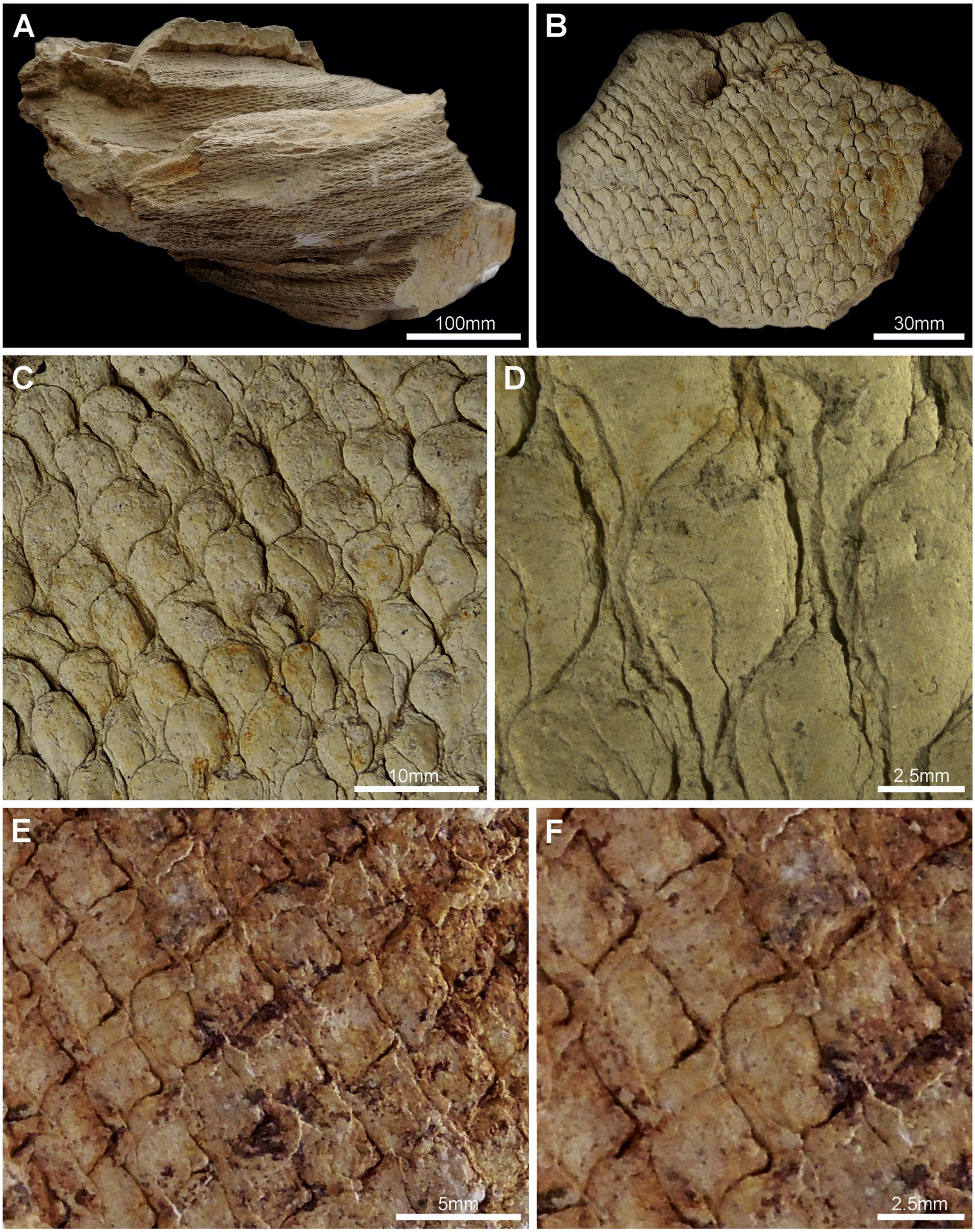

Fig. 6. Lycopsid macrofossils from the Quitéria outcrop. A) Vertically compressed stump presenting poorly preserved morphological characteristics (sample PbU 243). B) Horizontally bedded lycopsid impression bearing spirally arranged fusiform leaf cushions (sample PbU 548). C and D) Detail of the leaf cushions from specimen figured in B. E) Elongated rhomboidal leaf cushions spirally arranged (sample PbU 938). F) Detail of the leaf cushions from specimen figured in E. All these samples are deposited in the Palaeobotanical Collection of the *Museu de Ciências* of the *Universidade do Vale do Taquari*, Lajeado, RS, Brazil.

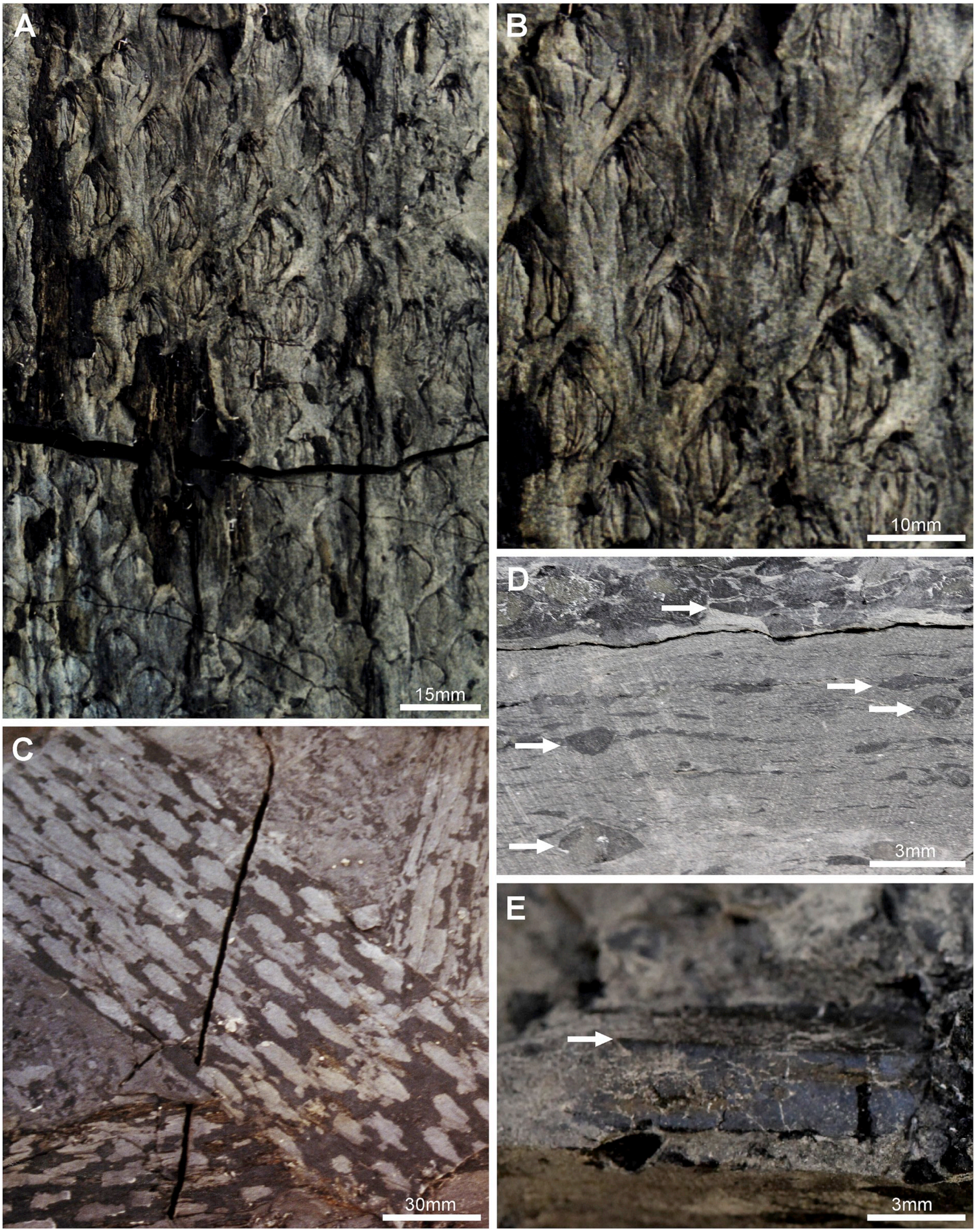

Fig. 7. Lycopsid macrofossils from the Figueira coalfield. A) Lycopsid axis bearing spirally arranged fusiform leaf cushions (sample GP/3E 7010a). B) Detail of the leaf cushions from specimen figured in A. C) Decorticated lycopsid axes (GP/3E 6010a1). These samples are deposited in the *Instituto de Geociências* of the *Universidade de São Paulo*, São Paulo, Brazil. D) Cross-section of siltstone bearing isolated microphylls (arrows) (sample CP1/565). E) Fragmented microphyll with a prominent central vascular bundle (arrow) in its abaxial face (sample CP1/564). These samples are deposited in the *Instituto de Geociências of Universidade Estadual de Campinas,* Campinas, SP, Brazil.

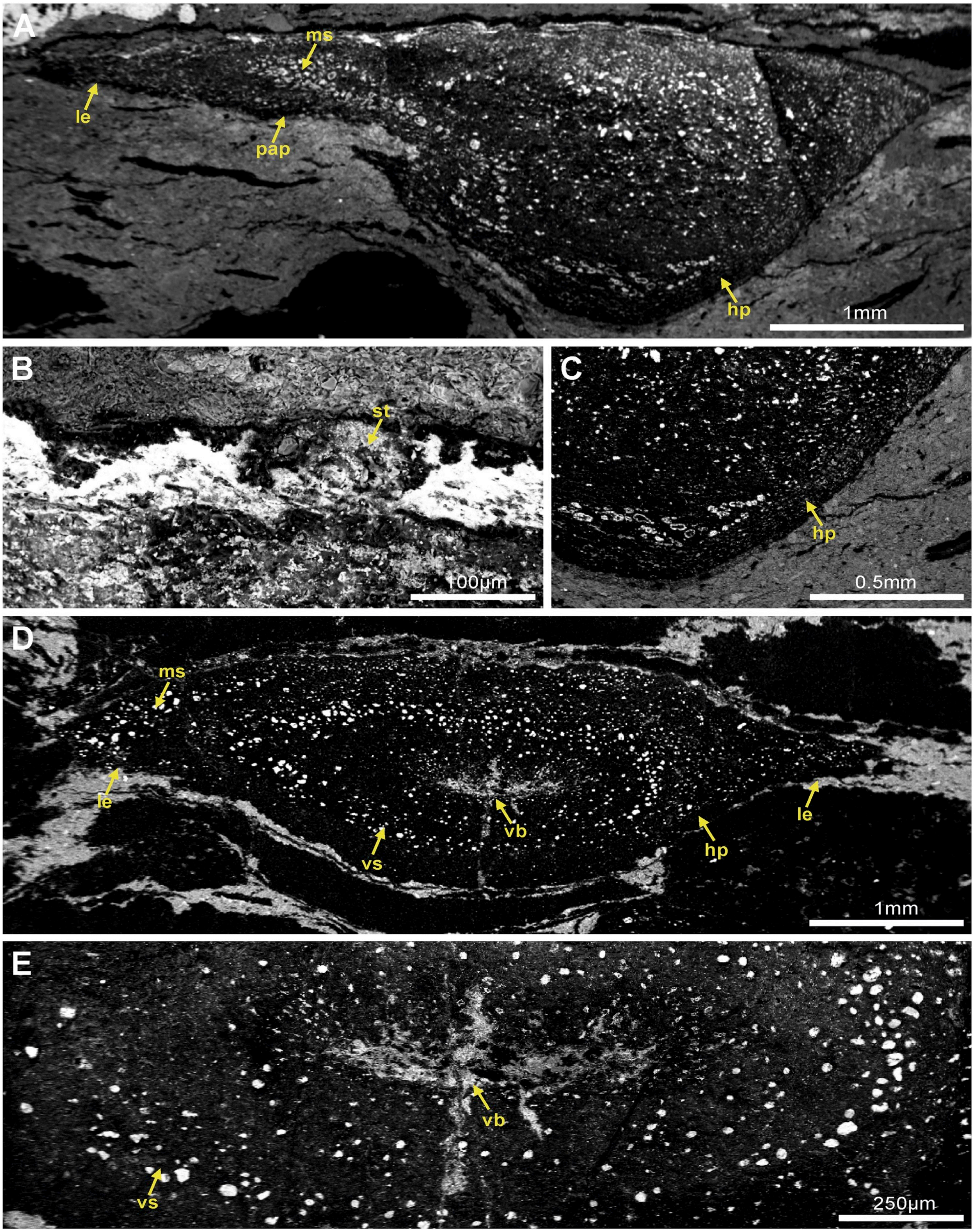

Fig. 8. Overview of the microphylls from the Figueira coalfield in cross-section. A) Microphyll bearing a single lateral expansion (le), a thin epidermis, and papillae (pap) in its abaxial face. Hypodermis (hp) and mesophyll (ms) are preserved. B) Detail of adaxial face of microphyll bearing a preserved stomata (st). C) Detail of microphyll showing the preserved hypodermis (hp). D) Specimen bearing lateral expansions (le) as well as a vascular bundle (vb) surrounded by a vascular sheath (vs). E) Detail of microphyll showing the vascular bundle (vb) and vascular sheath (vs). The images A–C are from sample Lam-DP1/566, while D and E are from sample Lam-DP1/564. This material is stored in the *Instituto de Geociências* of *Universidade Estadual de Campinas*. Figure from Marchetti (2013).

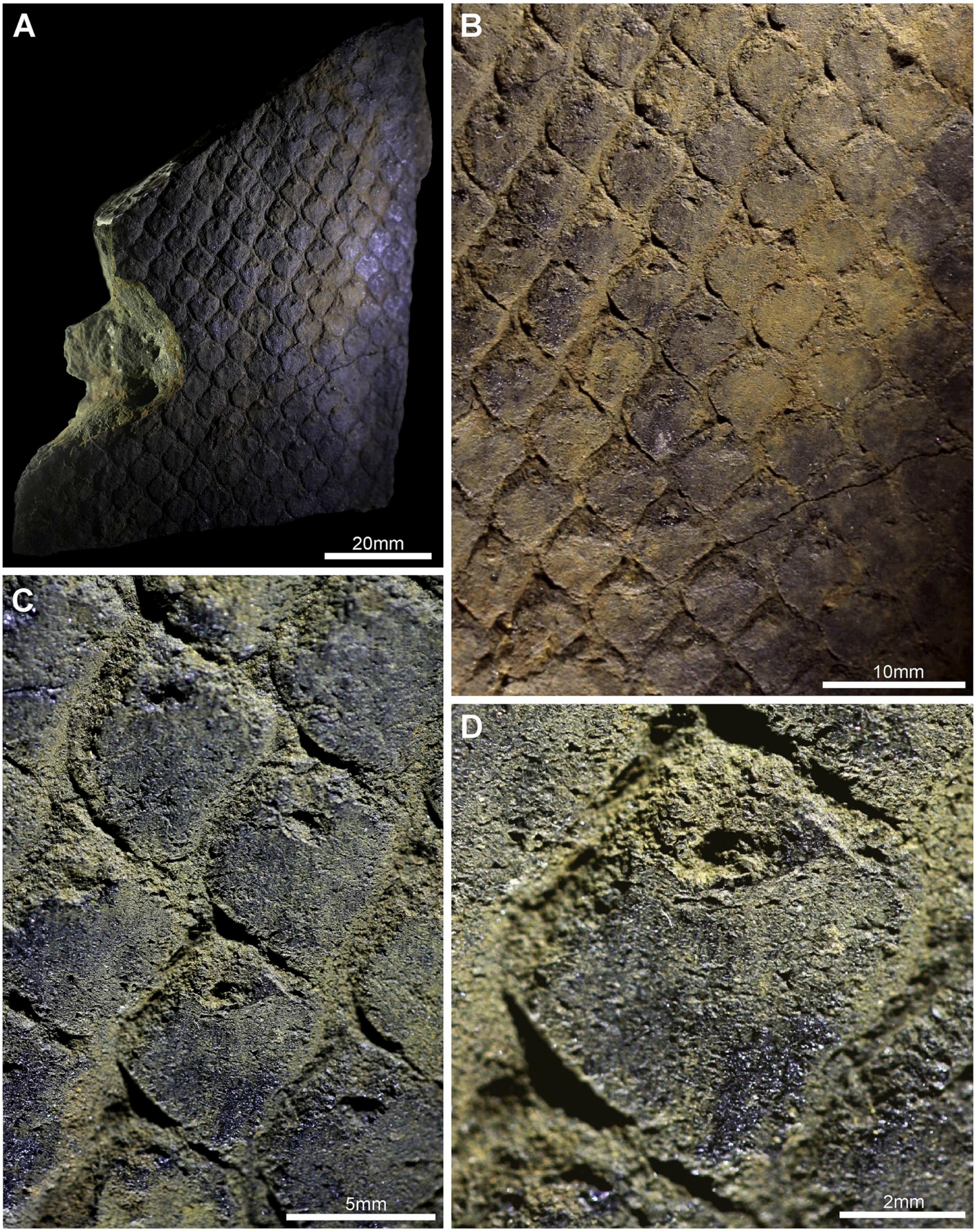

Fig. 9. Lycopsid macrofossil from Bonito I mine. Material classified as *Brasilodendron pedroanum* by Manfroi et al. (2012). A) Lycopsid cast from the clastic shale that overlies the coal-bearing strata of the mine. B) Spirally arranged rhomboidal leaf cushions. C) Detail of the rhomboidal leaf cushions. D) Detail of a leaf cushion bearing a leaf scar in its superomedial portion. Images are from sample PbU 766, deposited in the Palaeobotanical Collection of the *Museu de Ciências* of the *Universidade do Vale do Taquari*.

system, and the low lycopsid diversity in the area might be related to the stressful abiotic swampy conditions. The presence of hypautochthonous charred plant remains indicates that this peat-forming system and its surroundings were subjected to wildfires (Jasper et al., 2011).

3.2.4. *The lycopsid assemblage from the Bonito I mine*

The Bonito I mine is located in the municipality of Lauro Müller, Santa Catarina state. The coal-bearing layers of the mine are assigned to the Bonito coal seam, Siderópolis Member of the Rio Bonito Formation. The genesis of these coals is related to peat accumulation in an

Fig. 10. Clastic rock sample from Bonito I mine bearing a charred lycopsid remain and abundant gymnosperm-like charcoals. White arrow indicates the lycopsid charcoalified fragment. Sample PbU 790, deposited in the Palaeobotanical Collection of the *Museu de Ciências* of the *Universidade do Vale do Taquari*.

estuarine-barrier, shoreface depositional system (Kalkreuth et al., 2010). An Artinskian age for these deposits has been suggested based on sequence stratigraphy (Holz et al., 2010).

Lycopsid axes preserved as casts and impressions are abundant in the clastic shale that overlies the coal-bearing strata of this mine. Manfroi et al. (2012) investigated a total of 15 lycopsid specimens from this shale. According to the authors, these axes are covered by spirally arranged fusiform leaf cushions (Fig. 9A), which lack any extension in their upper and lower portion. Here we interpret that the leaf cushions figured by Manfroi et al. (2012) have a rhomboidal shape rather than fusiform (Fig. 9B and C). In their superomedial part, the cushions bear poorly preserved leaf scars (Fig. 9D), which lack any evidence of vascular bundle, parichnos, and ligule. Manfroi et al. (2012) assigned these specimens to *Brasilodendron pedroanum* and inferred a sub-arborescent growth habit for them. Mendonça Filho et al. (2013) also interpreted these axes as *Brasilodendron pedroanum* but suggested an arborescent growth habit for the plant.

The presence of some charred lycopsid remains (Fig. 10) in the Bonito I mine indicates that these plants had been affected by wildfires (Manfroi et al., 2012). Autochthonous-hypautochthonous charcoals with gymnosperm anatomy are also common components of the coal-bearing and clastic deposits of the mine. These charred remains testify that this peat-forming system and its surroundings were frequently subjected to wildfires (Jasper et al., 2011).

3.2.5. A mass-assemblage of lycopsid axes from the Morro do Papaléo outcrop

The Morro do Papaléo outcrop is located in the municipality of Mariana Pimentel, Rio Grande do Sul state. The upper interval of the outcrop is related to the Rio Bonito Formation and comprises conglomerates, carbonaceous layers and siltstones (Iannuzzi et al., 2009). Based on palynological data, an Asselian to Sakmarian age has been suggested for this outcrop (Smaniotto et al., 2006).

Spiekermann et al. (2018) conducted a taxonomic and taphonomic analysis of a lycopsid macrofossil assemblage preserved in the uppermost portion of the outcrop. This assemblage occurs in a light grey silt-grained layer interbedded between trough cross-bedded conglomerates, deposited in braided river channels. These lycopsids are preserved as impressions and are massively concentrated and distributed without any depositional orientation in this layer, constituting practically a monotypic assemblage (Fig. 11). According to these authors, this high-concentrated lycopsid assemblage is allochthonous and probably resulted from hydraulic sorting and transport under a decreasing fluvial discharge.

The lycopsids studied by Spiekermann et al. (2018) correspond to narrow unbranched axes presenting a completely preserved width that range from 12.6 to 46 mm (Fig. 12A). These fossils lack rooting system, apex, attached leaves as well as reproductive structures and are covered by spirally arranged leaf cushions. Three morphologically different leaf cushion patterns can be observed on distinct axes (Fig. 12B–G). The description of the morphologic characteristics of these leaf cushions is provided in Table 2. However, multivariate statistical analysis indicates that all the fossils are morphometrically similar, the three axes presenting a transition between the different leaf cushion morphological patterns (see Fig. 9 of Spiekermann et al., 2018), thus testifying that all these lycopsids belong to the same taxon, i.e. *Brasilodendron* cf. *pedroanum*. According to Spiekermann et al. (2018), the distinct leaf cushion patterns could represent different fracture planes of the fossils or might result either from decortication processes or (other) taphonomical alterations. Leaf cushion shape also may change ontogenetically in concert with determinate growth. The pattern of change is known for some Euramerican arborescent taxa, such as *Lepidodendron* and *Synchysidendron* (e.g. Opluštil, 2010; Moore et al., 2014). In contrast, little is known about the ontogenetic variations in the leaf cushions from the Gondwanan late Palaeozoic lycopsids taxa.

The presence of false leaf scars indicates that these lycopsids had

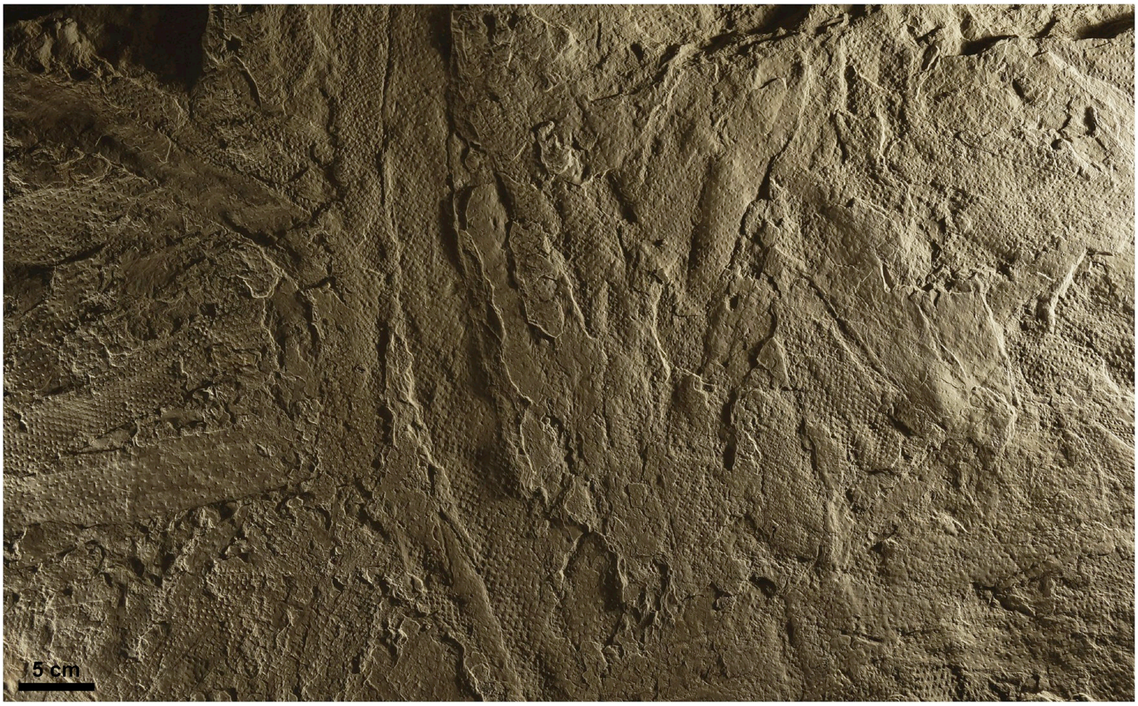

Fig. 11. Large slab showing the distribution and abundance of lycopsid axes preserved in the silt-grained layer N8b at the Morro do Papaléo outcrop. Sample PbUMCN 1162, deposited in the Palaeobotanical Collection of the *Museu de Ciências* of the *Universidade do Vale do Taquari*. From Spiekermann et al. (2018).

persistent leaves. However, the incomplete nature of the fossils precludes a reliable reconstruction of the growth habit of these plants, and the axes could represent stems of either monopodial sub-arborescent lycopsids or crown branches of an arborescent plant. Only the discovery of more completely preserved fossils of *Brasilodendron pedroanum* can solve this dilemma (Spiekermann et al., 2018).

3.2.6. Herbaceous lycopsids from the Rio Bonito formation

Herbaceous lycopsid impression fossils occur in association with the large *in situ* stumps preserved in the Asselian ash layer of the Quitéria outcrop. According to Salvi et al. (2008), these specimens are eligulate, and their narrow stems are covered by helically arranged microphyllous leaves (Fig. 13A and B). Some of them are fertile and bear ovate-elliptical sporangia at the sporophyll axils (Fig. 13C and D). However, no *in situ* spores have been found in these reproductive structures.

Salvi et al. (2008) assigned herbaceous lycopsids from the Quitéria outcrop to the genus *Lycopodites*. However, due to their unique set of morphological characteristics, the authors erected a new species and classified these fossils as *Lycopodites riograndensis*. So far, this is the only record of herbaceous lycopsids in deposits of the Rio Bonito Formation.

3.3. Lycopsids from the Frayle Muerto formation (Sakmarian – Artinskian, Uruguay)

Gutiérrez and Herbst (1995) described lycopsid remains from the vicinity of Vichadero, Department of Rivera, Uruguay. These remains occur in concretions within the sandstones from the lower section of the Melo Formation. The latter is currently divided into the Frayle Muerto, Mangrullo and Paso Aguiar formations (de Santa Ana et al., 2006), and reliable stratigraphic positioning of these fossils is difficult. However, as the specimens occur in the lower portion of Melo Formation, we tentatively included them into the Frayle Muerto Formation.

The lycopsid fossils studied by Gutiérrez and Herbst (1995) correspond to vegetative axes poorly preserved as impressions and casts. Spirally arranged leaf traces cover these fossils, and the less decorticated specimens present elongate rhomboidal leaf cushions. According to the authors, these lycopsids exhibit a ligule scar and two small depressions that could represent parichnos. Gutiérrez and Herbst (1995) interpreted these remains as sub-herbaceous ligulate lycopsids. It seems that the term sub-herbaceous, as used by these authors, indicates a growth habitat smaller than arborescent lycopsids like *Lepidodendron*, *Lepidophloios* and *Sigillaria*, but higher and more robust than taxa like *Selaginella* and *Lycopodium*. According to Bek et al. (2008), lycopsids with such a growth size should be classified as sub-arborescent. As the fossils were poorly preserved, Gutiérrez and Herbst (1995) assigned them to an informal Type A.

3.4. Lycopsids from the São Sepé outcrop (Palermo Formation, Artinskian, Brazil)

The São Sepé outcrop is composed of conglomerates, siltstones and sandstones, and is located in the municipality of São Sepé, Rio Grande state (Bortoluzzi and Veiga, 1981). This outcrop was first assigned to the Rio Bonito Formation (Zingano and Cauduro, 1959) and later to the Palermo Formation. According to Simões (1992), the São Sepé outcrop is an isolated exposure and its correlation with other late Palaeozoic units of the Paraná Basin is difficult. However, based mainly on palynological data, the author also assigned these deposits to the Palermo Formation. This stratigraphic positioning is not beyond doubt since conglomerates are not a typical lithology of this formation and the macroflora preserved in the outcrop has so far not been reported from other deposits attributed to this unit (Simões, 1992).

According to Bortoluzzi and Veiga (1981), lycopsid axes are abundantly preserved in the siltstones of this outcrop. These axes are incompletely preserved as impressions and casts and lack attached leaves, evidence of branching, rooting systems, and reproductive structures. The impressions are covered by spirally arranged fusiform leaf cushions (Fig. 14A–D), whereas the casts present a typical *Knorria*-like morphological pattern (Fig. 14E and F). Zingano and Cauduro (1959) informally interpreted them as *Lepidodendron*, but a detailed taxonomical analysis of these fossils has to be carried out yet.

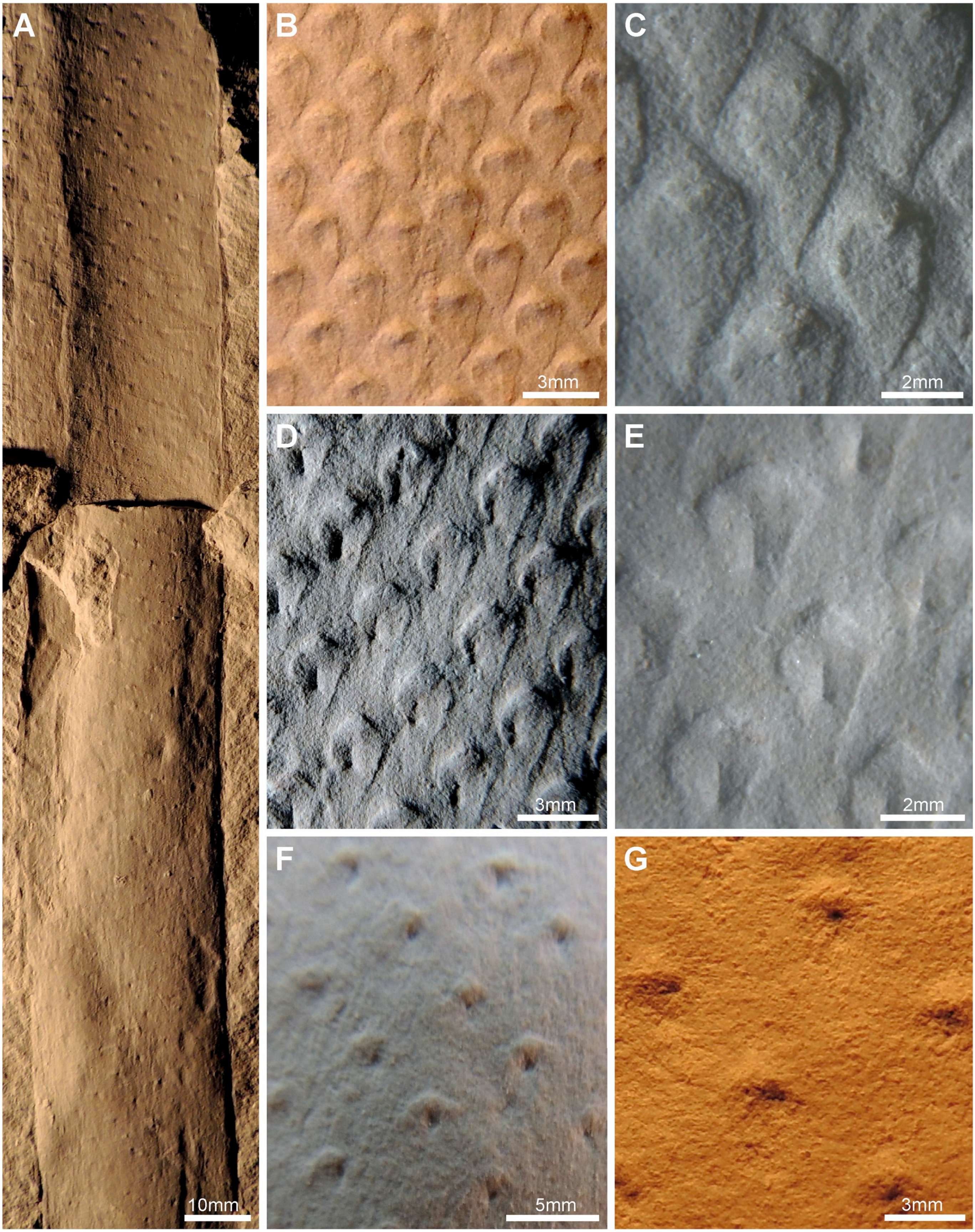

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Fig. 12. *Brasilodendron* cf. *pedroanum* axes from the Morro do Papaléo outcrop. A) Elongated unbranched lycopsid axis [Leaf cushion pattern 3 of Spiekermann et al. (2018), sample PbUMCN 1088]. B) Spirally arranged fusiform leaf cushions [Leaf cushion pattern 1 of Spiekermann et al. (2018), sample PbUMCN 990]. C) Detail of the leaf cushions from specimen figured in B. D) Spirally arranged fusiform leaf cushions [Leaf cushion pattern 2 of Spiekermann et al. (2018), sample PbUMCN 996]. E) Detail of the leaf cushions from specimen figured in D. F) Incompletely preserved leaf cushion [Leaf cushion pattern 3 of Spiekermann et al. (2018), sample PbUMCN 1003]. G) Detail of specimen figured in F. This material is deposited in the Palaeobotanical Collection of the *Museu de Ciências* of the *Universidade do Vale do Taquari*. Adapted from Spiekermann et al. (2018).

3.5. Lycopsid from the Irati Formation (Artinskian – Kungurian, Brazil)

Guerra-Sommer (1981) provided a preliminary description of a permineralized axis collected from the Irati Formation at the district of Assistência, municipality of Rio Claro, São Paulo state. According to this author, the external surface of the axis is covered by rhomboidal leaf cushions and circular appendices scars (Fig. 15A). The specimen presents a large central pith (Fig. 15B), and its primary xylem is composed of a small number of tracheids, whereas the secondary xylem is exclusively composed of tracheids and medullary rays. Based on both external and internal characteristics, Guerra-Sommer (1981) suggested that this specimen could be some type of *Sigillaria*. However, an ongoing re-analysis of this particular specimen indicates that it has secondary xylem solely composed of tracheids bearing bordered pits. This characteristic suggests that this axis is a gymnosperm rather than an arborescent lycopsid. The primary and secondary xylem of the Palaeozoic arborescent lycopsids is composed of tracheids bearing scalariform pitting with vertical fimbrils (also known as Williamson striations) that connect the horizontal bars of the pit (Taylor et al., 2009). This pitting pattern with fimbrils also occurs in Palaeozoic lycopsids from the Paraná Basin (Jasper et al., 2008) but it is not visible in the specimen from the Irati Formation.

Recently, Rios and Ricardi-Branco (2016) reported isolated microphyllous leaves from chert nodules of the Assistência Member, at the municipality of Santa Rosa do Viterbo, São Paulo state. These specimens are very small and incompletely preserved, and can be observed either in longitudinal or in cross-section (Fig. 15C). In cross-section, they have a triangular shape with lateral expansions (Fig. 15D, E). To date, these microphylls are the only putative evidence of lycopsid fossils for the Irati Formation.

3.6. Lycopsids from the Paso Aguiar Formation (Roadian)

Herbst (1986) reported two? fragmented lycopsid axes from a fossiliferous locality near the municipality of Melo, Department of Cerro Largo, east-northeast of Uruguay. Based on the morphology of their leaf cushions, Herbst (1986) assigned them to *Cyclodendron* cf. *leslii*, a taxon otherwise known from the early Permian of South Africa (e.g. Rayner, 1985) and Australia (e.g. Beeston, 1990).

3.7. *Cyclodendron andreisii* from the Yaguarí Formation (Roadian – Wordian)

Herbst and Gutiérrez (1995) reported abundant lycopsid fossils preserved in a fine-grained sandstone layer at the Cañada Sarandí de los Carpinchos, Department of Rivera, Uruguay. According to these authors, this sandstone is included in the lower portion of the Upper Member of the Yaguarí Formation, deposited during the Roadian-Wordian interval (Rocha-Campos et al., 2019).

The lycopsids described by Herbst and Gutiérrez (1995) correspond to unbranched axes preserved as impressions and casts. Their lengths range from 40 to 165 mm, and their widths range from 25 to 40 mm. However, the authors mentioned that they observed specimens with up to 2.8 m in length in the field. According to Herbst and Gutiérrez (1995), these axes present three different decortication stages. The most decorticated stage bear remains of helically arranged hexagonal and rhombic leaf cushions with a true leaf scar in their superomedial portion. The intermediary decortication stage presents helically arranged rhombic isodiametric leaf cushions bearing a well-defined leaf scar in their upper part. The less decorticated stage preserves the base of the leaves. The authors did not mention the presence of parichnos and ligule for any decortication stage. Herbst and Gutiérrez (1995) interpreted these axes as sub-herbaceous (interpreted here as sub-arborescent) and included them in a new taxon named as *Cyclodendron andreisii*.

3.8. Lycopsids from the Tacuary Formation (Guadalupian? Paraguay)

To date, only a few lycopsid macrofossils have been reported from the late Palaeozoic strata of the Paraguayan part of the Paraná Basin. Herbst (1972) reported the presence of lycopsid axes at the locality of Arroyo Vino, Colonia Independencia and interpreted them as parts of an arborescent plant. Later, Herbst and Gutiérrez (1995) suggested that they could belong to decorticated axes of *Cyclodendron andreisii*. Lycopsid impressions were also reported from the Paraguayan locality of Siraty, Department of San Pedro. According to Herbst (1986), these macrofossils correspond to vegetative axes covered by helically arranged leaf cushions that generally have a rhombic shape and exhibit a leaf scar bearing a vascular bundle scar. The author assigned these specimens to *Cyclodendron* cf. *leslii*.

The lycopsid fossils mentioned above were first assigned to the Independencia Formation/Series (Herbst, 1972, 1986), which is

Table 2
Morphometry and morphology of the three different leaf cushion patterns observed in the *Brasilodendron* cf. *pedroanum* specimens from Morro do Papaléo outcrop. Adapted from Spiekermann et al. (2018).

Characteristics	Leaf Cushion Pattern 1	Leaf Cushion Pattern 2	Leaf Cushion Pattern 3
Shape	Fusiform with slightly sigmoid extension in the upper and lower part, presenting a protuberance in the superomedial portion. Some leaf cushions present a central longitudinal narrow elongate depression	Fusiform with a prominent triangular to roundish shape in the upper portion, which taper downwards and ends acutely. Presents a central longitudinal narrow elongate depression, and a protuberance in the upper portion.	Incompletely preserved in length, and only the upper part is observable. This part has a triangular to roundish shape. Presents a protuberance in the upper portion, and a central longitudinal narrow depression.
Leaf scar	Absent	Absent	Absent
Parichnos	Not visible	Not visible	Not visible
Infrafoliar Bladder	Absent	Absent	Absent
Ligule	Absent	Absent	Absent
Size	2.1 mm × 4.6 mm (average)	1.8 mm × 4.3 mm (average)	Preserved part frequently between 1.4 mm and 1.8 mm in width
Phyllotaxy	Lepidodendroid (ranging from 40° to 67°)	Lepidodendroid (ranging from 43° to 66°)	Lepidodendroid (ranging from 43° to 66°)

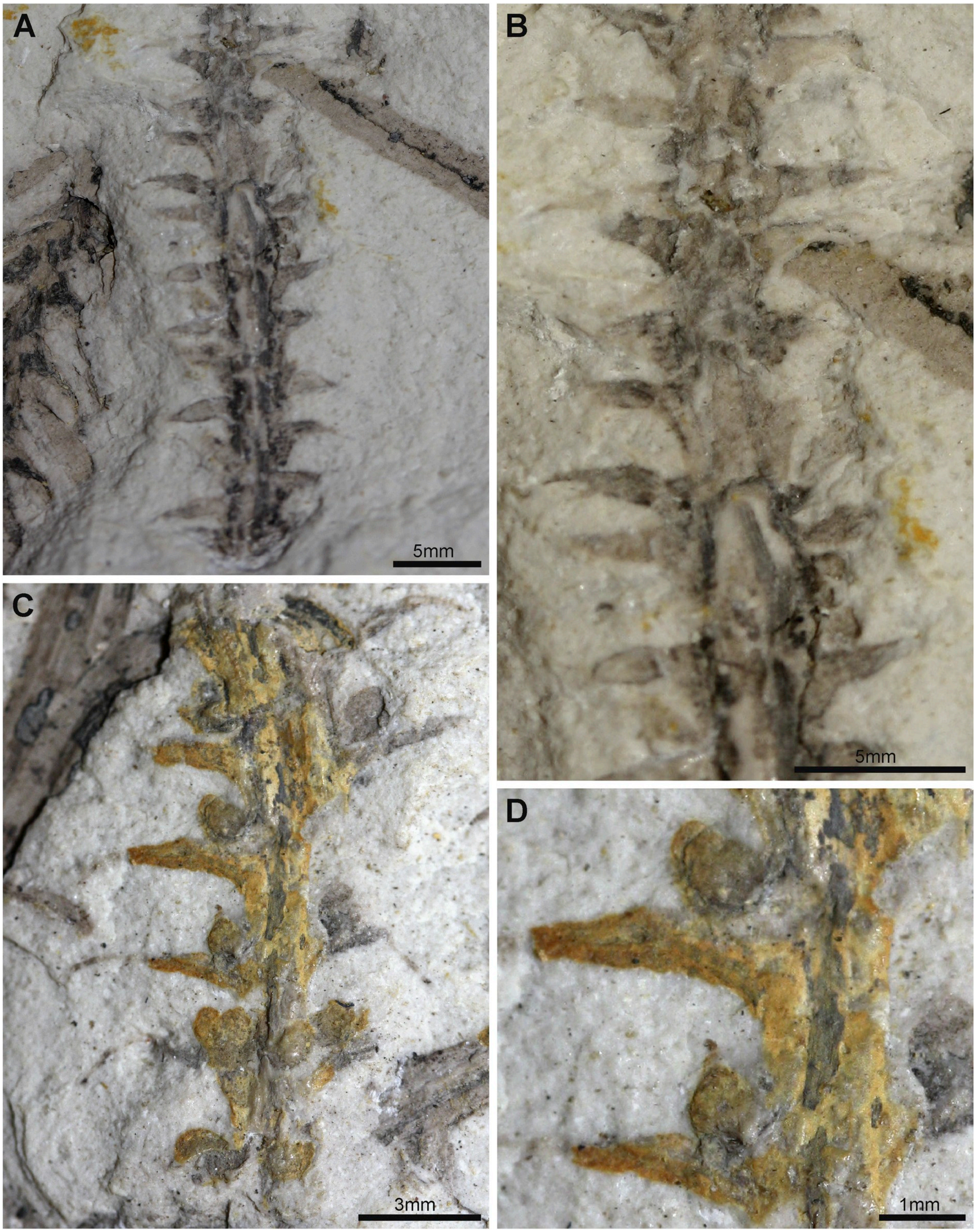

Fig. 13. *Lycopodites riograndensis* from the Quitéria outcrop. A) Specimen bearing helically arranged microphyll leaves (sample PbU 038). B) Detail of specimen figured in A. C) Fertile specimen bearing ovate-elliptical sporangia born on the sporophyll axils (sample PbU 190). D) Detail of the ovate-elliptical sporangia from specimen figured in C. This material is deposited in the Palaeobotanical Collection of the *Museu de Ciências* of the *Universidade do Vale do Taquari.*

currently divided into the San Miguel and Tacuary formations (Mapa Geológico del Paraguay, 1986). More recently, Herbst and Amábili (2011) informally mentioned these macrofossils as components of the Tacuary Formation. Here we tentatively include them in the latter stratigraphic unit.

3.9. Lycopsids from the Teresina and Corumbataí formations (Roadian – Wuchiapingian?)

Lycopsid macrofossils occur in both Teresina and Corumbataí formations and are represented by microphylls and axes generally assigned to *Lycopodiopsis derbyi* (Maack, 1947; Mendes, 1952; Kräusel,

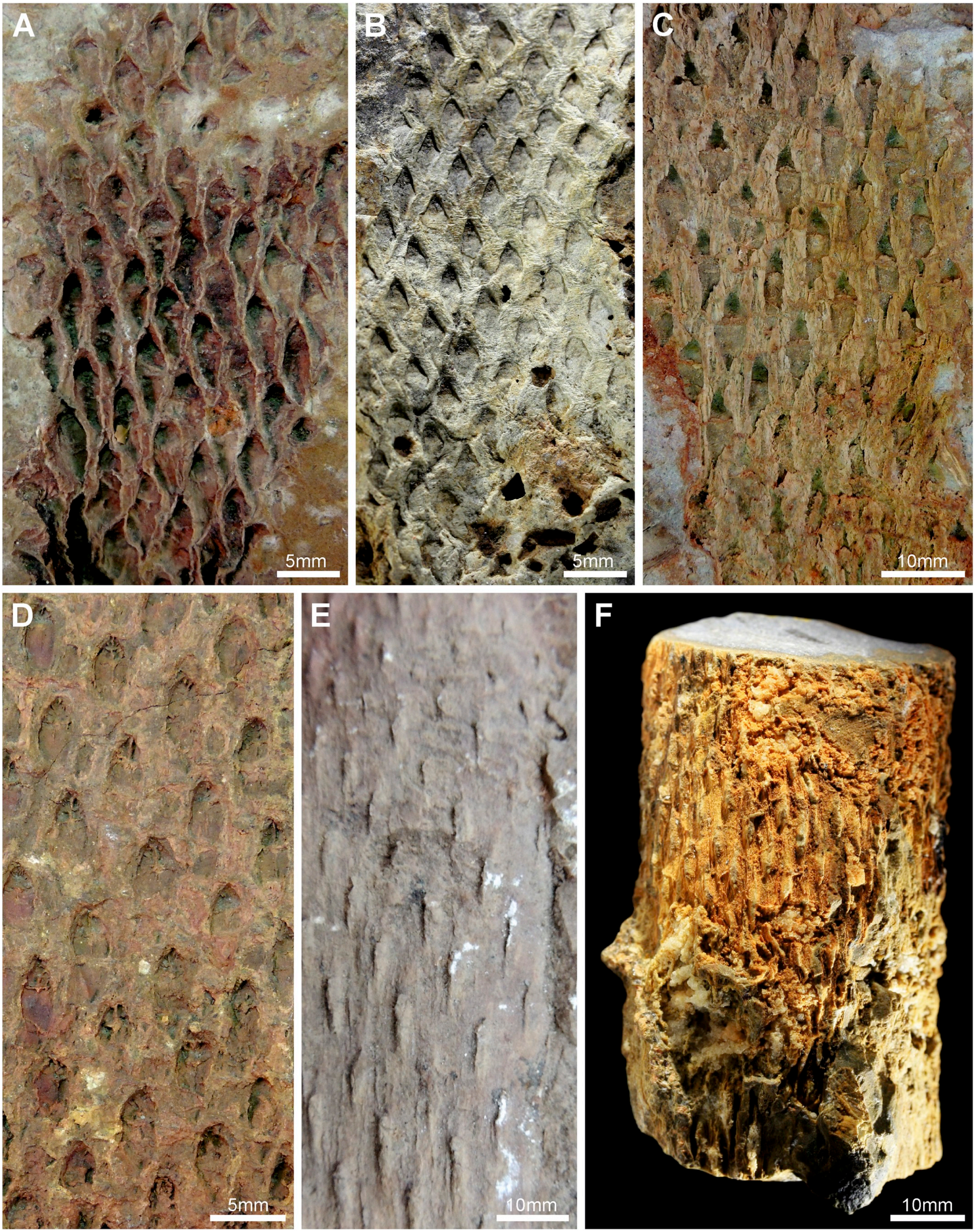

Fig. 14. Lycopsid macrofossils from the São Sepé outcrop. A–D) Impressions bearing spirally arranged fusiform leaf cushion (A, sample PbUMCN 1195; B, sample PbUMCN 1203; C, sample 1193; D, sample PbUMCN 1194). E) Detail of a cast, presenting *Knorria*-like longitudinally oriented ridges (sample PbUMCN 1198). F) Cast with a *Knorria* morphological pattern (sample PbUMCN 1191). These fossils are deposited in the Palaeobotanical Collection of the Museu de Ciências of the Universidade do Vale do Taquari.

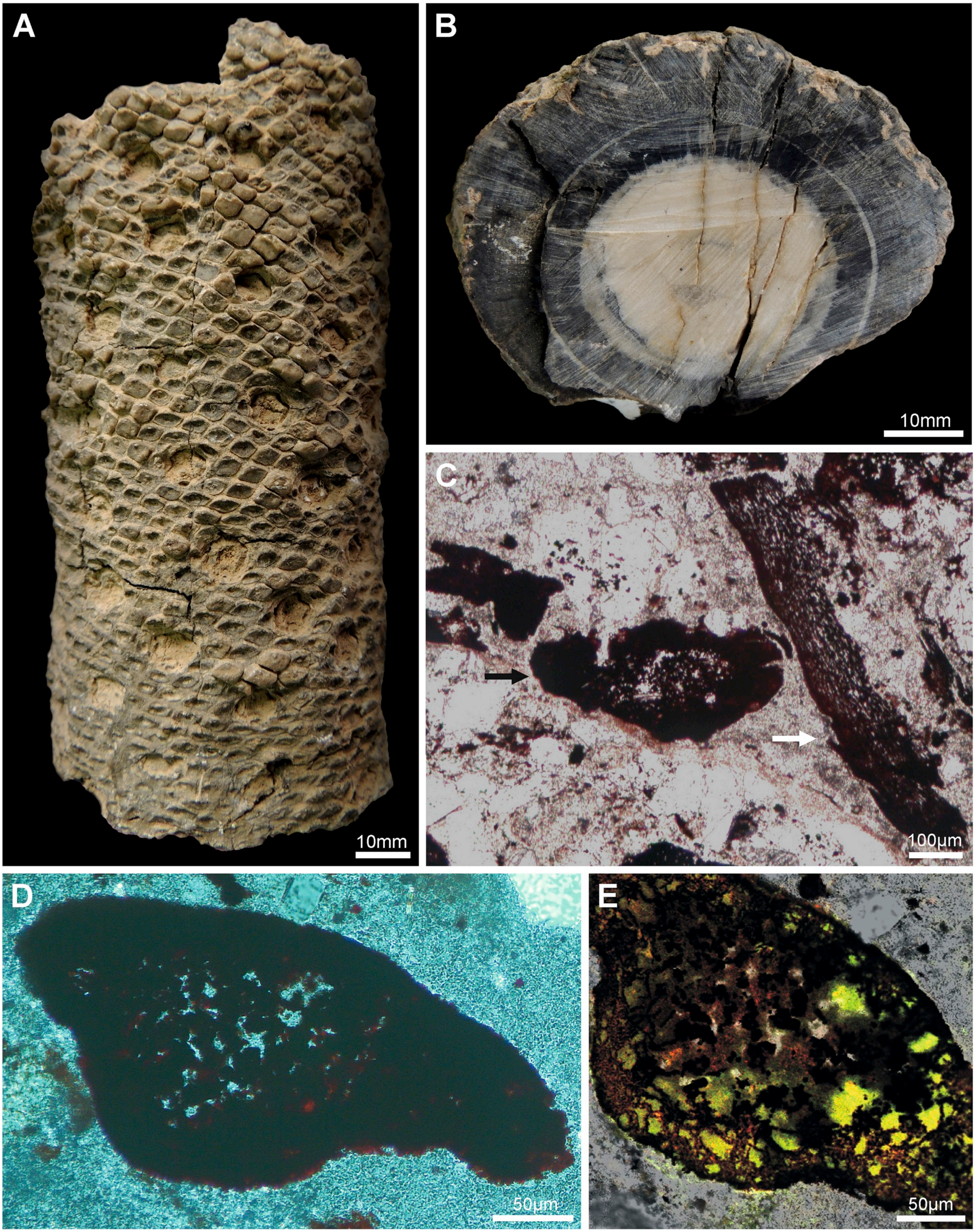

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Fig. 15. Fossil specimens from the Irati Formation. A) Permineralized axis originally interpreted as some type of *Sigillaria* by Guerra-Sommer (1981). B) Cross-section of the permineralized axis figured in A. This axis is stored in the *Departamento de Geociências* of the *Universidade Federal do Rio Grande do Sul*, Porto Alegre, RS, Brasil. C) Specimens interpreted as microphylls in longitudinal (white arrow) and in cross-section (black arrow). D) Cross-section of a microphyll showing its triangular shape with lateral expansions. E) Detail of the specimen figured in D showing the fluorescence of the organic matter under green waves between 498 nm and 561nm. This material corresponds to sample CP5/85-1 and is stored in the *Instituto de Geociências* of *Universidade Estadual de Campinas*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

1961; Oliveira-Babinski and Rösler, 1984; Simões and Fittipaldi, 1992; Alarcon, 1998; Alarcon and Bernardes-de-Oliveira, 1999; Faria et al., 2007, 2009; Faria and Ricardi-Branco, 2010). In the Paraná Basin, the early studies did not mention the lithostratigraphic unit from which the specimens were collected. Based on the lithology and geographical locality, we consider that all the lycopsid macrofossil reports presented below are related to the Teresina and Corumbataí formations.

3.9.1. The permineralized lycopsid Lycopodiopsis derbyi

Lycopodiopsis derbyi was erected by Renault (1890) based on silicified axes collected at the municipality of Piracicaba, São Paulo state. The exact location of the outcrop remains unknown, but it is probably in the Corumbataí Formation. According to Renault (1890), this taxon has a discontinuous xylem cylinder, differing from the Euramerican Carboniferous *Lepidodendron*, which has a continuous one.

Zeiller (1898) reinvestigated Renault's material and interpreted the cylinder as continuous, and considered that this lycopsid should be classified as *Lepidodendron derbyi*. White (1908) disagreed with Zeiller's interpretation, and classified a new specimen from the municipality of Bofete (São Paulo state) as *Lycopodiopsis derbyi*. Later, Steinmann (1924) described a well-preserved silicified axis of *Lycopodiopsis derbyi* from Piracicaba and considered that this species lacks parichnos and its stele cylinder is clearly discontinuous. Rao (1940) reinvestigated Steinmann's specimen, and a small silicified axis collected at the municipality of Tatuí, São Paulo state. Based on both fossils, the author confirmed the interpretation of a discontinuous stele cylinder for *Lycopodiopsis derbyi* and stated that this Gondwanan species differs from *Lepidodendron* (based on the anatomical knowledge about this taxon at this time). A discontinuous stele cylinder is not an exclusive character of *Lycopodiopsis derbyi*, since it is also known for the Euramerican Carboniferous taxon *Synchysidendron*. The latter has a primary xylem cylinder divided into wedges, separated by parenchyma, and these parenchymatous zones extend into the secondary xylem (DiMichele and Bateman, 1992).

According to Edwards (1952), *Lycopodiopsis derbyi* should be classified as *Lycopodiopsis pedroanus*. Kräusel (1961) reinvestigated the previously published records of *L. derbyi* and studied new impressions and silicified axes from São Paulo, Paraná, and Rio Grande do Sul states. This author disagreed with Edwards and considered that *L. derbyi* and *L. pedroanus* exhibit morphologically different leaf cushion patterns. However, both authors considered that these species had leaf cushions lacking ligule and parichnos. Lemoigne and Brown (1980) presented an emended diagnosis for *Lycopodiopsis* and considered it as ligulate. This interpretation was followed by Thomas and Meyen (1984), who considered the genus as ligulate in their identification key for the late Palaeozoic lycopsid impressions and compressions.

Faria et al. (2009) described impressions, compressions and silicified axes of *Lycopodiopsis derbyi* (Fig. 16A–C) collected from the Corumbataí Formation and emended the diagnosis of the species. According to Faria et al. (2009), *L. derbyi* was an arborescent lycopsid with dichotomizing growth architecture (Fig. 16B). Its pith cells are isodiametric, and the cortex is composed of internal parenchyma, a thin periderm, a zone with elongated cells and external parenchyma. Its vascular cylinder is siphonostelic, composed of a discontinuous ring of exarch xylem. The distal branches of *L. derbyi* exhibit indistinct incipient leaf cushions, whereas the intermediate branches have rhomboidal to circular leaf cushions bearing leaf scars in their upper portion and infrafoliar bladders. The proximal branches bear well-defined rhomboidal leaf cushions with leaf scars and infrafoliar bladders. All these leaf cushions lack parichnos and ligule according to the observations of these authors.

Lycopodiopsis derbyi is interpreted as a typical element of the southern *Glossopteris*-flora. This plant fossil is the most conspicuous element of the Teresina and Corumbataí formations, being considered as a biostratigraphic marker of these units (e.g. Mezzalira, 1980; Rohn, 1994; Rohn and Rösler, 2000).

3.9.2. Cyclodendron dolianitti from the Cerro Chato outcrop

The Cerro Chato outcrop is located in the municipality of Dom Pedrito, south-west portion of the Rio Grande do Sul state. According to Martins and Sobrinho (1951), this outcrop comprises limestones related to the Estrada Nova Group. Based on the presence of *Lycopodiopsis derbyi* (Martins and Sobrinho, 1951; Kräusel, 1961), the limestones of the Cerro Chato outcrop may be assigned to the Teresina Formation, which occurs in that region of Rio Grande do Sul.

According to Kräusel (1961), two lycopsid axes from Cerro Chato presented a unique morphological pattern, and the author classified them as the new taxon *Lycopodiophloios dolianitti*. Stems of the latter are covered by laterally elongated leaf cushions (5–7 mm wide and 1.5 mm high) that lack parichnos and ligule, and possess acicular microphylls that were at least 10 cm long and 1 mm wide. Rayner (1985) disagreed with Kräusel and considered that *Lycopodiophloios* is synonymous with *Cyclodendron*. One year later, Herbst (1986) reanalyzed *Lycopodiophloios dolianitti* and proposed the new combination *Cyclodendron dolianitti*.

3.9.3. Microphylls from Teresina and Corumbataí formations

Isolated microphylls occur in both Teresina and Corumbataí formations (Kräusel, 1961; Rohn et al., 1997a, b, c; White, 1908). However, so far, only a few of them have been studied in detail.

Faria and Ricardi-Branco (2010) described microphylls (Fig. 16D) collected from deposits of the Corumbataí Formation at São Paulo state. They are silicified and incompletely preserved, and in cross-section, their shape is triangular to slightly rhomboidal with short lateral expansions (Fig. 16E). They have a pronounced keel on the abaxial surface and sunken stomata on the adaxial one. Their xylem bundle is surrounded by a vascular sheet that is composed of five rows of elongated cells, which are isodiametric in cross-section. The mesophyll comprises of palisade parenchyma, while the hypodermis and epidermis are composed of longitudinally elongated cells. Based on this set of morpho-anatomical characteristics, Faria and Ricardi-Branco (2010) erected the new microphyll species *Lepidophylloides corumbataensis*. The species also occurs in the Teresina Formation at Paraná state (Faria and Ricardi-Branco, 2010).

According to Faria and Ricardi-Branco (2010), *Lepidophylloides corumbataensis* commonly occurs in association with axes of *Lycopodiopsis derbyi*. The latter presents true leaf scars and this indicates that leaf abscission naturally occurred in this species. Although they have not been found in organic connection, the authors suggested that *Lepidophylloides corumbataensis* could represent the leaves of *Lycopodiopsis derbyi*. The latter is included in the Gondwanan family Lycopodiopsidaceae (Chaloner and Boureau, 1967), whereas the form genus *Lepidophylloides* has been generally used to classify detached leaves of the late Palaeozoic lepidodendrid taxa from Euramerica and Cathaysia (Snigirevskaya, 1958; Wang et al., 2002; Dilcher et al., 2005). However, *Lepidophylloides* has little phylogenetic meaning, since it represents the

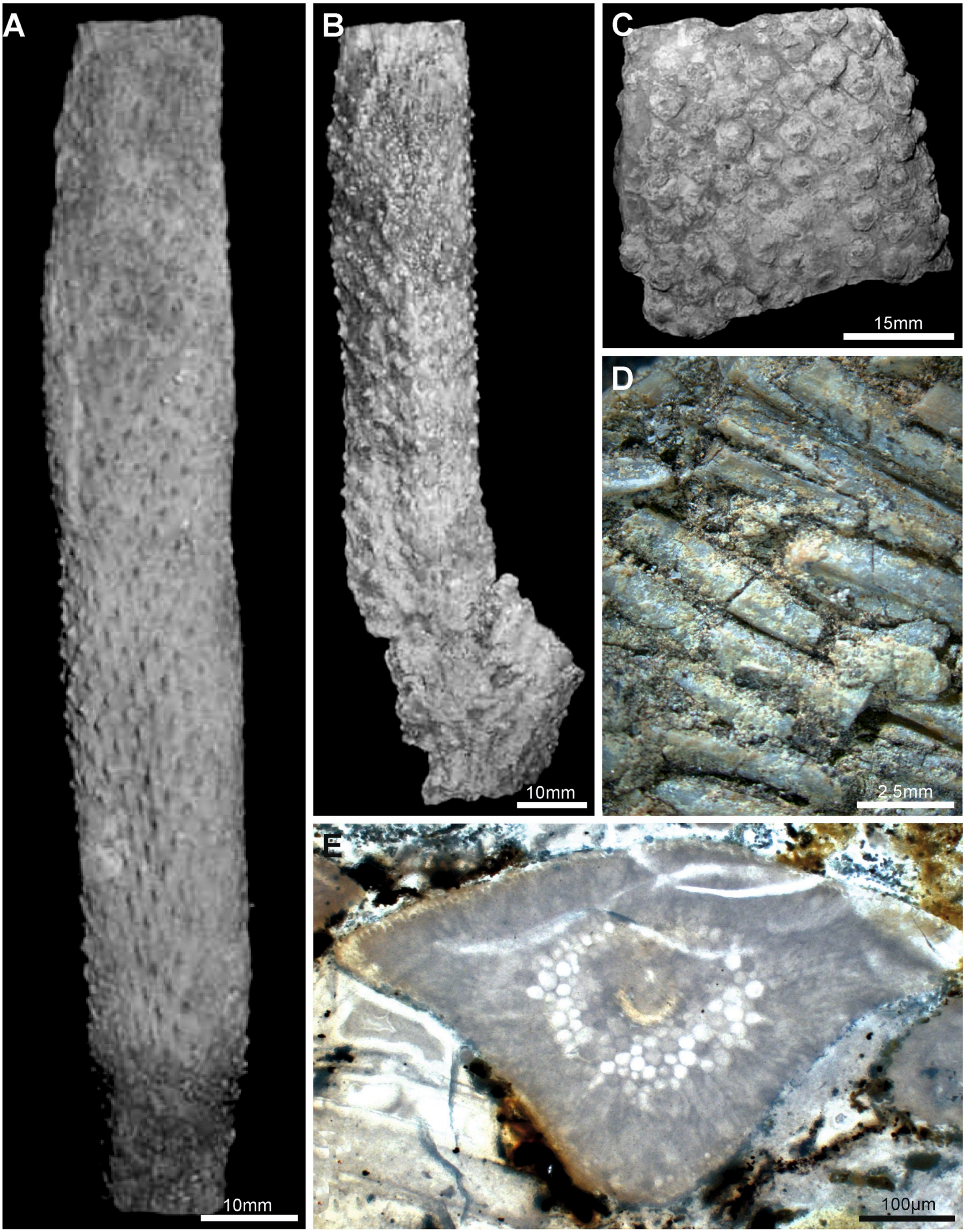

Fig. 16. Lycopsid fossils from the Corumbataí Formation. A) Permineralized axis taxonomically assigned to *Lycopodiopsis derbyi* (sample CP1/109). B) Dichotomous axis assigned to *Lycopodiopsis derbyi* (sample CP1/111). C) Fragment bearing typical leaf cushions of *Lycopodiopsis derbyi* (sample CP1/90A). Images A–C from Faria et al. (2009). D) Highly concentrated fragments of *Lepidophylloides corumbataensis* (sample CP1/155). E) Cross-section of *Lepidophylloides corumbataensis* (sample CP1/143). This material is stored in the *Instituto de Geociências* of *Universidade Estadual de Campinas*.

isolated microphylls of different lycopsid families such as Diaphorodendracae, Lepidodendraceae, and perhaps even Ulodendraceae (DiMichele pers. commun.).

4. Summary and final remarks

The macrofossil record of lycopsids from the late Palaeozoic of the Paraná Basin is mostly composed of very fragmented axes preserved as impressions and compressions. The only exception is *Lycopodiopsis derbyi*, which is permineralized and for this taxon internal anatomical details and external morphology are known. The permineralized axis (previously interpreted as *Sigillaria*) from the Irati Formation, exhibits secondary xylem composed of tracheids with bordered pits. This characteristic position this specimen in Gymnospermae rather than in Lycopsida.

The taxonomy of the lycopsid axes preserved as impressions and compressions has been based on their leaf cushions. The morphology of the latter is strongly influenced by taphonomy, decortication processes and ontogenetic development stages of the plant, and this has historically led to a profound taxonomical confusion concerning taxa based on such characters (Gensel and Pigg, 2010; Cleal et al., 2016). After several redescriptions and synonymization, the leaf cushion-based taxa that are currently used in the literature for the late Palaeozoic of the basin are *Bumbudendron millani*, *Bumbudendron* cf. *paganzianum*, *Leptophloeum* cf. *sanctae-helenae*, *Cyclodendron brasiliensis*, *Cyclodendron* cf. *leslii*, *Cyclodendron andreisii*, and *Brasilodendron pedroanum*. The lack of reproductive structures, as well as the poor and fragmented preservation of the lycopsid fossils reported so far for the late Palaeozoic of the basin, has resulted in a poor understanding about their taxonomy and systematic position. Efforts to discover more completely preserved specimens and reproductive structures, as well as a review of the fossils reported for the basin so far, are necessary to provide a robust taxonomical and systematical classification for these lycopsids. This review should strongly consider the intraspecific morphological variations of the leaf cushions, since an approach considering these variations could lead to a more natural taxonomy for these fossil plants.

Most of the lycopsid axis remains reported from the late Palaeozoic deposits of this basin seem to lack evidence of parichnos and ligule. The absence of these characteristics has been used to separate them from the Euramerican Carboniferous arborescent genera such as *Lepidodendron*, *Sigillaria* and *Lepidophloios* (Edwards, 1952; Kräusel, 1961; Sommer and Trindade, 1966). According to Iannuzzi and Pfefferkorn (2002), the occurrence of a ligule is typical for arborescent lycopsids growing in the Carboniferous tropics, whereas such a structure is unknown from lycopsids growing in cold climates during this period. However, the presence of ligule and parichnos in lycopsid fossils can be strongly influenced by a wide range of factors such as taphonomy, ontogenetic stage, decortication processes, as well as the mode of preservation (Meyen, 1972; Thomas and Meyen, 1984; Gensel and Pigg, 2010). For example, in modern *Selaginella* the ligule is a very small and flat structure, which is located very close to the leaf axil on the adaxial surface of the leaf (Webster, 1992). Considering the preservation of many of the fossils described here, small, papery, leaf-borne ligules might be virtually unidentifiable. Also, even in well-preserved fossils of *Lepidodendron* and *Sigillaria*, which clearly bore a ligule, evidence of the latter is not always preserved (Chaloner, 1968). Both parichnos and ligule were mentioned for some specimens from the Rio Bonito and Frayle Muerto formations (Read, 1941; Gutiérrez and Herbst, 1995), and *Lycopodiopsis* was considered as ligulate by Lemoigne and Brown (1980). The presence or absence of these features in the lycopsids of the Paraná Basin clearly requires further detailed observations.

The oldest record of lycopsid macrofossils from the late Palaeozoic of the Paraná Basin occurs in the Pennsylvanian interglacial strata of the Sítio Volpe outcrop, Itararé Group, Brazil. These fossils correspond to vegetative axes assigned to *Brasilodendron*, *Bumbudendron,* *Cyclodendron* sp. and *Leptophloeum* (Mune et al., 2012). The growth size of *Brasilodendron* remains uncertain (Spiekermann et al., 2018), whereas *Bumbudendron* includes sub-arborescent lycopsids (Archangelsky et al., 1981), and *Cyclodendron* and *Leptophloeum* are generally interpreted as arborescent forms (Rayner, 1985; Prestianni and Gess, 2014). However, *Cyclodendron* has also been mentioned as a sub-arborescent plant in recent literature (Álvarez-Vázquez et al., 2019). These plants may have inhabited periglacial areas, migrating to the new frost-free palaeoenvironments when the glaciers shortly retreated during an interglacial interval of the LPIA in the basin.

In the interglacial coal-bearing strata of the Sítio Volpe outcrop, lycopsids axes are abundant, forming even a hypautochthonous almost monotypic assemblage (Mune et al., 2012). Lycopsids have been considered as opportunistic pioneer elements in Pennsylvanian and Triassic palaeoenvironments (DiMichele and Phillips, 1985; Grauvogel-Stamm and Ash, 2005), and in modern environments, herbaceous ones play an important role as the pioneer vegetation of disturbed areas (Pigg, 1992; Pfefferkorn, 1999). A similar ecological strategy might be suggested for the lycopsids from the Sítio Volpe. These plants could have been components of the pioneer vegetation and may have opportunistically colonized the vacuity of the recently frost-free palaeoenvironment, contributing to the initiation of peat accumulation in that area.

According to Bernardes-de-Oliveira et al. (2016), the vegetated system of Sítio Volpe collapsed with the beginning of a new glacial stage. However, it seems that *Brasilodendron pedroanum* survived and continued to inhabit Pennsylvanian periglacial areas or frost-free refugia until the Cisuralian, since this species also occurs associated with the *Glossopteris*-flora in the post-glacial strata of the Rio Bonito Formation in southern Brazil.

As the late Palaeozoic ice caps retreated, lycopsids successfully colonized the Rio Bonito Formation palaeoenvironments from the Asselian up to the Artinskian. Vegetative axes, generally assigned to *Brasilodendron,* are abundantly preserved in the paralic fluvio-deltaic and peat-forming depositional systems of this Brazilian lithostratigraphic unit. Their growth habit and architecture remain unclear, but the size of the fossils reported so far indicates that they were rather small compared to the palaeotropical Carboniferous lepidodendrids. In contrast, understory herbaceous lycopsid macrofossils are rare in the Rio Bonito Formation as well as in the Itararé group, and only a few remains assigned to *Lycopodites* have been reported so far (Salvi et al., 2008). The scarcity of macrofossils from these herbaceous forms might be related to taphonomic factors or even human bias (overlooked or ignored in the field), since at least for the Rio Bonito Formation, abundant spores potentially related to these plants have been reported from coal-bearing intervals (e.g. Jasper et al., 2006; Pereira et al., 2019). Such a possible human bias against herbaceous lycopsids is also known from the Euramerican realm (Thomas, 1997).

The considerable number of lycopsid fossils associated with the coal-bearing strata of the Rio Bonito Formation indicates that they were important components of the biomass that formed the Cisularian coal measures of Brazil. This interpretation is supported by palynological studies, which have reported abundant megaspores and microspores potentially related to lycopsids for different coal-bearing areas of this formation (e.g. Trindade and Sommer, 1966; Ricardi-Branco et al., 2002; Cazzulo-Klepzig et al., 2005; Jasper et al., 2006; Pereira et al., 2019). In the Quitéria outcrop and Figueira coalfield, arborescent/subarborescent taxa were even the dominant vegetation of the peat-forming palaeoenvironments (Ricardi-Branco and Rösler, 2004; Jasper and Guerra-Sommer, 1998). The Quitéria outcrop can be included in the first stage of coal formation in the Rio Bonito Formation during the Asselian (Griffis et al., 2018), whereas the Figueira coalfield was deposited during a second coal forming interval, in the Artinskian (Griffis et al., 2018; Jurigan et al., 2019).

The Rio Bonito Formation coal levels exhibit a large amount of mineral matter, and most of them have been interpreted as hypautochthonously formed under sub-aquatic conditions (Correia da Silva, 1989, 1991). However, at least at the Quitéria outcrop, an *in situ* assemblage of corm-like lycopsids indicates that these plants could grow inside the peat swamp during the deposition of the Rio Bonito oldest coal-forming stage in the Asselian. These plants may have contributed to autochthonous peat accumulation in this area. This is the only *in situ* lycopsid assemblage published for the Paraná Basin so far. A future detailed taphonomical investigation of this assemblage can probably shed important light on the palaeoecology of the late Palaeozoic post-glacial lycopsid groves from Gondwana.

Autochthonous/hypautochthonous gymnospermous macro-charcoals have been reported from several coal-bearing deposits of the Rio Bonito Formation (Jasper et al., 2011; Benício et al., 2019), indicating that the lycopsids from this unit grew in a palaeoenvironment frequently subjected to wildfires. However, only a few charred lycopsid remains were reported for this formation (Jasper et al., 2008; Manfroi et al., 2012). The paucity of charred lycopsid remains in the Rio Bonito Formation coal-bearing strata might be related to a wide range of factors, and different hypotheses can be suggested to explain it.

The scarcity of lycopsid charcoals in the Rio Bonito coal-bearing strata could be related to their lower potential for preservation when compared to charred gymnosperm secondary xylem. Another possibility is that these plants might have inhabited more water-saturated areas of these peat swamps that acted as a protective barrier against the wildfires (Glasspool, 2003). However, the late Palaeozoic elevated atmospheric O_2 levels may have increased fire activity and the high amount of inertinites and charcoals reported from several Permian coals have been interpreted as evidence of wildfires in these peat-forming palaeoenvironments and nearby areas (e.g. Glasspool, 2003; Glasspool and Scott, 2010; Glasspool et al., 2015; Jasper et al., 2017). An alternative explanation is an experiment conducted by Vogel et al. (2011), who subjected modern *Lycopodium* strobili to fire and observed that they exhibited a natural resistance against it. As this genus inhabits modern non-fire prone areas, it was suggested that such an adaptation could have an early evolutionary origin that lies in the Carboniferous, when lycopsids grew in a high-fire world (e.g. Scott and Jones, 1994; Glasspool et al., 2015). Hypothetically, the lycopsids of the Rio Bonito Formation could also be resistant to fire, since they successfully flourished in an environment frequently subjected to wildfires. This resistance could have led to the scarcity of charcoal remains of these plants in this unit. These hypotheses remain speculative, and all the factors mentioned above may have acted together.

The maximum flooding interval (related to a marine transgression) of the Paraná Basin occurred during the middle Artinskian. It coincides with the termination of the Rio Bonito paralic fluvio-deltaic and peat-forming systems in most areas of the basin. This may have affected the abundant lycopsid communities that flourished in the Rio Bonito peat swamps. Only a single lycopsid assemblage composed of axes bearing fusiform leaf cushions and *Knorria*-like morphological pattern was reported for the Palermo Formation (middle Artinskian) at the São Sepé outcrop (Bortoluzzi and Veiga, 1981). However, it is not clear if this outcrop is related to the Palermo or the Rio Bonito Formation. Besides, from the overlying Irati Formation, only a few specimens can be putatively interpreted as putative lycopsid microphylls (Rios and Ricardi-Branco, 2016).

In deposits of the Brazilian Teresina and Corumbataí formations, lycopsids are again significant components of the fossil record. However, *Brasilodendron* disappeared and was replaced mainly by *Lycopodiopsis derbyi*. The latter grew as a branched pole, but its growth size remains unclear (Faria et al., 2009). Recent radiometric dating suggested a Wordian-Capitanian age for the Teresina Formation and a Wuchiapingian age for the Corumbataí (Rocha-Campos et al., 2019). If this Lopingian age is confirmed by further studies, an assumed *Lycopodiopsis derbyi* biochron would be extended significantly. Other taxa for this interval are microphylls classified as *Lepidophylloides corumbataensis* and two axes assigned to *Cyclodendron dolianitti*. The type material of the latter was deposited in the collection of the Museu Nacional, (Rio de Janeiro). At the moment it is unknown whether it survived the catastrophic fire that struck this museum in September 2018.

So far most of the late Palaeozoic lycopsid records are from the Brazilian part of the Paraná Basin. For the Paraguayan and Uruguayan parts, only a few lycopsid macrofossils have been published. An exception is an assemblage composed of abundant axes of *Cyclodendron andreisii* from the Tacuary Formation in Uruguay (Herbst and Gutiérrez, 1995). Further investigations in the non-Brazilian parts of the basin are needed to explain whether this disparity results from distinct palaeoecological conditions or a lack of collecting efforts and specific palaeobotanical studies. However, what is observable for all the parts of the basin is that after the increasing aridity in South America during the upper Permian (Limarino et al., 2014), lycopsids seem to have disappeared from the fossil record of the Paraná Basin.

Declaration of interests

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

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Appendix A. Supplementary data

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Appendix: Lycopsid macrofossils taxa from the Late Palaeozoic of the Paraná Basin. First taxonomic status (original taxonomic assignment), current taxonomic status (last synonymy or taxonomical mention of the material), dashes (material that remains with the first taxonomic classification).

Country	Locality	Formation	First taxonomic status	Current taxonomic status	References
Brazil	Sítio Volpe outcrop, Monte Mor, São Paulo state	Campo Mourão?	*Lepidodendron pedroanum*, *Lycopodiopsis pedroanus*, *Lycopodiopsis derbyi*, *Lycopodiopsis* sp.	*Leptophloeum* cf. *sanctae-helenae*, *Bumbudendron millani*, *Bumbudendron* cf. *paganzianum*, *Brasilodendron pedroanum*, *Brasilodendron* sp., *Cyclodendron* sp.	Millan (1972, 1980); Mune et al. (2012)
Brazil	Sítio Toca do Índio outcrop, Cerquilho, São Paulo state	Taciba	*Lycopodites* sp.	—	Salvi et al. (2008)
Brazil	Candiota coalfield, Candiota, Rio Grande do Sul	Rio Bonito	*Flemingites pedroanus*	*Brasilodendron pedroanum*	Carruthers (1969); Chaloner et al. (1979)
Brazil	Arroio dos Ratos coalfield, Arroio dos Ratos, Rio Grande do Sul state	Rio Bonito	*Lepidodendron pedroanum*	*Brasilodendron pedroanum*	Zeiller (1895); Kräusel (1961); Chaloner et al. (1979)
Brazil	Arroio dos Ratos coalfield, Arroio dos Ratos, Rio Grande do Sul state	Rio Bonito	*Lepidophloios laricinus*	*Brasilodendron*?	Zeiller (1895); Kräusel (1961); Chaloner et al. (1979)
Brazil	São Jerônimo, Rio Grande do Sul state	Rio Bonito	*Lepidodendron pedroanum*, *Lepidophloios laricinus*, *Sigillaria brardii*	*Brasilodendron*?	White (1908); Kräusel (1961); Chaloner et al. (1979)
Brazil	Rio do Rastro Road, Lauro Müller, Santa Catarina state	Rio Bonito	*Sigillaria australis*	*Brasilodendron*?	White (1908); Kräusel (1961); Chaloner et al. (1979)
Brazil	Arroio dos Cachorros, Rio Grande do Sul state	Rio Bonito	*Sigillaria brardii*, *Sigillaria* sp.	*Brasilodendron*?	Lundqvist (1919); Kräusel (1961); Chaloner et al. (1979)
Brazil	Cambuí, Figueira coalfield, Paraná state	Rio Bonito	*Sigillaria*	This material was not figured by Oliveira (1927), and its morphological characteristics are obscure.	Oliveira (1927)
Brazil	Cambuí, Figueira coalfield, Paraná state	Rio Bonito	*Lepidodendron pedroanum*, *Lycopodiopsis pedroanus*, *Lycopodiopsis* sp.	*Brasilodendron pedroanum*?	Read (1941); Rösler (1972); Chaloner et al. (1979); Ricardi-Branco and Ricardi (2003)
Brazil	Rio Carvãozinho, Figueira coalfield, Paraná state	Rio Bonito	*Lepidodendron*, *Lepidodendron pedroanum*	*Brasilodendron pedroanum*?	Oliveira (1927); Read (1941); Chaloner et al. (1979); Ricardi-Branco and Ricardi (2003)
Brazil	São João do Triunfo, Paraná state	Rio Bonito	*Lycopodiopsis pedroanus*	*Brasilodendron* cf. *pedroanum*?	Rösler (1972); Ricardi-Branco and Ricardi (2003)
Brazil	Figueira coalfield, Paraná state	Rio Bonito	*Brasilodendron* cf. *pedroanum*	—	Ricardi-Branco and Ricardi (2003)

Continuation

Country	Locality	Formation	First taxonomic status	Current taxonomic status	References
Brazil	Rio Ferreira outcrop, Treviso, Santa Catarina state	Rio Bonito	*Lepidostrobus* sp.	Vegetative structure, lacking evidence of sporangia (Chaloner et al., 1979)	Read (1941); Chaloner et al. (1979)
Brazil	Rio Ferreira outcrop, Treviso, Santa Catarina state	Rio Bonito	*Lepidodendron pedroanum*	*Brasilodendron pedroanum*?	Read (1941); Chaloner et al. (1979)
Brazil	Rio Ferreira outcrop, Treviso, Santa Catarina state	Rio Bonito	*Cyclodendron brasiliensis*	—	Lejal-Nicol and Bernardes-de-Oliveira (1979)
Brazil	Quitéria outcrop, Encruzilhada do Sul, Rio Grande do Sul state	Rio Bonito	*Brasilodendron*, isolated microphyllous	*Brasilodendron pedroanum*	Jasper and Guerra-Sommer (1998); Jasper et al. (2006); Guerra-Sommer et al. (2008); Boardman et al. (2012)
Brazil	Quitéria outcrop, Encruzilhada do Sul, Rio Grande do Sul state	Rio Bonito	*Lycopodites riograndensis*	—	Salvi et al. (2008)
Brazil	Bonito I mine, Lauro Müller, Santa Catarina state	Rio Bonito	*Brasilodendron pedroanum*	—	Manfroi et al. (2012); Mendonça-Filho et al. (2013)
Brazil	Morro do Papaléo outcrop, Mariana Pimentel, Rio Grande do Sul state	Rio Bonito	*Brasilodendron* cf. *pedroanum*	—	Spiekermann et al. (2018)
Uruguay	Vichadero, Department of Rivera, Uruguay	Frayle Muerto	Lycopsida Type A	—	Gutiérrez and Herbst (1995)
Brazil	São Sepé outcrop, São Sepé, Rio Grande state	Palermo	*Lepidodendron*	Lycopsida vegetative axes	Zingano and Cauduro (1959); Bortoluzzi and Veiga (1981); This work
Brazil	Assistência, Rio Claro, São Paulo state	Irati	*Sigillaria*	Cycadophyte-like plant	Guerra-Sommer (1981); This work
Brazil	Santa Rosa do Viterbo, São Paulo state	Irati	Lycopsida microphyllous	—	Rios and Ricardi-Branco (2016)
Uruguay	Melo, Department of Cerro Largo	Paso Aguiar	*Cyclodendron cf. leslii*	—	Herbst (1986)
Uruguay	Cañada Sarandí de los Carpinchos, Department of Rivera	Yaguarí	*Cyclodendron andreisii*	—	Herbst and Gutiérrez (1995)
Paraguay	Arroyo Vino, Colonia Independencia	Tacuary	*Cyclodendron andreisii*	—	Herbst (1972); Herbst and Gutiérrez (1995)
Paraguay	Siraty, Department of San Pedro	Tacuary	*Cyclodendron* cf. *leslii*.	—	Herbst (1986)

Continuation

Country	Locality	Formation	First taxonomic status	Current taxonomic status	References
Brazil	Tereza Cristina, margins of Ivaí river, Paraná state	Teresina	*Lycopodiopsis derbyi*	—	Mack (1947)
Brazil	Prudentópolis, margins of Patos river, Paraná state	Teresina	*Lycopodiopsis derbyi*	—	Mack (1947)
Brazil	Joaquim Tavorá, Paraná state	Teresina	*Lycopodiopsis*?	—	Kräusel (1961)
Brazil	Reserva, Paraná state	Teresina	*Lycopodiopsis derbyi*	—	Kräusel (1961)
Brazil	Cerro Chato outcrop, Dom Pedrito, Rio Grande do Sul state	Teresina	*Lycopodiopsis derbyi*, *Lycopodiopsis* sp., *Cyclodendron dolianitti*	—	Kräusel (1961); Herbst (1986)
Brazil	Fluviópolis, São Mateus do Sul, Paraná state	Teresina	*Lycopodiopsis?*	—	Oliveira-Babinski and Rösler (1984)
Brazil	Quarries, Prudentópolis, Paraná state	Teresina	*Lycopodiopsis derbyi*	—	Rohn (1994)
Brazil	Quarry (*Pedreira velha*), Fluviópolis, Paraná state	Teresina	*Lycopodiopsis* sp.	—	Rohn (1994)
Brazil	District of Gonçalves Júnior, Paraná state	Teresina	Microphylls	—	Rohn et al. (1997a)
Brazil	Rio Preto quarry, Paraná state	Teresina	Microphyllous	*Lepidophylloides corumbataensis*	Rohn et al. (1997a); Faria et and Ricardi-Branco (2010)
Brazil	Cândido de Abreu-Reserva region, Paraná state	Teresina	Microphyllous	—	Rohn et al. (1997b)
Brazil	Canoinhas outcrop, Canoinhas, Santa Catarina state	Teresina	Microphyllous	*Lepidophylloides corumbataensis*	Rohn et al. (1997c); Faria et and Ricardi-Branco (2010)
Brazil	Piracibaba, São Paulo state	Corumbataí	*Lycopodiopsis derbyi* and microphylls	—	Renault (1890); Steinmann (1924); Alarcon (1998); Alarcon and Bernardes-de-Oliveira (1999)
Brazil	Bofete, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	White (1908)
Brazil	Tatuí, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	Rao (1940)
Brazil	Conchas, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	Kräusel (1961)
Brazil	Batovi, vicinities of Conchas, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	Kräusel (1961)
Brazil	Corumbataí, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	Kräusel (1961)

Continuation

Country	Locality	Formation	First taxonomic status	Current taxonomic status	References
Brazil	Porangaba, São Paulo state	Corumbataí	*Lycopodiopsis derbyi* and isolated microphyllous	—	Kräusel (1961)
Brazil	Rio Claro, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	Simões and Fittipaldi (1992)
Brazil	Cantagalo-Ipeúna Highway, Ipeúna, São Paulo state	Corumbataí	*Lycopodiopsis*?	—	Mendes (1952)
Brazil	Laras, Laranjal Paulista, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	Mezzalira (1980)
Brazil	Castelo-Branco Highway, Km 164, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*	—	Faria et al. (2007); Faria et al. (2009)
Brazil	Santa Terezinha, Piracicaba, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*, *Lepidophylloides corumbataensis*	—	Faria et al. (2009); Faria et and Ricardi-Branco (2010)
Brazil	São Roque Novo, Bofete, São Paulo state	Corumbataí	*Lycopodiopsis derbyi*, *Lepidophylloides corumbataensis*	—	Faria et al. (2009); Faria and Ricardi-Branco (2010)

Publication 2

A fresh look on the morphology of Azaniadendron Rayner: a ligulate lycopsid from the Permian of Gondwana

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R. Spiekermann: author position, 1; scientific ideas, 90%; data generation 90%; analysis and interpretation, 90%; paper writing, 90%.
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M.K. Bamford: author position, 3; scientific ideas, 2%; data generation 3%; analysis and interpretation, 3%; paper writing, 3%.
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A fresh look on the morphology of *Azaniadendron* Rayner: a ligulate lycopsid from the Permian of Gondwana

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ABSTRACT

The monotypic *Azaniadendron fertile* Rayner, a lycopsid from the Guadalupian of Gondwana, is investigated providing new data on the morphology of its leaf cushions and their variation in shape. Evidence for a ligule is presented for the first time, elucidating, at least for this genus, a dilemma about the presence of this structure in lycopsids from the Permian *Glossopteris* flora. New data on its fertile axes question the assumption that the taxon produced true cones. We hypothesise that the genus belong to the Isoetales. Unequivocal evidence of the taxon is so far known only from the South African Vryheid Formation and its equivalent beds.

1. Introduction

Many lycopsid fossils, assumed to represent sub-arborescent (*sensu* Bek et al., 2008) to arborescent forms, are known from the Permian strata of Gondwana (e.g., Edwards, 1952; Anderson and Anderson, 1985; Spiekermann et al., 2020). In several localities, such lycopsids are considered important elements of the *Glossopteris* flora, but the study of their remains is largely hampered by their fragmented state in allochthonous assemblages (e.g., Kräusel, 1961; Spiekermann et al., 2020). In the few occurrences of *in situ* Permian lycopsids known from Gondwana, preservation of taxonomically important surface structures, such as details of leaf cushions, is often not good enough to allow precise taxonomic determination (e.g., Jasper and Guerra-Sommer, 1998; Mottin et al., 2022). Some *in situ* fossils, for example, can only be assigned to Lycopsida (e.g., Azcuy et al., 1987). Therefore, our knowledge about these plants is still incomplete, especially when compared to the well-known and often ubiquitous sub-arborescent and arborescent lycopsid fossils from the Carboniferous of the Euramerican floral province (e.g., Pigg and Rothwell, 1983a; Bateman et al., 1992; DiMichele and Bateman, 2020). Many systematic assignments found in the literature for Permian Gondwanan lycopsids have to be considered questionable due to these facts (e.g., Spiekermann et al., 2020).

Most of these southern lycopsids are incompletely preserved, lacking one or more characters with systematic value (e.g., Kräusel, 1961; Rayner, 1986; Chaloner et al., 1979; Spiekermann et al., 2020). Characters with systematic value include: type of rooting system, evidence for the presence/absence of secondary tissues and ligule, as well as reproductive structures (e.g., Meyen, 1987; DiMichele and Bateman, 1996; Gerrienne et al., 2018). They are poorly understood as whole plants, and it is difficult to apply well-established taxonomic/systematic concepts developed for late Palaeozoic Euramerican lycopsids (e.g., DiMichele and Bateman, 1996) to them. Due to their fragmentary condition, it is often even difficult to provide reliable generic determinations for such material. In addition, the original diagnoses and descriptions of many of the currently recognized taxa are based only on a few, fragmentary specimens representing the type-material of the corresponding taxa, which do not cover the range in morphological variation. This adds to the problems with identifying many of the fragmentary remains of these plants. An approach to overcome these difficulties to reliably identify individual taxa is to characterize, as far as possible, the variability of morphological structures of a larger suite of fragments (from a single or only a few localities), which can unambiguously be assigned to one taxon (e.g., Spiekermann et al., 2018).

This approach includes not only the description of the biological variability resulting from positional, functional or ontogenetic differences.

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It should also consider taphonomical induced changes (e.g., shape distortion, decortication, and decay, all common in lycopsid fossils; Gensel and Pigg, 2010; Bateman and DiMichele, 2021) to clarify the entire variability of morphological characters that may occur in fossils belonging to an individual taxon. When this approach is applied to different taxa, it might be possible to identify which preservational states of certain morphological characters are suitable for taxonomical purposes (i.e. on the level of genera and species) and which are not. Concerning the Gondwanan sub-arborescent to arborescent lycopsids, it is clear that some of the morphological variability visible in their fossil remains is due to taphonomy. Unfortunately, in many cases, it is still difficult or even impossible to provide sound interpretations of these taphonomical-induced changes due to the fragmentary nature of most specimens and the lack of anatomical preserved material in most taxa. At some point, however, we must begin to take a fresh, descriptive look at the fossils of these plants.

Here we apply this approach to the monotypic genus *Azaniadendron* Rayner from the Guadalupian of South Africa. This taxon is based on impressions and compressions of defoliated and sporophyll-bearing axes (Anderson and Anderson, 1985; Rayner, 1986) from three localities exhibiting deposits of that epoch. Sporophyll-bearing axes of *Azaniadendron fertile* Rayner yielded *in situ* micro and megaspores. Rayner (1986) analysed the spores and interpreted that micro and megasporangia were aggregated in bisporangiate cones. This author also examined epidermal details of the taxon's leaf cushions based on cuticles recovered from compressions, plus scanning electron microscope analyses of epidermal cells impressed on specimens lacking cuticles. *Azaniadendron fertile* has so far been interpreted as an arborescent lycopsid, lacking evidence of ligules (Anderson and Anderson, 1985; Rayner, 1986). However, especially for this minute structure, absence of evidence is not evidence of absence (cf. Meyen, 1972), and such a presumed eligulate condition needs to be validated.

Rayner (1986) assigned *Azaniadendron* to Lycopodiopsidaceae and Lepidodendrales. The Lepidodendrales are now lumped into the Isoetales based on their bipolar rhizomorphs and secondary growth, being considered the most derived isoetaleans due to their monosporangiate cones (DiMichele and Bateman, 1996). Later, the genus was placed in Azaniodendraceae, based on a classification proposal that remains unpublished to date (Bek, 2017). Thus, the diagnostic characteristics of this family remain unknown. So far, our knowledge of the genus is based on Rayner (1986) and Anderson and Anderson (1985). Anderson and Anderson (1985) referred to the taxon as *Azaniodendron* Rayner *in press*. This generic name does not fulfil the requirements of the Shenzhen Code (Turland et al., 2018), as it was given by referencing a study that had, yet, to be validly published. Rayner's (1986) proposal of *Azaniadendron* and *A. fertile* meets all demands of the code and should be considered the protologue of this genus and species.

This paper reviews the published aspects of *Azaniadendron*, supplemented by new morphological data gathered from a suite of fossils, many of which are so far not figured in the literature. They reveal new information about the morphological variability of the leaf cushions. Evidence for the occurrence of a ligule is reported, at least for this genus, demonstrating the presence of this structure in lycopsids from the *Glossopteris* flora. Last, but not least, new evidence questions whether the taxon produced true cones.

2. Material and methods

Seventy-one fossils form the basis of this study (see repository and accession numbers in Table 1). They come from collections made prior to 1985 at the Leeukuil, Hammanskraal, and West Driefontein quarries in the Gauteng Province, South Africa (Anderson and Anderson, 1985; Fig. 1). Today, the strata of these quarries are largely inaccessible.

2.1. Leeukuil quarries

This set of adjacent quarries (26°42'12"S; 27°54'27"E) lies southwest of the town of Vereeniging, on the northern side of the Vaal River (le Roux and Anderson, 1977; Fig. 2a). They have been inactive for many years and are flooded, infilled, or covered by vegetation today. Fossils recovered from the quarries include lycopsids, ferns, sphenophytes, glossopterids, cordaitaleans, and conifers (Anderson and Anderson, 1985). Most, including those studied here, are preserved in laminated, buff-coloured silty claystones (le Roux and Anderson, 1977; Prevec et al., 2008). Among lycopsids, fossils assigned to *Cyclodendron leslii* (Seward) Kräusel prevail, and the locality yielded only a few remains assignable to *Azaniadendron* (Anderson and Anderson, 1985; Rayner, 1986). We examined three *A. fertile* specimens from these quarries (Table 1). They represent fragmented defoliated axes impressions.

The quarries are assigned to the Vryheid Formation, Ecca Group, of the northern part of the main Karoo Basin (Anderson and Anderson, 1985; Adendorff et al., 2003). Overall, the Vryheid beds represent a fluvio-deltaic system associated with swamps (e.g., Johnson et al., 1996; Cairncross, 2001). Recent palynological studies indicate that its deposition began in the Artinskian and continued into the Wordian

Table 1
List of the *Azaniadendron fertile* Rayner specimens examined in this study. They are stored in the Fossil Herbarium of the Evolutionary Studies Institute at the University of the Witwatersrand, Johannesburg, South Africa.

Specimens	Type of fossil	Locality	Source strata
BP/2/13267; BP/2/13368; BP/2/13420	Impressions of defoliated axes	Leeukuil Quarries, Gauteng Province, South Africa (26°42'12"S; 27°54'27"E)	Vryheid Formation, Ecca Group
BP/2/7255; BP/2/7257; BP/2/7263; BP/2/7266; BP/2/7302 (holotype); BP/2/7362; BP/2/7365; BP/2/7366; BP/2/7371; BP/2/7372; BP/2/7373; BP/2/7375; BP/2/7376	Compressions and impressions of defoliated and sporophyll-bearing axes	Hammanskraal Quarry, Gauteng Province, South Africa (25°27'57"S; 28°17'47"E)	Vryheid Formation equivalent, Ecca Group
BP/2/16548; BP/2/16604; BP/2/16625; BP/2/16628; BP/2/16636; BP/2/16653; BP/2/16655; BP/2/16658; BP/2/16661; BP/2/16669; BP/2/16672; BP/2/16680; BP/2/16684; BP/2/16690; BP/2/16691; BP/2/16692; BP/2/16695; BP/2/16696; BP/2/16697; BP/2/16699; BP/2/16700; BP/2/16701; BP/2/16704; BP/2/16710; BP/2/16715; BP/2/16717; BP/2/16723; BP/2/16732; BP/2/16733; BP/2/16736; BP/2/16742; BP/2/16744; BP/2/16746; BP/2/16747; BP/2/16764; BP/2/16766; BP/2/16767; BP/2/16750; BP/2/16780; BP/2/16784; BP/2/16790; BP/2/16793; BP/2/16794; BP/2/16796; BP/2/16802; BP/2/16808; BP/2/16812; BP/2/16870; BP/2/16872; BP/2/16873; BP/2/16875; BP/2/16877; BP/2/16878; BP/2/16879; BP/2/21545	Impressions of defoliated axes	West Driefontein Quarry, Gauteng Province, South Africa (26°23'43"S; 27°28'45"E)	Vryheid Formation?, Ecca Group

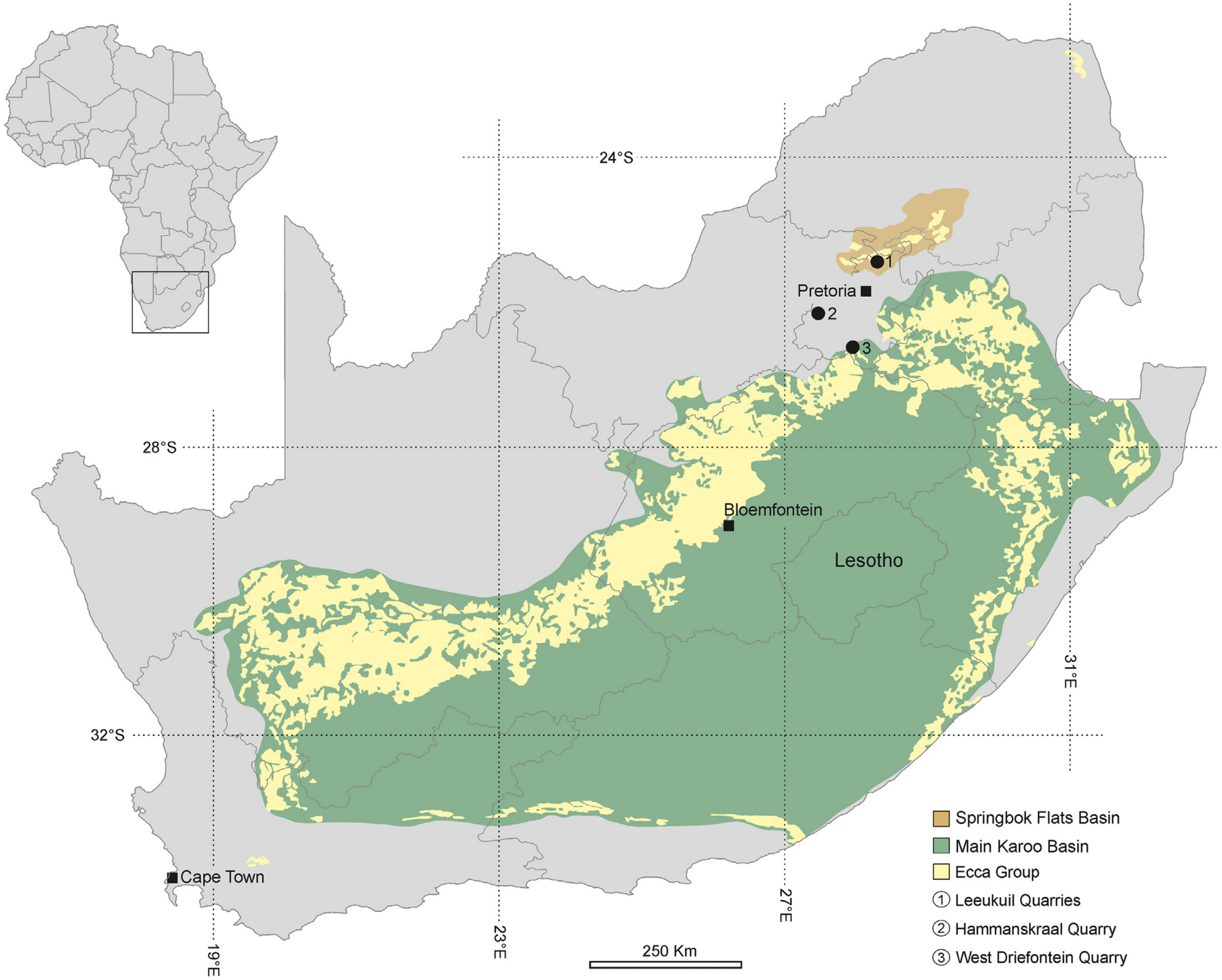

Fig. 1. Map of South Africa showing the main Karoo and Springbok flats basins and the location of the Leeukuil, Hammanskraal, and West Driefontein quarries. Adapted from Barbolini et al. (2018).

(Barbolini et al., 2018; Fig. 3). The quarries' strata did not yield palynomorphs (Rayner, 1986) but lie above the Vereeniging top coal seam (Millsteed, 1994). This top seam is equivalent to the No. 4 seam of the Witbank coalfields, and their uppermost part is assigned to the Roadian, according to the palynoflora (Barbolini et al., 2018). Thus, the quarries' strata are younger than these coal seams but not younger than Wordian, lying within the Guadalupian.

2.2. Hammanskraal quarry

This quarry (25°27′57″S; 28°17′47″E) is situated south-southeast of the Hammanskraal station (Adendorff et al., 2003; Fig. 2b). It has been inactive for many years and long since filled with water. The Hammanskraal flora includes lycopsids, ferns, sphenophytes, glossopterids, and cordaitaleans (e.g., Anderson and Anderson, 1985). Lycopsid macrofossils are rare elements, assigned to *Cyclodendron leslii* and *Azaniadendron fertile* (Rayner, 1985, 1986). The holotype of *Azaniadendron fertile,* a sporophyll-bearing axis, comes from this quarry (Rayner, 1986). We studied thirteen *Azaniadendron fertile* fossils, including the holotype, as well as other sporophyll-bearing and defoliated axes (Table 1). They represent fragmented compressions and impressions in grey mudstones.

The quarry lies within the Springbok Flats Basin (Fig. 1). Its strata are considered equivalent to the Vryheid Formation (Adendorff et al., 2003; Barbolini et al., 2019). This unit comprises a lower and upper coal zone, and these coals represent peat accumulating areas in fluvial and upper delta plain settings, respectively (Barbolini et al., 2019). The strata exposed in this quarry may have resulted from deposition in proximal-inland settings (Barbolini et al., 2019). Palynologically, the upper coal zone and the Hammanskraal fossil site correlate with Biozone E of the Waterberg Coalfield of the Ellisras Basin (MacRae, 1988; Barbolini et al., 2019). Palynostratigraphic analyses indicated that the upper coal zone accumulated during the Roadian–Wordian (Barbolini et al., 2019; Fig. 3). The Hammanskraal Quarry seems to be more or less contemporaneous with the Leeukuil Quarries and thus is probably of Guadalupian age.

2.3. West Driefontein quarry

This quarry (26°23′43″S; 27°28′45″E) is situated east of Carltonville, circa 50 km from Johannesburg (Fig. 2c). Rayner (1986) mentioned that after the collection of plant fossils at the locality, a brick manufacturing company fully extracted these fossiliferous deposits. Strata exposed in this quarry originated from sedimentation in a small isolated basin

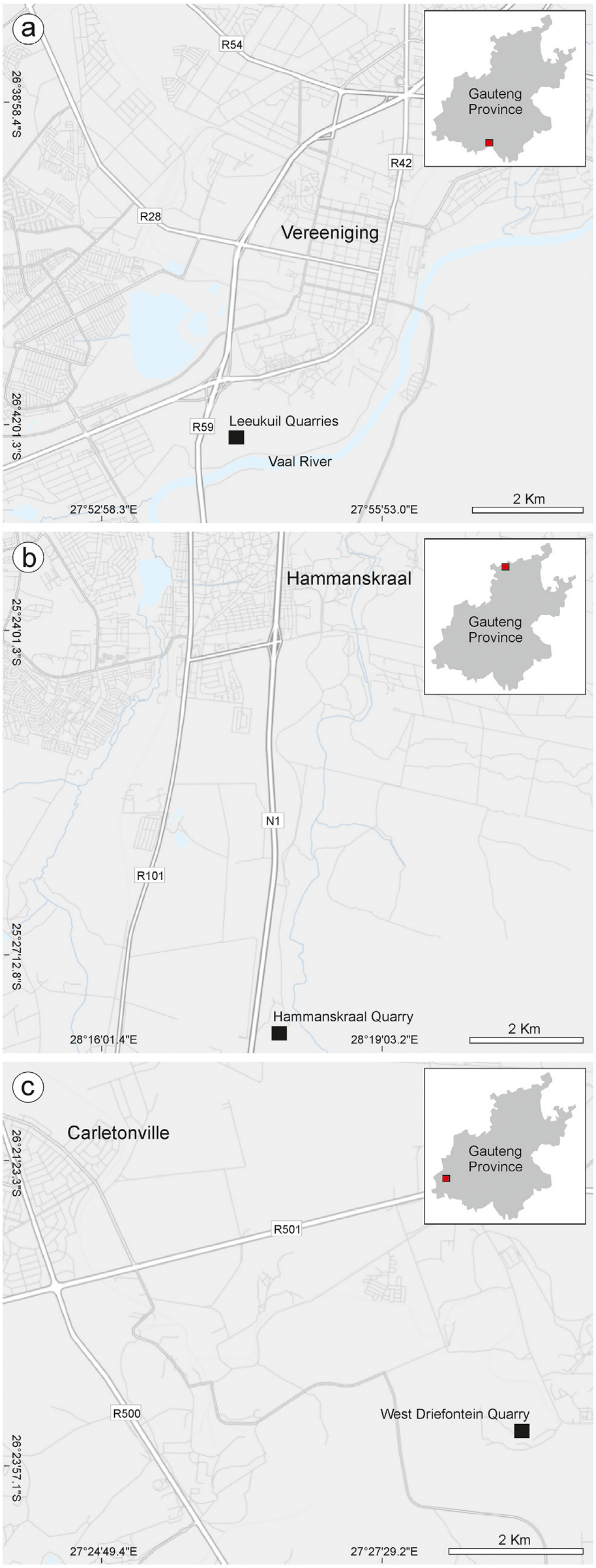

Fig. 2. Maps showing the location of the Leeukuil, Hammanskraal, and West Driefontein quarries in the Gauteng Province, South Africa. (a) Leeukuil Quarries. (b) Hammanskraal Quarry. (c) West Driefontein Quarry. Maps created using ArcGIS® online software by Esri. ArcGIS®

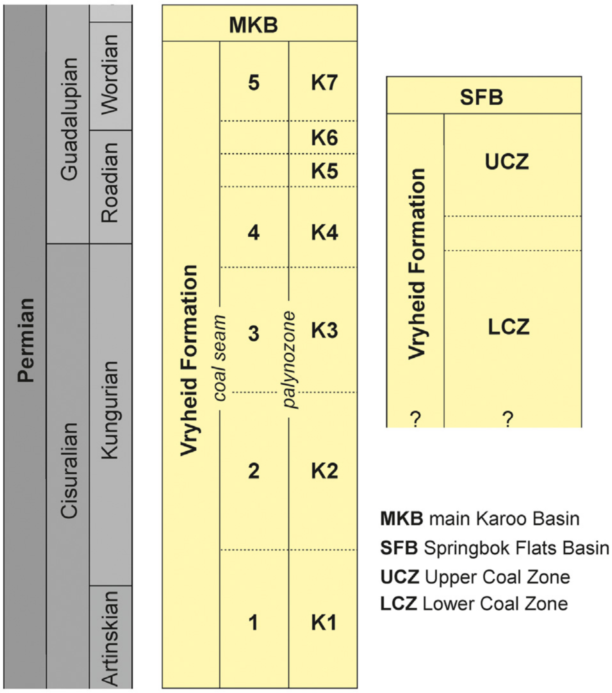

Fig. 3. Palynostratigraphic correlation between the Vryheid Formation coal beds from the main Karoo and Springbok Flats Basin. The Leeukuil Quarries lie above the upper Vereeniging coal seam (equivalent to the No. 4 seam of the Vryheid Formation in the main Karoo Basin). The Hammanskraal Quarry correlates palynologically with the upper coal zone of the Vryheid Formation in the Springbok Flats Basin. Adapted from Barbolini et al. (2019).

and yielded only a few fossil types, including *Azaniadendron fertile* and several glossopterids (Rayner, 1986). The quarry seems to be part of Anderson and Anderson's Libernon Gold Mine superlocality, placed in the middle Ecca-Vryheid Formation (Anderson and Anderson, 1985). Based on the occurrence of *A. fertile*, West Driefontein might be, more or less coeval, with the Leeukuil and Hammanskraal quarries, because this taxon is reported to have regional biostratigraphic significance (Rayner, 1986).

Azaniadendron fertile remains dominate the fossil collection (Rayner, 1986). They are impressions of fragmented defoliated axes in white silty claystones. We investigated fifty-five *A. fertile* axes (Table 1). They were selected due to the quality of preservational state, which yielded new data about the variability of leaf cushions of this taxon.

2.4. Methodology

This study was conducted according to the rules governing work on non-hominid fossils stored in the collections of the University of the Witwatersrand. Specimens were investigated and photographed with an Olympus SZX16 stereomicroscope equipped with an Olympus UC30 camera. Photographs showing their overall morphology were taken using a Canon PowerShot G11 camera. Measurements were taken from calibrated images using ImageJ-NIH (Schneider et al., 2012).

We measured the width and height of the largest and the smallest leaf cushion of each geometry occurring in each specimen. The widths × heights of the cushions in these specimens were plotted in a scattered diagram. One subordinate type of cushion, which has a laterally fused-like appearance, was not included in the plot as it was impossible to define its lateral boundaries and measure its width. For three selected axes, showing transitions between typical *Azaniadendron*-like cushions to ones with a distinct wider-than-high geometry, we measured the width and height of all cushions occurring on them. We plotted the widths × heights of the cushions occurring in these three specimens in a scattered diagram, comparing them with the other specimens.

The angles of the fossil's hypothetical left-to-right and right-to-left parastichies were measured following Benca et al. (2014; Fig. 4). The terminology used in the description follows mainly Bateman et al. (1992). The term "leaf cushion" is used in a broad sense (*sensu* Chaloner and Meyer-Berthaud, 1983). We did not extract new *in situ* spores from the fertile axes and did not recover further cuticles from the leaf cushions of the specimens. A descriptive overview of the current knowledge about those is presented based on the literature, complementing our macromorphological investigation and showing the current state of the art of the taxon.

3. Systematics

Class: Lycopsida Scott, 1909
Order: Isoetales *sensu* Meyen, 1987
Family: Incertae sedis
Genus: **Azaniadendron** Rayner, 1986 emend. Spiekermann, Jasper, Bamford et D. Uhl
Type species: *Azaniadendron fertile* Rayner, 1986
Emended diagnosis: The same as for the type species.

Species: *Azaniadendron fertile* Rayner, 1986 emend. Spiekermann, Jasper, Bamford et D. Uhl
Type locality: Hammanskraal Quarry (25°27'57"S; 28°17'47"E).
Holotype: BP/2/7302 designated by Rayner (1986; pl. II, 8; pl. III, 1–3, 5). Here figured in Plate II, 1–5.
Repository: Fossil Herbarium, Evolutionary Studies Institute, University of the Witwatersrand.
Additional studied material: Listed in Table 1.
Stratigraphic horizon: Vryheid Formation equivalent, Guadalupian.

Rationale for emending the diagnosis of the taxon: The generic-specific diagnosis is emended based on the variable shapes of the leaf cushions observed in this taxon, the leaf scars, the occurrence of a ligule pit, and new information on its fertile axes. The considerable variation of leaf cushion shapes, a potential result of taphonomy, is included in the diagnosis to allow readily identification of the taxon regardless of preservational condition. This is in accordance with the Art. 1.2. of the ICBN (Turland et al., 2018). The emended parts are in bold.

Emended generic-specific diagnosis: Lycopod with spiral phyllotaxis; microphylls/**sporophylls** present on narrow **and on broader axes**; broad **defoliated** axes covered with closely **to widely** spaced, **variably** rhomboidal, **drop-shaped, pyriform, and** oval to circular leaf cushions with a central elongate scar **situated within a not always evident large leaf scar; small ligule pit scar or notch at the top of the cushions not always preserved**; epidermal cells isodiametric to elongate, in a radiating pattern in the vicinity of leaf scars; heterosporous bisexual **fertile areas** made up of megasporangia that contain a single tetrad of spores up to 2 mm in diameter with a spiny surface, and strong contact faces delimited by curvaturae; microspores 30–40 μm in diameter with curvaturae, a cingulum and granulate sculpture; sporophylls recurved close to the point of attachment; sporangia borne in the curve in the sporophyll.

Synonymies and selected references (including the three given in the protologue and additional ones):

1969 *Lycopodiopsis* Renault sp.; Plumstead, Trans. Geol. Soc. S. Afr. 72 (annex.), pl. XIV, 2.

1973 *Lycopodiopsis derbyi*? Renault; Plumstead in Hallam (Ed.), Atlas Palaeobiogeogr., pl. II, 2.

1978 *Cyclodendron leslii* (Seward) Kräusel; Smithies, Ph.D. Thesis, University of the Witwatersrand, S. Afr., fig. 5A, D.

1980a *Lycopodiopsis* Renault; Lemoigne and Brown, Geobios 13 (4), pl. 1, 1–3, pl. 4, 1–3, pl. 5, 1.

1980b *Lycopodiopsis derbyi* Renault; Lemoigne and Brown, Geobios 13 (4), pl. 1, 3–5.

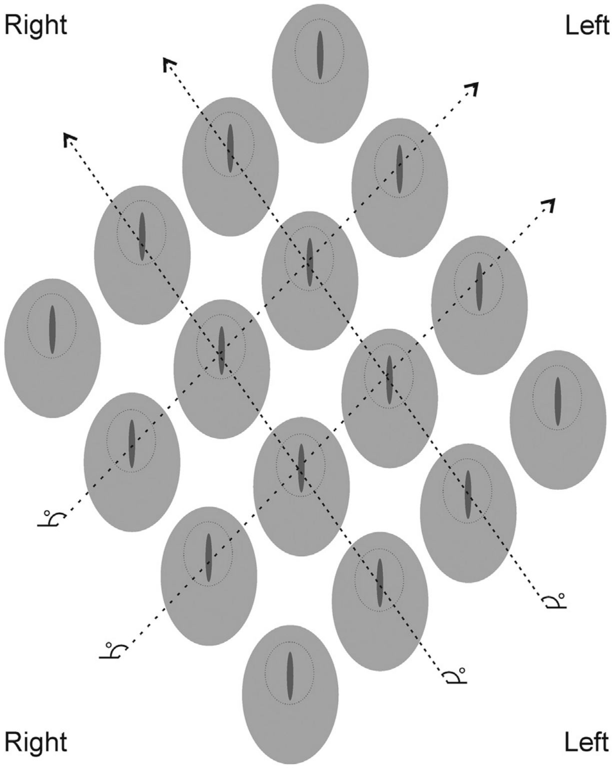

Fig. 4. Diagram showing method for measuring parastichies angles. Based on Benca et al. (2014). When specimens are external moulds, left-to-right and right-to-left parastichies are usually inverted.

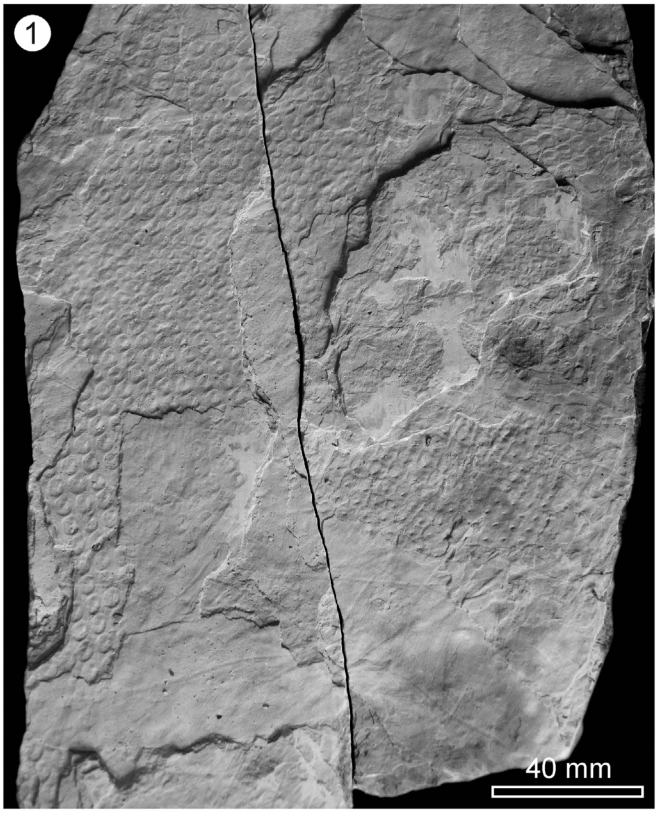

Plate I. *Azaniadendron fertile* Rayner. Small slab from West Driefontein Quarry containing fragmented defoliated axes. This fragmented condition characterizes all studied defoliate axes. Sample BP/2/16655.

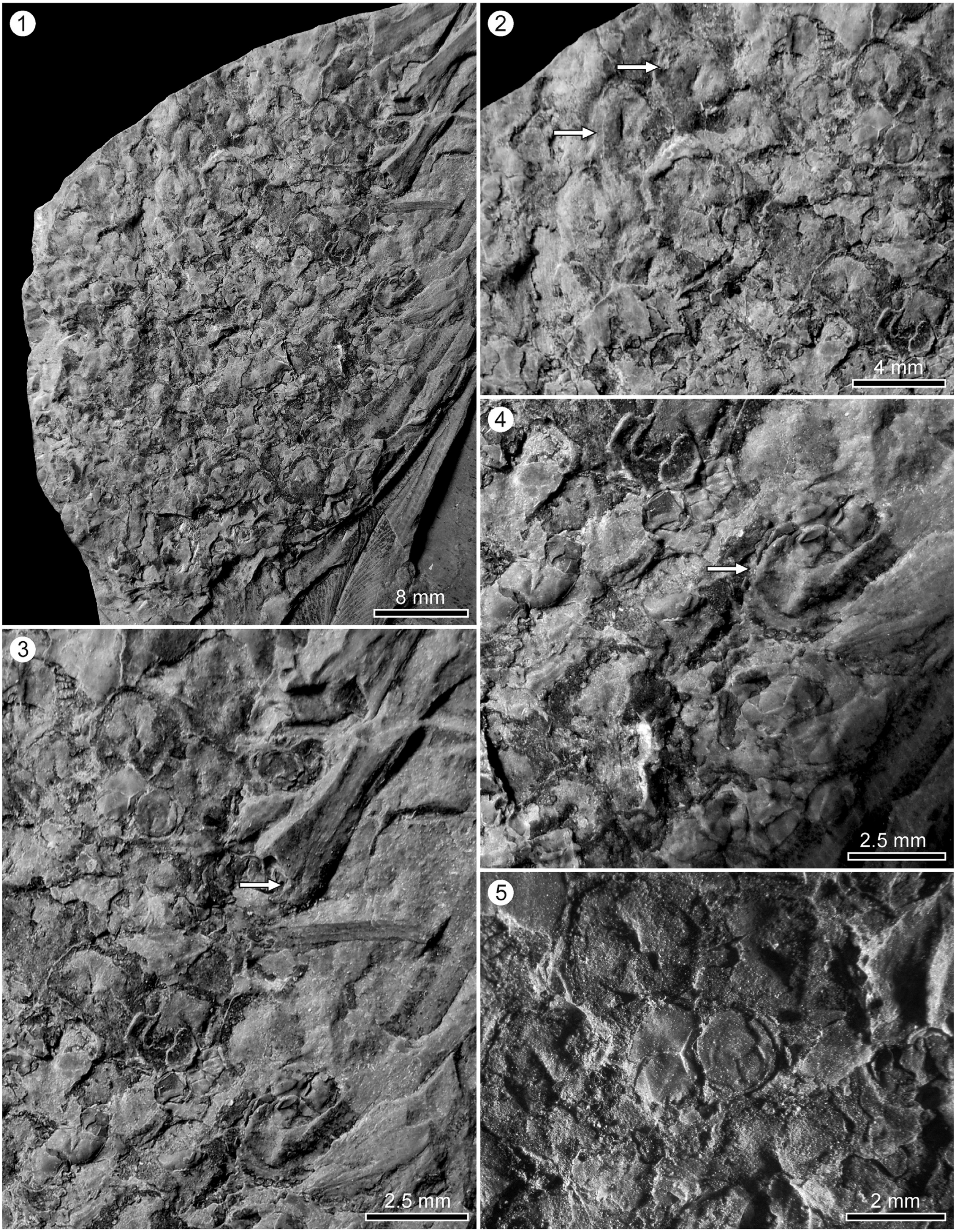

Plate II. *Azaniadendron fertile* Rayner. Holotype; specimen BP/2/7302. (1) Overview of the type specimen. (2) Detail of its leaf cushions (arrows). (3) Megasporangiate zone. Note the apparently slightly expanded megasporophyll pedicel (arrow). (4) Detail of megasporophyll pedicel (arrow). (5) Megaspores preserved on the surface of the holotype.

1985 *Azaniodendron fertile* Rayner; Anderson and Anderson, Palaeoflora South. Afr. Prodromus S. Afr. megafloras, Devonian to Lower Cretac., pl. 21, 1a–4, pl. 22, 1, 3a–3b, pl. 23, 1–7.

1986 *Azaniadendron* fertile Rayner; Rayner, Rev. Palaeobot. Palynol. 47, pl. I, 1–9, pl. II, 1–10, pl. III, 1–7.

1995 *Azaniadendron fertile* Rayner; Balme, Rev. Palaeobot. Palynol. 87, pp. 120–120.

2017 *Azaniodendron* Rayner; Bek, Palaeontograph. Abt. B 296, pp. 48–48.

Description: The sixty-seven defoliated axes examined here are 1.8–19.5 cm long, broken at both ends, and limited by slab size. They are 1.5–9.8 cm wide but broken at the laterals, precluding the determination of their original widths. This fragmented state gives them irregular outlines (Plate I, 1). None shows evidence of branching, and the rooting system of the taxon remains unknown.

The four studied sporophyll-bearing axes include the holotype. They are broken at both ends. The measures below are based on the axis proper. The holotype axis is 5.1 cm long and 3.1 cm wide; its proper left margin is preserved, but the right margin is irregularly broken (Plate II, 1). The other fertile axes have their complete width preserved. Among those, the largest fertile axis is 4 cm wide and 15 cm long (Plate III, 1), and the narrowest is 1.3 cm wide and 6.4 cm long (Plate IV, 1). The narrowest fertile axis, described by Rayner (1986, pl. II, 7), is 1 cm wide and curved.

We state from the outset that we agree with Rayner's (1986) interpretation that such defoliated and sporophyll-bearing axes belong to a

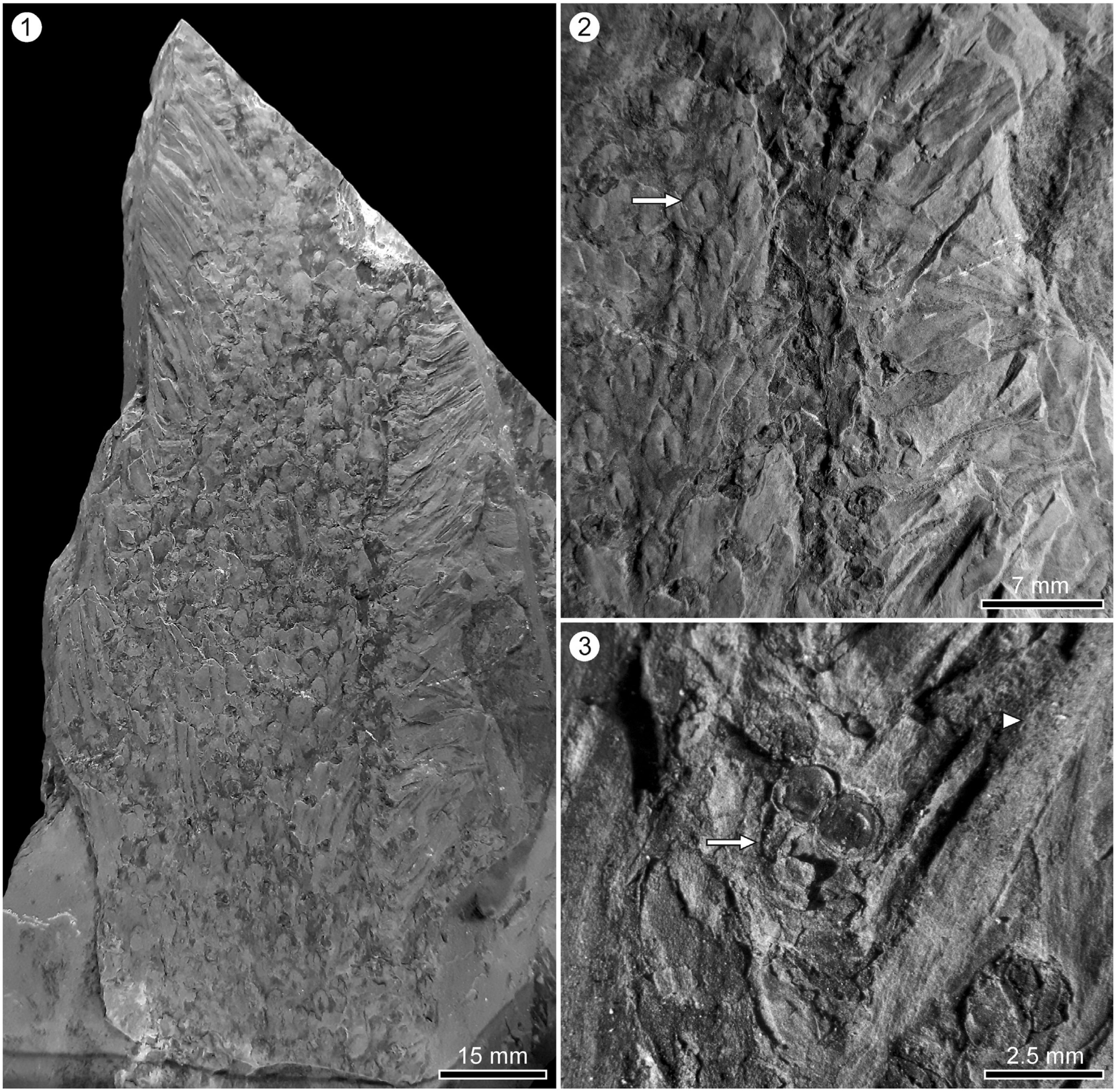

Plate III. *Azaniadendron fertile* Rayner. The thickest sporophyll-bearing axis of the taxon; specimen BP/2/7255. (1) Overview of the robust fertile axis. (2) Detail showing its leaf cushions (arrow) and poorly preserved megasporophylls. (3) Megasporangia with megaspores (arrow) and lamina of megasporophyll (arrowhead).

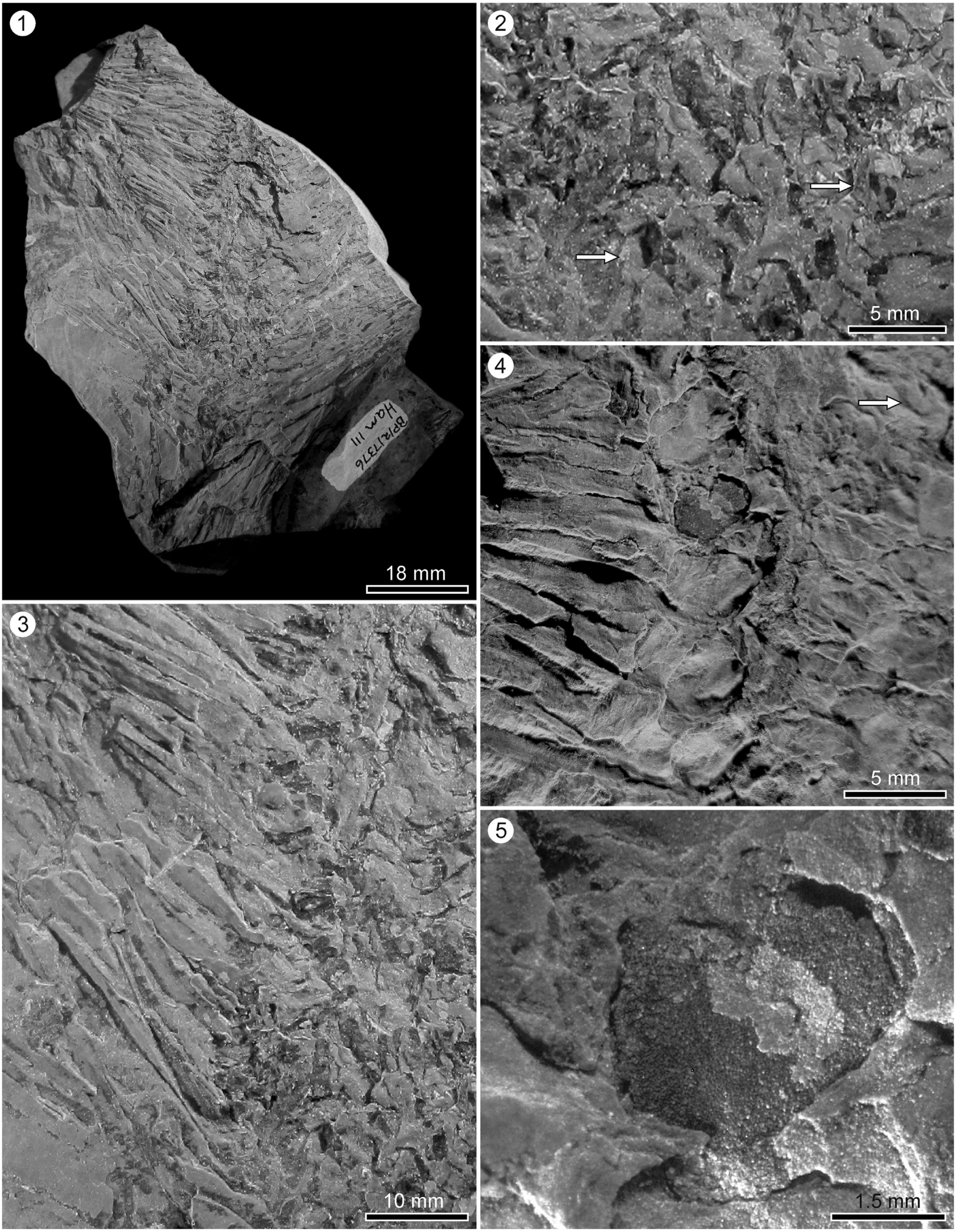

Plate IV. *Azaniadendron fertile* Rayner. (1) Narrow fertile axis. Specimen BP/2/7376. (2) Detail of specimen in 1 showing poorly preserved remains of leaf cushions (arrows). (3) Detail of specimen in 1 showing sporophylls. (4) Part of fertile axis showing microsporangia and a poorly preserved cushion remain (arrow). Specimen BP/2/7365. (5) Microsporangium from the specimen in 4.

single species. Both the holotype and largest fertile axis show identical leaf cushions to those of the defoliated axes (Plate II, 2 arrows; Plate III, 2 arrow). The other fertile axes are not well-preserved. Yet, they come from the same locality (Hammanskraal) and stratum as the better-preserved ones, show sporophylls similar to those (Plate IV, 1, 3–4), and leaf cushion remains comparable to the defoliated axes (Plate IV, 2 arrows, 4 arrow). Further, Rayner (1986) studied the epidermal details of these fertile and defoliated axes and demonstrated the morphological similarity between their epidermal tissues.

Sporophylls and sporangia. Rayner (1986, pl. II, 1, 10) demonstrated that the sporophyll-bearing axes were bisporangiate. New data indicate that sporophylls formed fertile areas not only on narrow (1–1.3 cm wide) but also on robust axes (4 cm wide) with a nearly undifferentiated vegetative-like morphology (Plate III, 1).

Sporophylls are helically arranged and incomplete in length, not showing their apices (Plate III, 1; Plate IV, 1). The longest incomplete sporophyll is about 30 mm long. Micro and megasporophylls seem to have been similar, and it is difficult to distinguish both, based only on their gross morphology. Their pedicels seem to have been short and slightly expanded as compared to the laminae (Plate II, 3 arrow). Laminae are strap-like, have apparently entire margins and are narrow, 0.8–2.5 mm wide in the preserved parts in face view (Plate III, 1, 3 arrowhead; Plate IV, 1, 3–4).

Sporangia were borne on sporophyll axils (Plate II, 4 arrow; Plate III, 3 arrow; Plate IV, 4). Megasporangia are highly compressed, usually broken and open, with their exact outline not preserved. One can readily identify them due to the presence of megaspores visible to the naked eye (Plate II, 3 arrow, 4 arrow, 5; Plate III, 3 arrow). A megasporangium bears a single tetrad of megaspores (Anderson and Anderson, 1985; Rayner, 1986). Microsporangia have a granulate aspect and are highly flattened with a disk-like shape (Plate IV, 4–5).

Overview of the spores. Megaspores have sub-circular to circular amb and a diameter of circa 1400–2000 μm (Rayner, 1986, pl. III, 1). They are trilete, curvaturate, exhibit prominent contact areas, and distal surface covered by coni and spines (Rayner, 1986; Bek, 2017). Coni and spines are small and up to 5 μm high (Rayner, 1986, pl. III, 2), but did not cover densely the spore surface. Triradiate rays are straight to very slightly sinuous, becoming higher at the spore apex, building a low pyramidal elevation (Rayner, 1986, pl. III, 1).

Microspores are trilete and cingulizonate, with a subtriangular amb and diameter of circa 21–36 μm (Rayner, 1986, pl. III, 6–7). The cingulum and zona are about a tenth of the diameter of the spore (Rayner, 1986). The zona is laevigate, occasionally perforated or punctate, and the proximal and distal surfaces of the spores are microgranulate (Rayner, 1986; Bek, 2017). Triradiate rays are straight rather than sinuous, extending to the outer part of the central body or until the equatorial margin in some specimens (Rayner, 1986, pl. III, 6–7).

Leaf cushions. The leaf cushions (Fig. 5; Fig. 6) are helically arranged on the axes, forming left-to-right and right-to-left crossing and ascending parastichies (e.g., Plate V, 1–4; Plate VI, 1; Plate VII, 1–2). They are protuberant or slightly protuberant. The most notable detail of the cushions is a narrow, elongated, and vertically oriented depression situated in their centre (e.g., Plate V, 1–4; Plate VI, 1–6). In external moulds, this depression is visible as a positive ridge (Rayner, 1986; Plate V, 2). Rayner (1986) also elected this feature as the most typical aspect of the cushions. In a few cushions, this elongated depression in their centre appears divided into two parts (Plate VII, 4 arrows).

Examination of defoliated axes revealed that this elongated structure is located in a not always evident leaf scar and does not extend beyond the limits of such a leaf abscission area (e.g., Plate VI, 2 arrow; Plate VII, 5 arrow; Plate VIII, 5–6 arrows). There is no evidence of two foliar and two infrafoliar parichnos scars. Although not preserved in all cushions, evidence for a ligule pit occurs at the top of at least thirty-one of them (Plate VI, 2–4 arrowheads, 6 arrowhead). Sometimes, the pit seems to be represented by a small notch (e.g., Plate VII, 6 arrowhead; Plate VIII, 3 arrowhead), such as in some Euramerican lycopsid impressions (cf. Gensel and Pigg, 2010). The spiralling degree, spacing, size, and shape of the leaf cushions varies among distinct defoliated axes

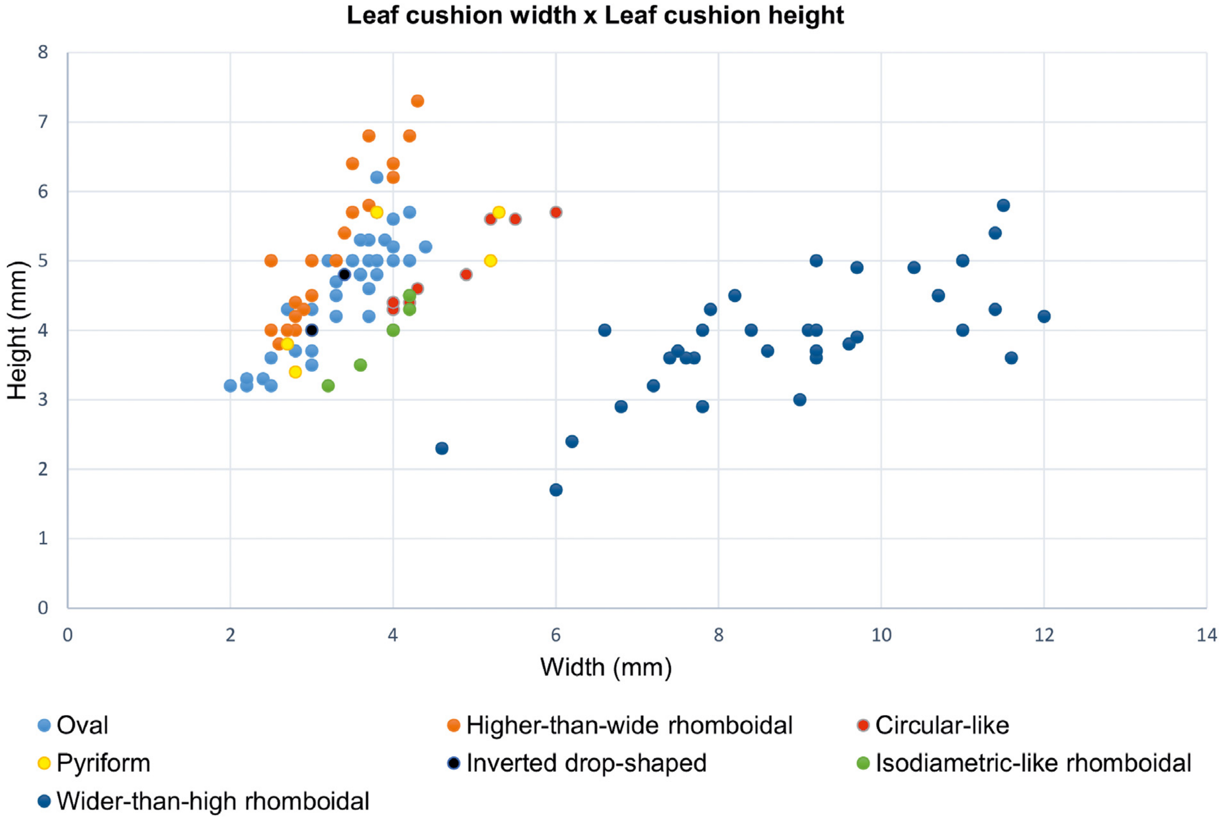

Fig. 5. Scatter diagram showing the width × height of the different cushion types. Based on the smallest and largest leaf cushion of each different geometry in each specimen.

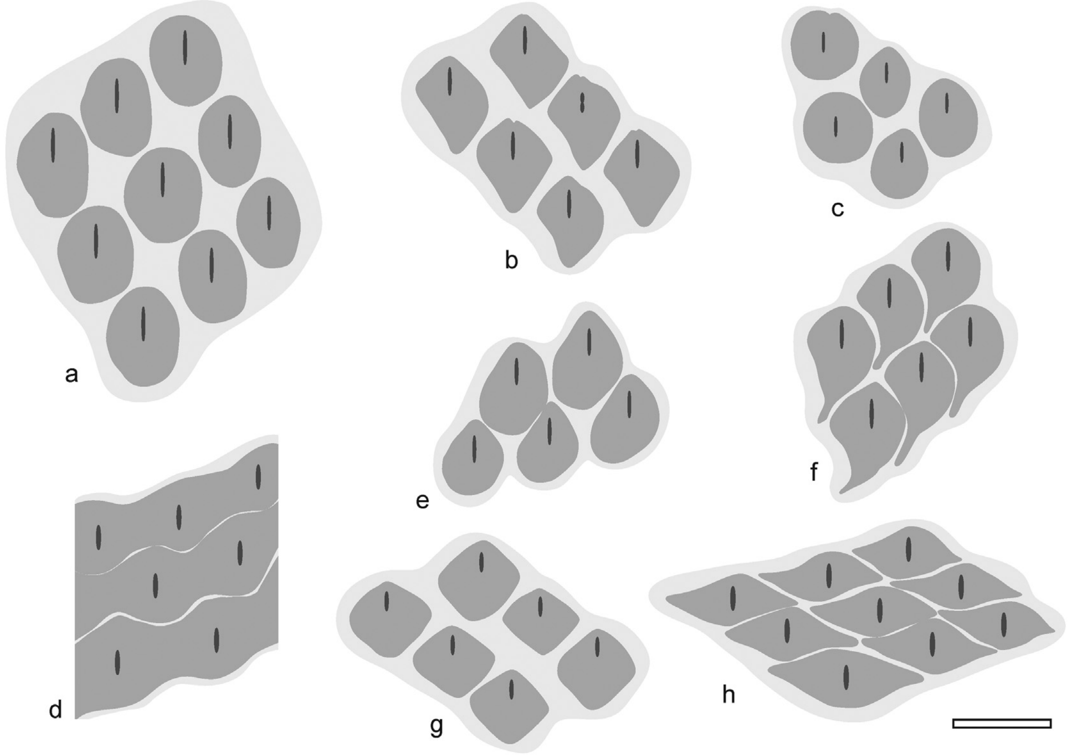

Fig. 6. Line drawings of different leaf cushion shapes. (a) Oval (e.g., Plate VI, 1). (b) Higher-than-wide rhomboidal (e.g., Plate VII, 3). (c) Circular-like associated with oval forms (e.g., Plate VIII, 2). (d) Laterally fused-like (e.g., Plate VIII, 4). (e) Pyriform (e.g., Plate IX, 3). (f) Inverted drop-like (e.g., Plate X, 4). (g) Isodiametric-like rhomboidal (e.g., Plate XI, 2). (h) Wider-than-high rhomboidal (e.g., Plate XIII, 2). Scale bar = approximately 5 mm.

and within a single axis (Fig. 5; Fig. 6). The morphology of the main cushion types, and subsidiary forms occurring among them, is described below in detail. It has to be pointed out, that the cushion categories are not organized in a gradational pattern from their presumed most to less pristine preservational state. There are relatively good-preserved cushions of virtually all types. These cushion types occur more or less randomly associated with each other on the axes, and defining a sequence from their presumed most to their less pristine state remains problematic based on the fragmentary nature of the specimens, at least for the time being without larger/longer and more informative specimens.

● Oval cushions (Fig. 6a): They are one of the most typical cushions, occurring in defoliated and sporophyll-bearing axes (Plate III, 2 arrow; Plate V, 1–4). These cushions form left-to-right parastichies with angles of 107–138° and right-to-left ones with inclinations of 114–151° (Plate V, 1–4). They are generally closely arranged within the parastichies (Plate V, 1–3; Plate VI, 1). However, one axis exhibits oval cushions widely spaced within the right-to-left parastichy and laterally (Plate V, 4). From the base to the top of this axis, the size of the cushions decreases progressively. The cushions are 4 mm wide and 6 mm high at the base and 3 mm wide and 3.5 mm high at the top of the specimen (Plate V, 4).

In the other specimens, the oval leaf cushions are 2.2–4.4 mm wide and 3.2–6.2 mm high, and their outline is symmetrical or asymmetrical (Plate VI, 1–6). Leaf scars are not always evident. We did not detect evidence of leaf scars in the sporophyll-bearing axes (Plate III, 2 arrow), probably because those have not been shed but were taphonomically detached or broken off. However, in the defoliated axes, at least forty-three of oval cushions bear a smooth leaf scar. These leaf scars have oval, rhomboidal, or onion-like shapes. They are 2.2–2.8 mm wide and 2.3–3.0 mm high, covering nearly the entire upper field of the cushions and sometimes part of the lower field (Plate VI, 2 arrow). Some but not all cushions bear a keel-like structure in their lower field (Plate VI, 5 arrow).

● Higher-than-wide rhomboidal cushions (Fig. 6b): Some defoliated axes exhibit rhomboidal cushions, which are higher than wide and are associated with oval-shaped ones (Plate VII, 1–2). These are 2.5–4.3 mm wide, 3.8–7.3 mm high, and have rounded edges (Plate VII, 1–6). They usually form left-to-right parastichies of 122–140° and right-to-lefts of 121–148°. Generally, they are closely spaced in the left-to-right parastichies but slightly more widely spaced within the right-to-left ones (Plate VII, 2). Most cushions with this shape lack clear evidence of a leaf scar. The leaf scars detected have a rounded rhomboidal outline, are about 2.0–3.0 mm wide and 2.2–3.0 mm high, and cover nearly the entire upper field of the cushions (Plate VII, 5 arrow).

● Circular-like cushions (Fig. 6c): This cushion type is 4.0–6.0 mm wide and 4.0–5.7 mm high (Plate VIII, 1–3). One axis exhibits circular cushions with subsidiary oval ones distributed among them (Plate VIII, 1–2). In this specimen, the circular cushions lie within left-to-right parastichies of 145° and right-to-left ones of 132°. They are close to each other in the right-to-left parastichies but slightly more spaced within the left-to-right ones in this axis (Plate VIII, 1–2). Another specimen, with more or less circular cushions, shows a transition from those into laterally fused ones, which form contiguous, slightly inclined horizontal rows (Plate VIII, 4; Fig. 4, d). Leaf scars are not always noticeable but occur in some circular cushions. When evident, they have rhomboidal shapes and are 2.5–3.6 mm wide and 2.2–2.7 mm high, covering almost the entire upper field of the cushions (Plate VIII, 5–6 arrows).

● Pyriform cushions (Fig. 6e): The axis partially dominated by circular cushions shows a transition from those into pyriform-shaped ones (Plate VIII, 1–2). These are 2.7–3.0 mm wide and 3.8–4.0 mm high in this specimen. This type of cushion also occurs among oval ones in some axes (Plate V, 3 arrow). Another specimen exhibits an area covered by pyriform cushions (Plate IX, 1). In this fossil, their sizes range from 2.8–3.8 mm in width and 3.4–5.7 mm in height. They are situated above a zone of small cushions and below an area covered by cushions with more or less oval to rhomboidal shapes, which form a

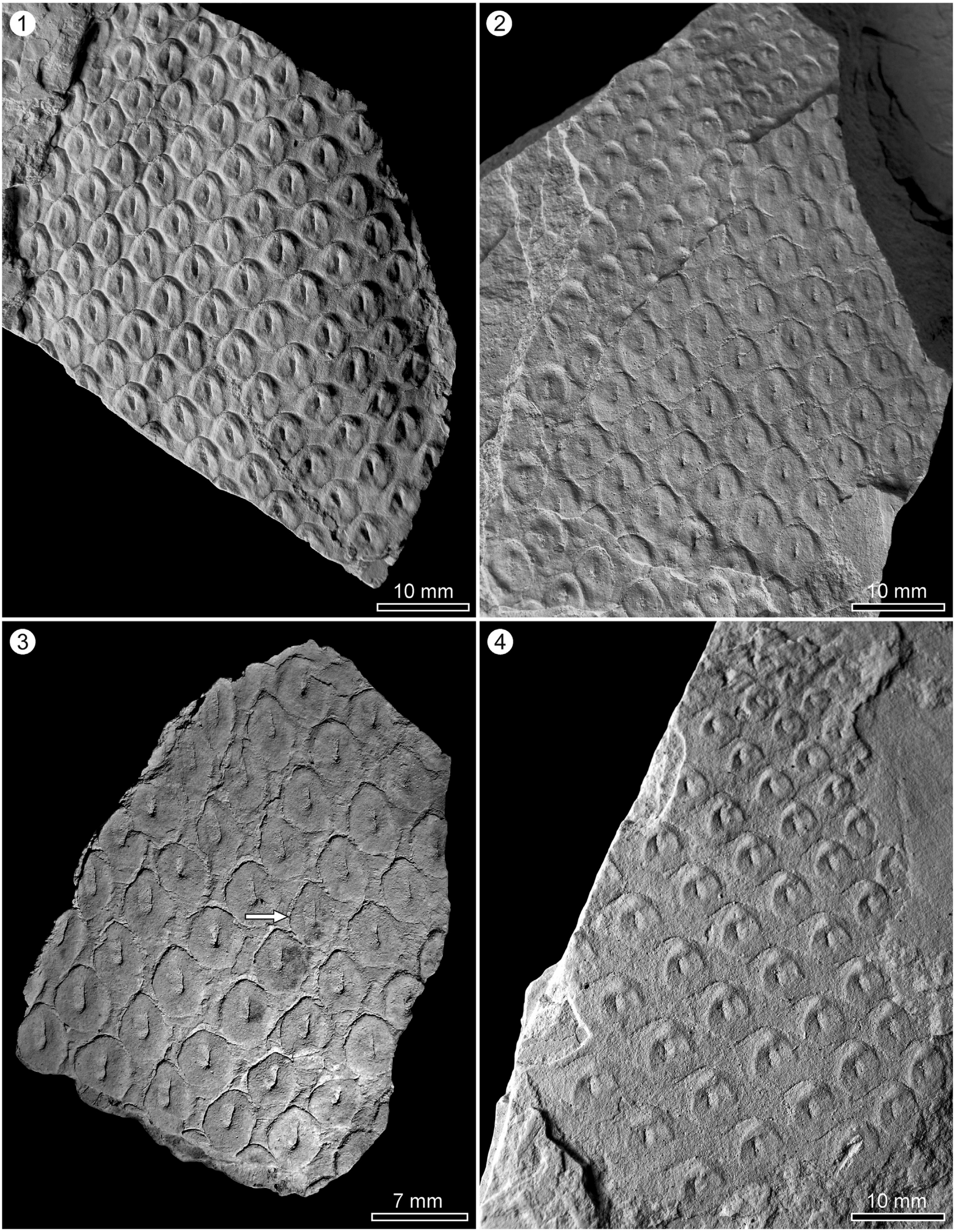

Plate V. *Azaniadendron fertile* Rayner. (1) Axis exhibiting oval leaf cushions. Specimen BP/2/16878. (2) Axis bearing oval cushions, and partially preserved as external mould. Specimen BP/2/16684. (3) Axis bearing oval cushions as well as a pyriform-like one (white arrow). Specimen BP/2/16723. (4) Axis showing widely spaced oval cushions. Note the decrease in their size from the base to the top of the axis. Specimen BP/2/16710.

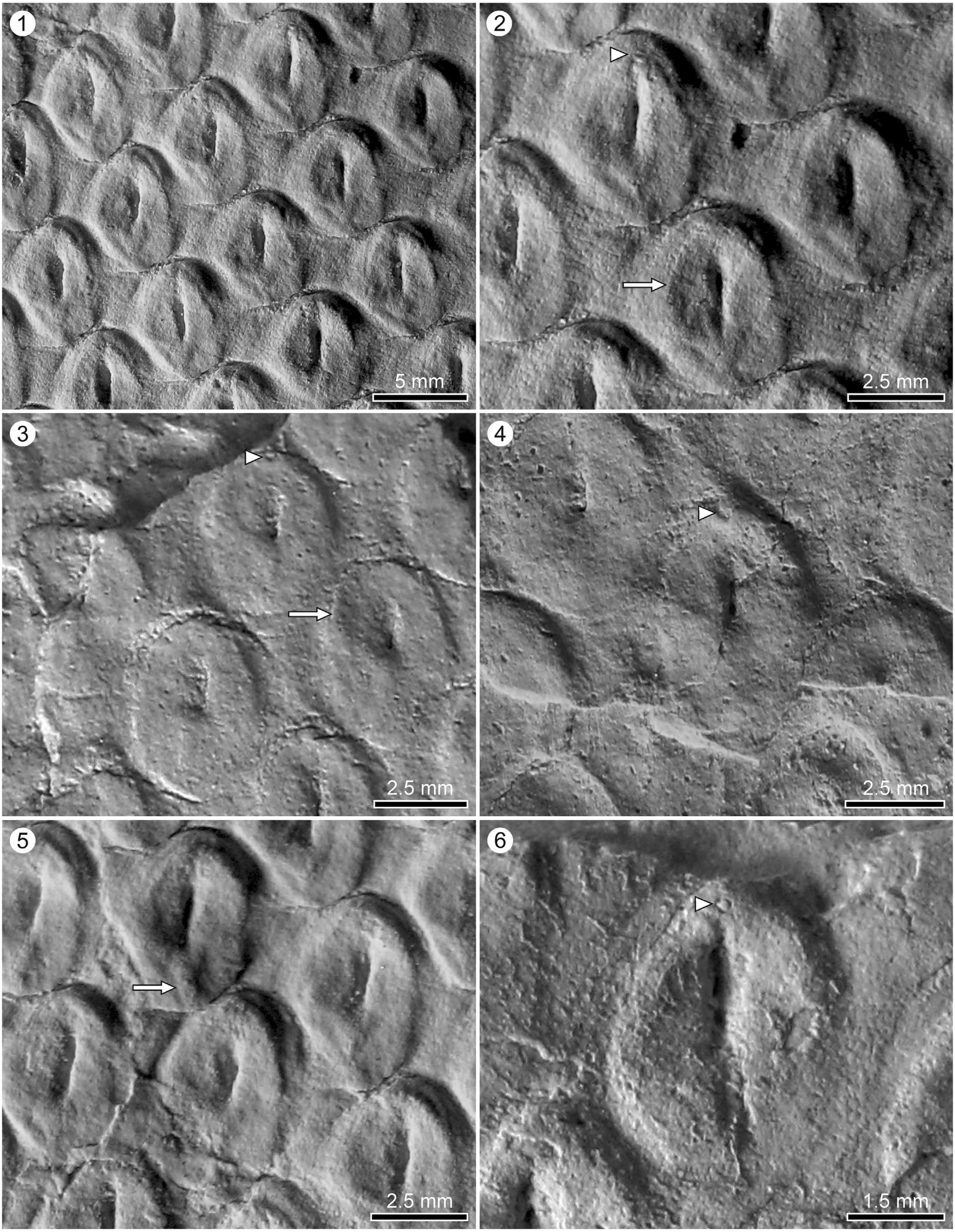

Plate VI. *Azaniadendron fertile* Rayner. (1) Detail of oval cushions. Specimen BP/2/16878. (2) Oval cushion with a large leaf scar (arrow), and another with ligule pit (arrowhead). Note the narrow elongated structure in the leaf scar. Specimen BP/2/16878. (3) Oval cushion with leaf scar (arrow) and another with ligule pit (arrowhead). Specimen BP/2/16684. (4) Oval cushion exhibiting ligule pit (arrowhead). Specimen BP/2/16684. (5) Cushions with asymmetrical outlines. Some bear a keel-like structure (arrow). Specimen BP/2/16878. (6) Oval cushion exhibiting ligule pit (arrowhead). Specimen BP/2/16604.

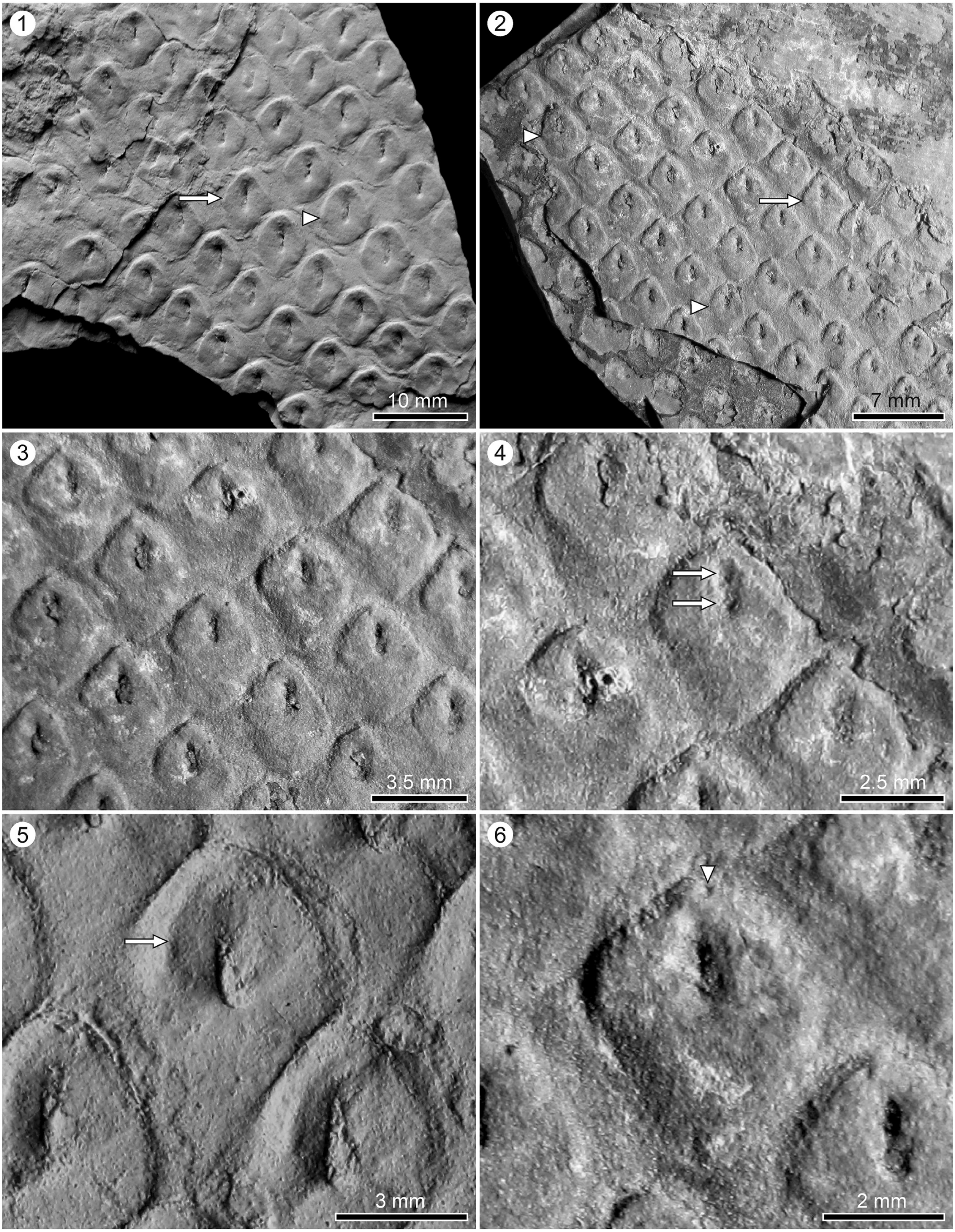

Plate VII. *Azaniadendron fertile* Rayner. (1) Axis exhibiting oval leaf cushions (arrowhead) and some with higher-than-wide rhomboidal shape (arrow). Specimen BP/2/16548. (2) Axis bearing a few oval cushions (arrowheads) and many higher-than-wide rhomboidal ones (arrow). Specimen BP/2/7366. (3) Detail of higher-than-wide rhomboidal cushions. Specimen BP/2/7366. (4) Cushion showing that the narrow and elongated structure in its centre seems to have been divided into two tissues (arrows). Specimen BP/2/7366. (5) Higher-than-wide cushion with large leaf scar (arrow). Note that the narrow and elongated structure is situated in the leaf scar. Specimen BP/2/16736. (6) Cushion with small notch at its top (arrowhead). Specimen BP/2/7366.

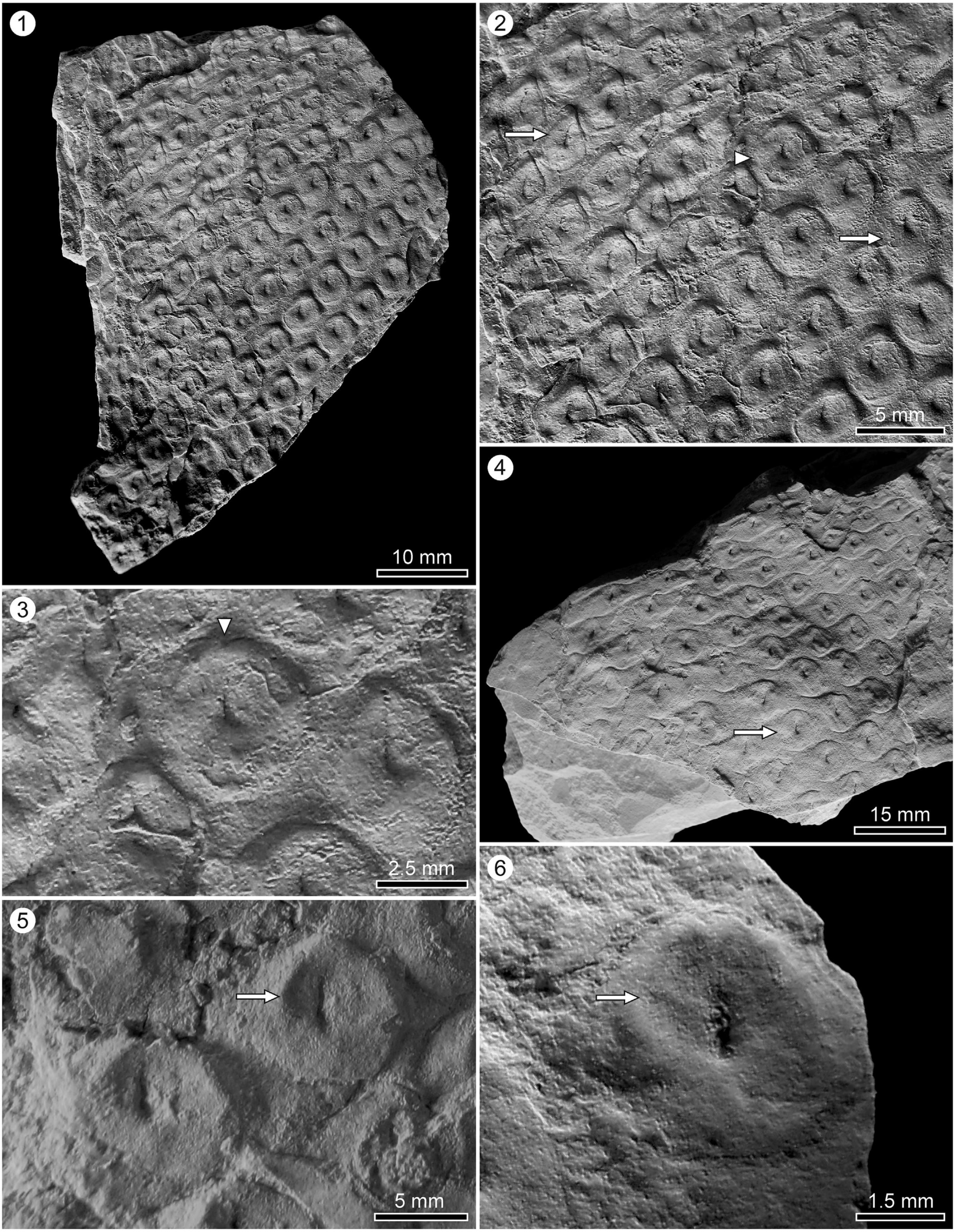

Plate VIII. *Azaniadendron fertile* Rayner. (1) Axis bearing circular and some oval cushions, showing a transition from those into pyriform-shaped ones. Specimen BP/2/16669. (2) Detail of specimen in 1 showing circular-like (arrowhead), oval (lower arrow), and pyriform cushions (upper arrow). (3) Circular cushion exhibiting small notch at its top (arrowhead). Specimen BP/2/16669. (4) Axis with circular-like cushions (arrow), showing a transition from those into laterally fused ones (upper part of the axis). Specimen BP/2/16690. (5) Cushion with large leaf scar (arrow). Specimen BP/2/16794. (6) Circular-like cushion with large leaf scar (arrow). Note the narrow and elongated structure in the leaf scar. Specimen BP/2/16812.

pseudowhorled pattern (Plate IX, 1–3). Sometimes, these pyriform cushions can have a more squat-like form, and these are 5.2–5.3 mm wide and 5.0–5.7 mm high (Plate X, 1 arrow). The outline of the leaf scar is not evident in these cushions. They lie within left-to-right parastichies of 123°–145° and right-to-left ones of 121°–130°. Usually, they are closely organized or very slightly spaced (Plate IX, 1).

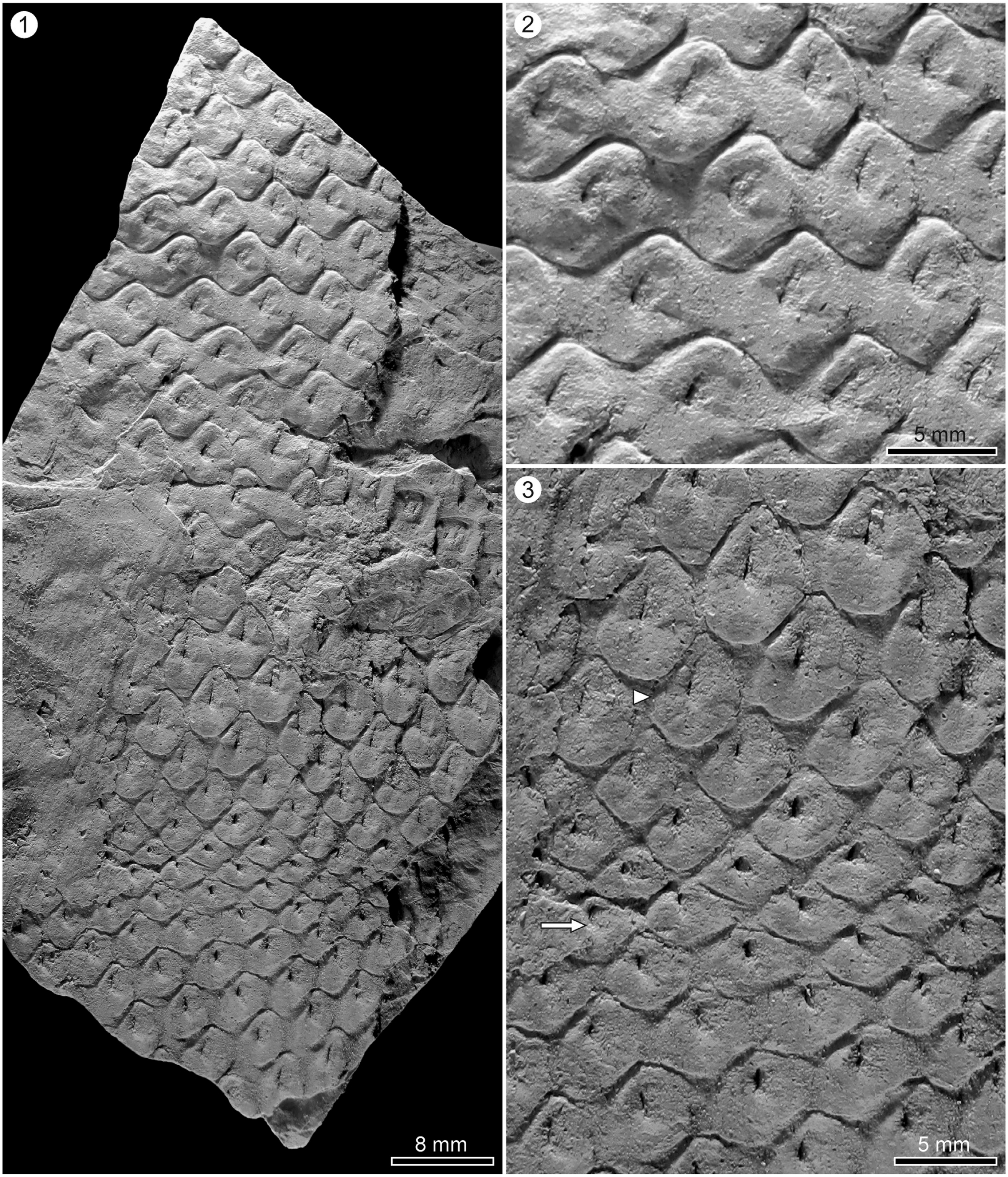

Plate IX. *Azaniadendron fertile* Rayner. (1) Axis covered by a zone of pyriform leaf cushions and also by cushions with very variable shapes and sizes. Specimen BP/2/16697. (2) Detail of the upper part of the axis in 1, showing cushions with more or less oval to rhomboidal shapes, which have a laterally fused appearance. (3) Detail of middle and lower parts of the axis in 1, showing pyriform cushions (arrowhead) above a zone of much smaller cushions (arrow), which increase in size again downwards.

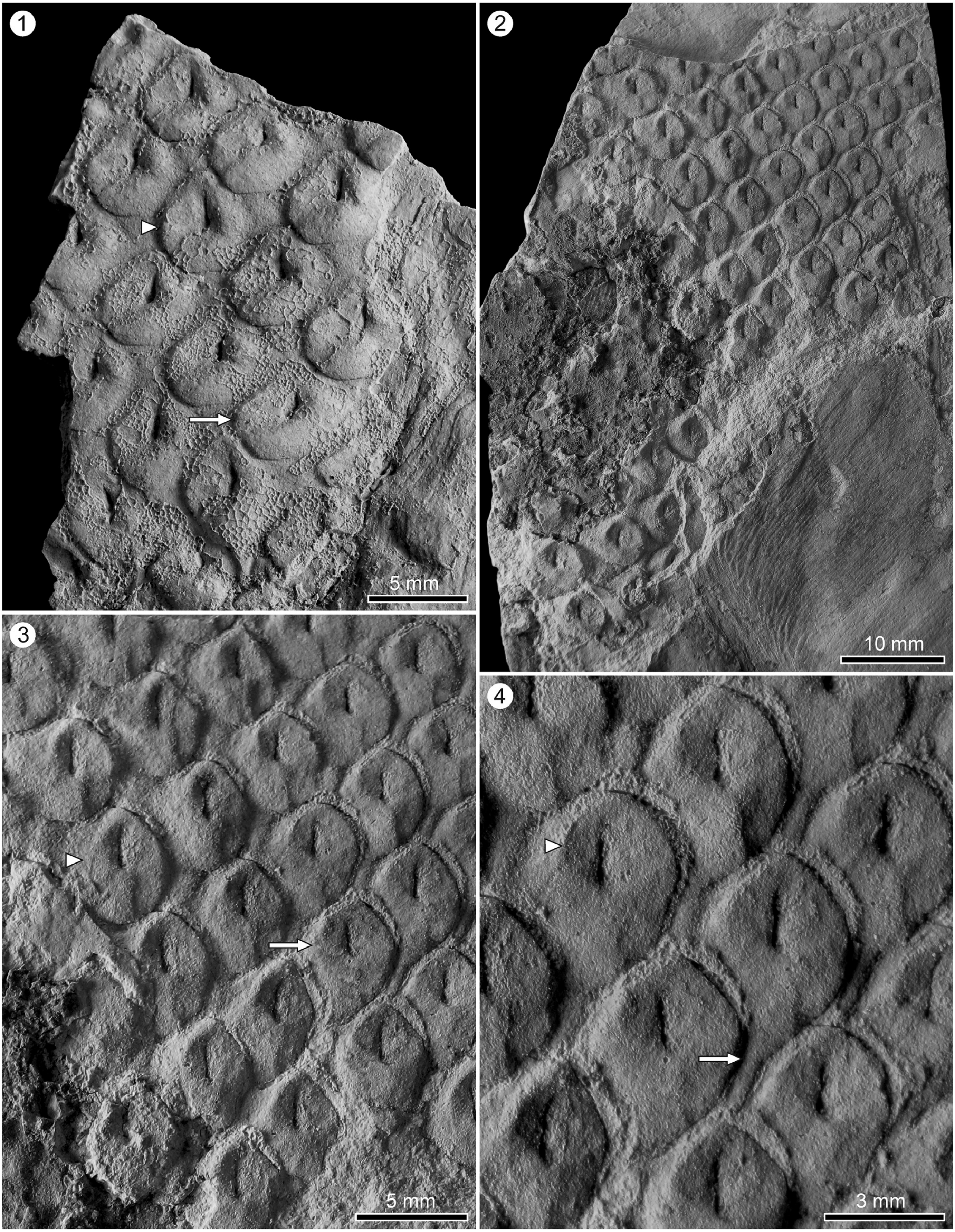

Plate X. *Azaniadendron fertile* Rayner. (1) Axis bearing a typical pyriform leaf cushion (arrowhead) and some with more squat pyriform shape (arrow). Specimen BP/2/16699. (2) Axis bearing oval (top-left of the image) and a few circular-like (bottom-left of the image) cushions, also showing drop-shaped cushions (top-right of the image). Specimen BP/2/16794. (3) Detail of specimen in 2, showing an oval cushion (arrowhead) and the inverted drop-like cushions (arrow). (4) Detail of the drop-like shaped cushions of specimen in 2, showing leaf scar (arrowhead) and a caudate-like extension in their lower part (arrow). Note that the narrow and elongated structure does not extend beyond the leaf scar. Specimen BP/2/16794.

● Inverted drop-shaped cushions (Fig. 6f): This type of cushion with an inverted drop-like shape was detected only in one specimen that also exhibits oval and circular-shaped cushions (Plate X, 2–3). The inverted drop-shaped cushions are 3.0–3.4 mm wide and 4.0–4.8 mm high and sometimes bear a caudate-like extension in their lower part (Plate X, 3–4 arrow). The leaf scars are well-defined, have more or less rhomboidal shapes, and are 1.7–2.2 mm wide and 1.8–2.0 mm high, covering almost the entire upper field of the cushion (Plate X, 3–4 arrowhead). In these cushions, it becomes clear that the narrow elongated and vertically structure visible in the centre all leaf cushions is situated within the leaf scar (Plate X, 4 arrowhead). They are arranged tightly, "squashing" against each other within left-to-right parastichies of 110° and right-to-lefts of 139° (Plate X, 2–3).

● Isodiametric-like rhomboidal cushions (Fig. 6g): One axis shows a transition from higher-than-wide rhomboidal cushions into ones with an almost isodiametric-like rhomboidal shape (Plate XI, 1–2). This cushion type also occurs associated with oval and pyriform to bell-shaped cushions (Plate XI, 3–5). The isodiametric-like rhomboidal cushions are 3.2–4.2 mm wide and 3.2–4.5 mm high. They form left-to-right parastichies of 125–146° and right-to-left ones of 114–155°. The narrow and elongated depression in their centre is sometimes more reduced (Plate XI, 2). The leaf scar is not evident in most of them, but in some, we detected a smooth mark that may be the leaf abscission area (Plate XI, 6 arrow).

● Wider-than-high rhomboidal cushions (Fig. 6h): Many defoliated axes bear laterally elongated wider than high cushions. These have a more or less rhomboidal outline and variable size, ranging from 4.6–12.0 mm wide and 1.7–5.8 mm high (Plate XII, 1–2; Plate XIII, 1–4). Some specimens show transitions between other cushion types and those. One axis, for instance, exhibits cushions with a basic oval-like shape, grading laterally into wider-than-high rhomboidal ones (Plate XII, 1; Fig. 7). Other specimens show wider-than-high rhomboidal cushions associated with pyriform-like and isodiametric-like rhomboidal ones (Plate XII, 2; Plate XIII, 1–2; Fig. 7). The wider-than-high cushions form left-to-right parastichies of 138–166° and right-to-left ones of 131–160° (Plate XII, 1–2; Plate XIII, 1). They are close or more loosely arranged within the parastichies. The narrow and elongated depression in their centre is sometimes more reduced (Plate XIII, 3). Leaf scars occur in some of them and are 1.2–3.4 mm wide and 1.4–3.0 mm high, with a rounded rhomboidal-like outline, covering almost the entire central part of the cushion (Plate XIII, 4 arrow).

Overview of the leaf cushion epidermis: Rayner (1986) described the leaf cushion epidermal tissue in detail. The epidermis lack stomata and consist of isodiametric to irregular-elongate cells (Rayner, 1986, pl. I, 8–9, pl. II, 2–5). Epidermal cells are narrow and elongated near leaf scars, where the cuticle covering some of them shows small perforations (Rayner, 1986, pl. II, 4–5).

Comparison and systematics: *Azaniadendron* is a member of Lycopsida (Lycopodiopsida); it has sporangia borne in the axil of sporophylls (Taylor et al., 2009). Characters such as leaf cushions, ligula, and heterospory suggest that the genus has affinities with Isoetales (e.g., Meyen, 1987; DiMichele and Bateman, 1996; Pigg, 2001). Both heterospory and a ligule also occur in Selaginellales, but all known living and extinct members of this order are exclusively small herbs (Taylor et al., 2009). Based on the available evidence, we hypothesise that *Azaniadendron* could belong to the Isoetales. One of the key characters of Isoetales is secondary growth (DiMichele and Bateman, 1996), found even in the small *Isoëtes* (Stokey, 1909). Unfortunately, the lack of anatomically preserved fossils precludes testifying if *Azaniadendron* produced secondary tissues.

Azaniadendron differs from "lepidodendralean" isoetaleans belonging to Sigillariaceae, Diaphorodendraceae, and Lepidodendraceae. Members of these families bore monosporangiate cones and are more derived than isoetaleans with bisporangiate fertile structures (Bateman et al., 1992; DiMichele and Bateman, 1992, 1996). Therefore, *Azaniadendron* belongs to, or descends, from a group of less derived lycopsids. Among those, the genus resembles sub-arborescent taxa such as *Omphalophloios* White (= *Sporangiostrobus* Bode; Brousmiche-Delcambre et al., 1995) from the Pennsylvanian of Euramerica (e.g., Opluštil et al., 2019), and Iberian terrains (e.g., Wagner and Álvarez-Vázquez, 2010).

Omphalophloios/*Sporangiostrobus* has been placed in different family concepts including Chaloneriaceae (Pigg and Rothwell, 1983b; Looy et al., 2021), Sporangiostrobaceae (Bek et al., 2015; Opluštil et al., 2019), or Isoetaceae *sensu lato* (*sensu* DiMichele and Bateman, 1996). *Azaniadendron* shares several aspects with the *Omphalophloios* plant. Both were ligulate, had leaf cushions with leaf scars lacking convincing evidence of two parichnos scars, and robust bisporangiate fertile axes bearing leaf-like sporophylls (cf. Wagner, 1989; Brousmiche-Delcambre et al., 1995; Opluštil et al., 2010; Bek et al., 2015). However, *Omphalophloios* produced densospores microspores and coronate megaspores (Bek et al., 2015; Opluštil et al., 2010, 2019).

At this point, we classify *Azaniadendron* as a potential less derived *incertae sedis* isoetalean. Attempts to include it in a family would be provisional due to the limited set of characters available in its fossils (e.g., unknown rooting system and growth architecture), which prevents any well-supported phylogenetic hypothesis. We avoid placing the genus in the Lycopodiopsidaceae concept (*sensu* Chaloner and Boureau, 1967), which is still frequently used to classify Gondwanan sub-arborescent lycopsids (e.g., Mune et al., 2012; Spiekermann et al., 2018; Carvalho et al., 2022). Two of the characters used to unite taxa in this family are deeply plesiomorphic in Lycopsida (spirally arranged leaves and presence of leaf cushions) and of little suprageneric weight. The other (absence of cones) has systematic value but also occurs in members of Chaloneriaceae or Isoëtaceae *sensu lato* (Pigg and Rothwell, 1983a; DiMichele and Bateman, 1996). Moreover, among taxa placed in Lycopodiopsidaceae by some authors to date (e.g., Chaloner et al., 1979; Rayner, 1985, 1986), reproductive structures are known only from *Cyclodendron* and *Azaniadendron*. Unlike *Azaniadendron*, fertile areas of *Cyclodendron* are interpreted as monosporangiate (Rayner, 1985). We also avoid erecting a new family name, such as the still unpublished Azaniodendraceae, to classify the genus for the reason stated above.

Rayner (1986) stressed the differences between *Azaniadendron* and selected Palaeozoic taxa from Gondwana and Angara. Some of those, such as *Angarophloios* Meyen (1972), *Bumbudendron* Archangelsky et al. (1981), and *Ufadendron* Naugolnykh (2014) exhibit the so-called infrafoliar bladders. In *Ufadendron*, for instance, the infrafoliar bladders resemble the narrow and elongated depression visible in the centre of *Azaniadendron's* cushions. However, this depression in *Azaniadendron*'s leaf cushions is situated within a not always evident large leaf scar and had an intrafoliar position. Before the genus *Azaniadendron* was established, some South African axes from the Permian belonging to it were assigned to *Lycopodiopsis* (e.g., Lemoigne and Brown, 1980a). Among the variety of *Azaniadendron* cushions, its isodiametric-like rhomboidal ones are similar to those of *Lycopodiopsis* specimens from Brazil (cf. Steinmann, 1924; Faria et al., 2009). The narrow and elongated structure conspicuous in the centre of all *Azaniadendron* cushions, and its large but not always evident leaf scars, may represent useful characters to differentiate the leaf cushions of both taxa. Further comparisons are not possible, as *Lycopodiopsis* is based also on anatomical details of permineralized axes (cf. Renault, 1890; Faria et al., 2009) and its reproductive structures remain unknown.

4. Discussion

4.1. General remarks on the plant

Rayner (1986) interpreted *Azaniadendron fertile* as an arborescent lycopsid based on the size of its axes. If our hypothesis that the genus belongs to Isoetales is correct, *Azaniadendron fertile* may have been "technically" arborescent as secondary growth is a synapomorphy of

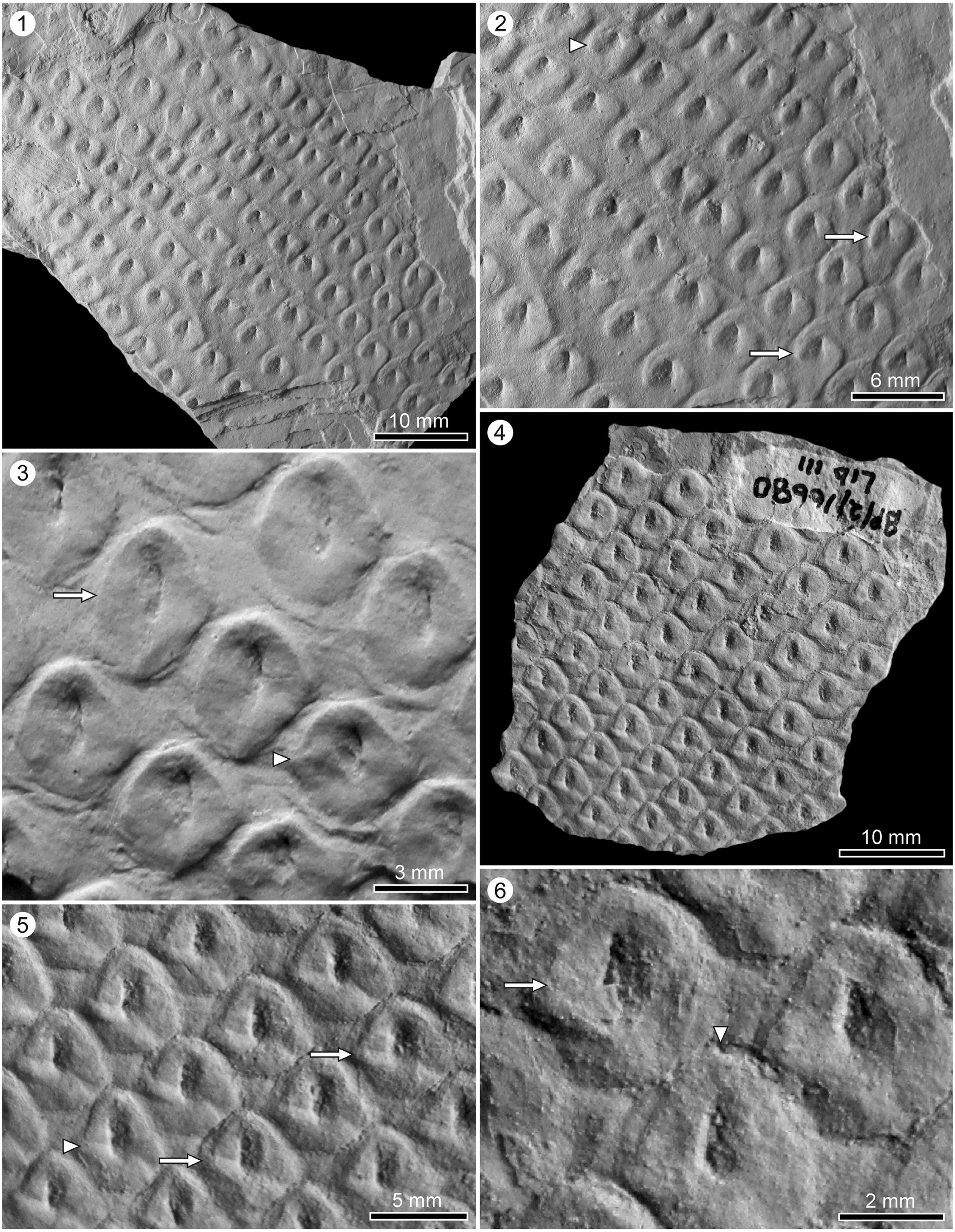

Plate XI. *Azaniadendron fertile* Rayner. (1) Axis showing a transition from higher-than-wide rhomboidal cushions into isodiametric-like rhomboidal ones. Specimen BP/2/16715. (2) Detail of fossil in 1, showing higher-than-wide rhomboidal cushions (arrows) and isodiametric-like rhomboidal ones (arrowhead). Note that some cushions are widely laterally spaced. (3) Detail of axis exhibiting isodiametric-like rhomboidal cushions (arrowhead) and oval ones (arrow). Specimen BP/2/16548. (4) Axis exhibiting mainly rounded, isodiametric-like rhomboidal cushions. Specimen BP/2/16680. (5) Detail of fossil in 4, showing isodiametric-like rhomboidal cushions (arrows) and some with a pyriform shape (arrow). (6) Detail of isodiametric-like rhomboidal cushions, showing one with leaf scar (arrow) and another with small notch at its top (arrowhead). Specimen BP/2/16680.

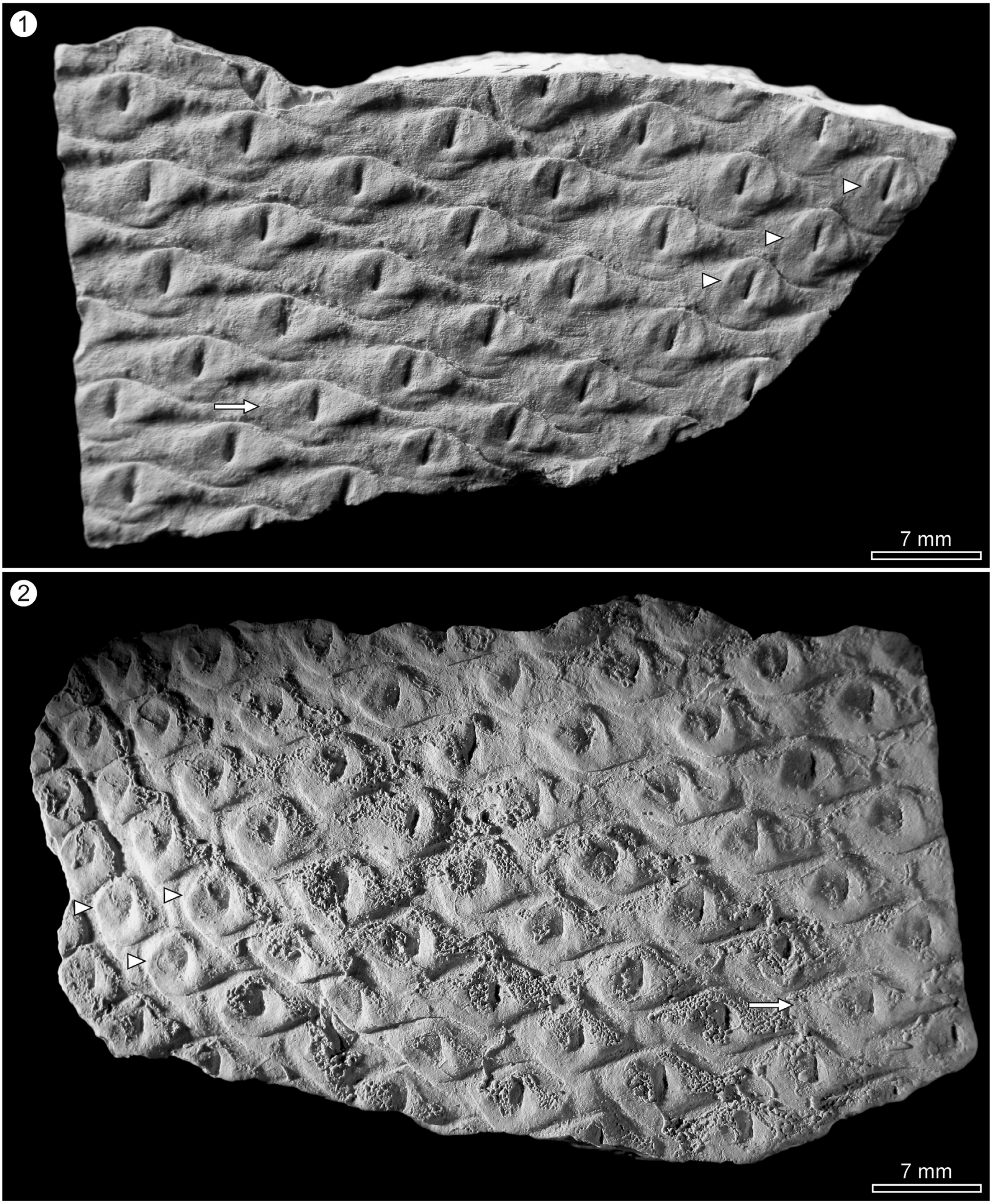

Plate XII. *Azaniadendron fertile* Rayner. (1) Axis bearing cushions with an essentially oval shape (arrowheads) and also cushions with a wider-than-high rhomboidal outline (arrow). Specimen BP/2/16875. (2) Axis showing isodiametric-like rhomboidal cushions (arrowheads) and wider-than-high rhomboidal cushions (arrow). Specimen BP/2/21545.

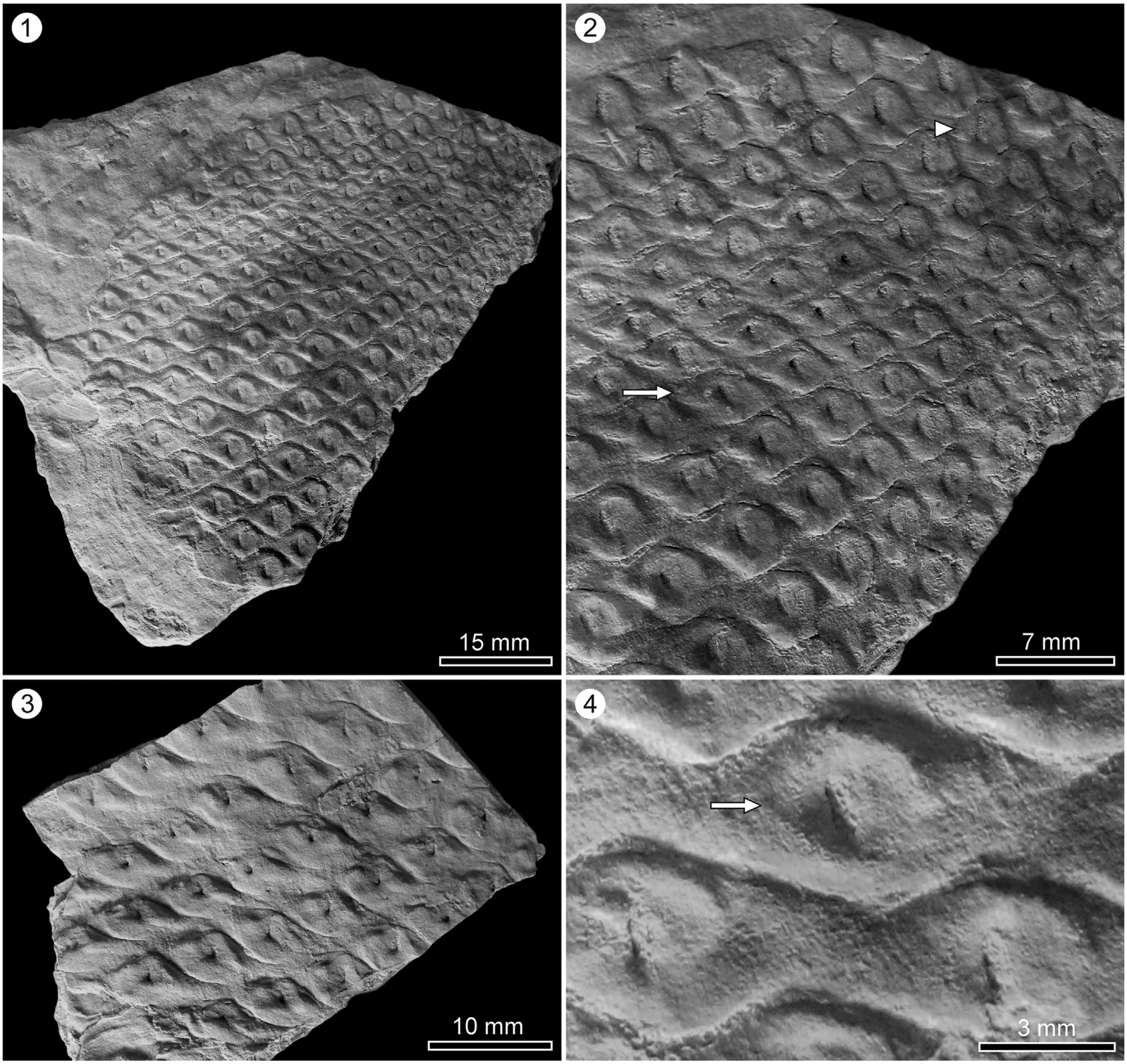

Plate XIII. *Azaniadendron fertile* Rayner. (1) Axis bearing mainly wider-than-high rhomboidal leaf cushions. Specimen BP/2/16691. (2) Detail of specimen in 1, showing a pyriform shaped cushion (arrowhead) and wider-than-high rhomboidal ones (arrow). (3) Axis bearing wider-than-high rhomboidal cushions. Note the reduced size of the depression in their centre. Specimen BP/2/16701. (4) Wider-than-high rhomboidal cushion exhibiting large leaf scar (arrow). Specimen BP/2/16691.

this order (DiMichele and Bateman, 1996). However, there is no evidence that it was a tall arborescent plant such as those found in the lepidodendrids. Based on its potential affinities with less derived isoëtaleans such as *Omphalophloios*, it may have been a smaller modest form with a sub-arborescent size. Due to the fragmented state of its fossils, at the moment, it is only possible to state that *A. fertile* was far more robust than *Selaginella* Beauvoir or *Isoëtes*-like growth forms.

Despite not always apparent, the leaf cushions covering the defoliated axes exhibit leaf scars. Most of these defoliated axes possibly represent proximal or middle parts of the mature plant where leaves already had abscised. An intriguing feature of these leaf cushions is the ubiquitous narrow, elongated, vertically oriented depression situated in their centre. Rayner (1986) interpreted this whole central structure as a vascular bundle scar. Our data show that this structure lies within a not always evident leaf scar. Therefore, it was an intrafoliar structure, and at least part of it indeed may correspond to a vascular bundle scar.

We identified broad and narrow fertile axes of *Azaniadendron*. The sporangia borne on the narrow axes yielded well-developed *in situ* spores (Rayner, 1986, pl. III, 6–7). This indicates that sporangia on these thin fertile axes already had reached a sporogenesis state. Therefore, immaturity does not explain why these particular fertile axes are considerable narrower than the broad fertile axis. The relatively broad sporophyll-bearing axis has an undifferentiated vegetative-like morphology, unlike the typical thin axes of lycopsid cones (e.g., Bonacorsi and Leslie, 2019). It seems most likely that sporophylls have formed fertile areas on different parts or types of unspecialised axes rather than determinate organs like cones. The narrow fertile axes probably occupied more distal parts of the plant. The broader one possibly had an

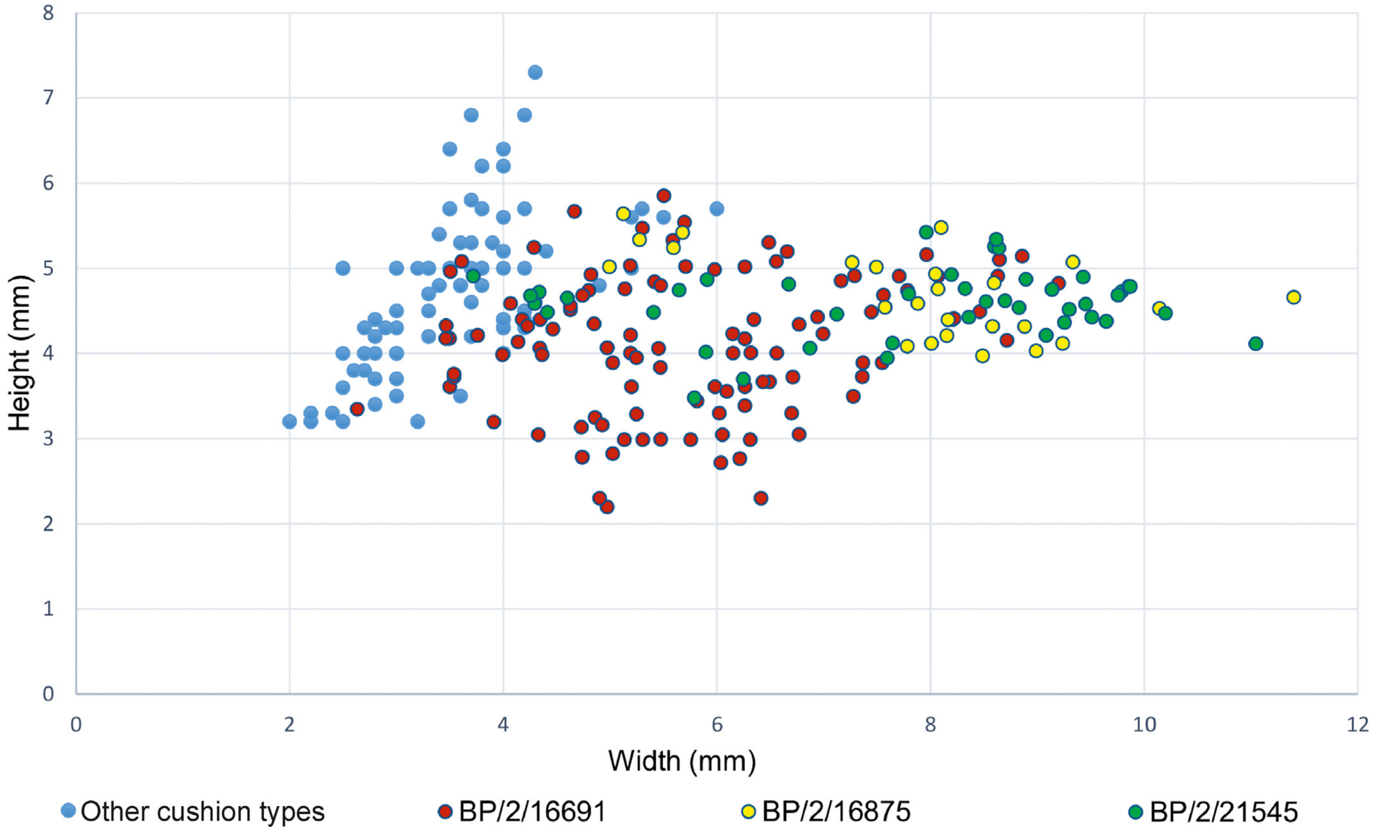

Fig. 7. Scatter diagram showing the width × height of all leaf cushions of three selected specimens (BP/2/16691; BP/2/16875; BP/2/21545), which exhibit mainly wider-than-high but also typical *Azaniadendron fertile* leaf cushions. The leaf cushion geometries in these three specimens are compared with the other *A. fertile* cushions in this diagram.

aerial position, but its exact place within a shoot remains unknown due to its fragmentary preservation. We did not detect reliable evidence of vegetative leaves in the specimens or may have overlooked them due to their poor preservation and possible similarity with the leaf-like sporophylls. Rayner (1986) mentions microphylls, but it is not clear whether he was referring to the leaf-like sporophylls or vegetative leaves. Sporophylls with a simple leaf-like appearance could represent a primitive state, and also occur in taxa such as *Lepidodendropsis* Lutz and *Pinakodendron* Weiss, which bore fertile areas or zones on unspecialised axes rather than compact cones (Chaloner and Boureau, 1967; Phillips, 1979).

4.2. Remarks on the spores

As suggested by Glasspool (2003a), the megaspores recovered from *Azaniadendron fertile* resemble *Sublagenicula turnaui* (Dijkstra) Dybová-Jachowicz et al. Specimens of *S. turnaui* do not exhibit a well-expressed subgula and sometimes it is difficult to distinguish this structure from the trilete rays (Glasspool, 2003a). This dispersed megaspore taxon, reported from some Vryheid Formation coal beds in South Africa (Dijkstra, 1972; Glasspool, 2003a, 2003b), seems to be restricted to this formation.

The microspores of *Azaniadendron fertile* have been assigned to different dispersed spore taxa. Rayner (1986) compared them with the miospore genera *Lycospora tritriangularis* Hart and *Zinjisporites congoensis* Maheshwari & Bose. According to Balme (1995), *Indotriradites* Tiwari is the most appropriate taxon for these microspores. However, more recently they have been placed in *Lycospora* Schopf et al. (Bek, 2012, 2017). Further analyses of these spores, which were not the aim of this morphological study, using modern palynological approaches may provide a better understating of their morphology, allowing more conclusive comparisons with dispersed spore taxa.

4.3. Leaf cushion variability

One of the most notable aspects of the *Azaniadendron fertile* defoliated fossils is the variable shapes of their leaf cushion. What essentially varies is their outline, as all of them bear the same characters, especially the narrow, elongated, and vertically oriented structure preserved in their centre. The latter, situated in a not always evident leaf scar, can be homologised throughout all different leaf cushion shapes. Many fossils exhibit transitions between such different cushion shapes, indicating that they belonged to one taxon. We included the specimens studied here in *A. fertile*, rather than splitting them into different fossil taxa. As pointed out by Cleal et al. (2016), the outcome of using such a taxonomic approach will still be a fossil taxon but may represent far more the organism that yielded such different leaf cushions shapes. This does not apply only to variations formed at the time when the plant was alive and functioning, but also to the range of morphologies its remains can display after having undergone variable decay before preservation.

The defoliated axes seem to show the same fracture planes, and the splitting of the host rock does not explain all the different leaf cushion types occurring throughout short distances. It seems unlikely that the random association of several distinct cushions geometries in an individual fossil in a very short distance represents variations resulting from a growing determinate meristem when the plant was alive and functioning. In our interpretation, it is more realistic that the random association of leaf cushions with distinct geometries resulted from taphonomical-induced changes. In the case of the oval, circular-like, pyriform, inverted drop-shaped and higher-than-wide to isodiametric-like rhomboidal cushions, these taphonomical changes may have included post-mortem decay and taphonomical/diagenetic distortion of a basic shape. The degree of decay resulting in decortication was not so advanced to the point that the cushions lost their morphological features. Many impressions from West Driefontein, which exhibit the largest variety of cushion shapes, show a considerable degree of distortion (e.g., Plate I, 1; Plate VIII, 4; Plate IX, 1), which may have played a key role in the formation of the different cushion geometries. Elucidating all transformations that the surface of *Azaniadendron* fossils may have experimented due to taphonomy, and defining the sequence from the presumed most to less pristine leaf cushion preservational state, remains problematic and requires more completely preserved specimens where variations in the external surface can be seen over the course of a larger distance. Regardless of what was or not the most pristine state of these cushions, documenting their variations for fossils belonging to a single taxon remains important. Found isolated they could eventually lead to new names, taxonomical confusions, and inflation of species numbers.

The wider-than-high cushions are somewhat distinct from the other types. Rayner (1986) figured two cushion types in his paper (ovals, and wider-than-high ones) and assigned both to *Azaniadendron fertile*. Despite having a different outline, they exhibit all *A. fertile* characters, especially that narrow elongated structure in their centre that characterize all other cushions of the taxon. Further, some specimens show transitions/overlapping between other typical *Azaniadendron* cushions and these wider-than-high ones (Plate XII, 1–2; Plate XIII, 1–2; Fig. 7). At the moment, we agree with Rayner's (1986) interpretation and maintain these wider-than-high forms placed in *A. fertile* as there is no evidence to justify the proposal of a new taxon. The gradational reduction in cushion size, resulting in some wider-than-high shapes (e.g., Plate XIII, 1–2), could reflect variations in the plant growth rate (e.g., Wnuk, 1985; Cleal et al., 2016). They probably represented vegetative areas rather than sporophyll-bearing ones, since leaf cushions preserved on fertile axes exhibit oval and higher-than-wide shapes.

4.4. Ligule in sub-arborescent lycopsids from the Glossopteris flora

Most sub-arborescent to arborescent lycopsid remains from the *Glossopteris* flora have been traditionally interpreted to lack evidence of ligules (e.g., Kräusel, 1961; Chaloner and Boureau, 1967; Rayner, 1986; Cariglino et al., 2012; Spiekermann et al., 2018). Exceptions include a few defoliated axes from the Permian of Vereeniging (Leeukuil Quarries? South Africa), considered ligulate and placed in *Lycopodiopsis* Renault (Lemoigne and Brown, 1980a). However, it seems possible that at least some of those assumed ligulate *Lycopodiopsis* axes were interpreted and figured upside down. If rotated by 180°, leaf cushions covering them become identical to those of *Azaniadendron* (Lemoigne and Brown, 1980a, pl. 1, 2–3), and their assumed ligule pit would be situated below the leaf scar, representing something else. Cuticles mentioned as also coming from *Lycopodiopsis* leaf cushions from Vereeniging provide evidence of ligule (Lemoigne and Brown, 1980a, pl. 2, 1–2). However, it was not explicitly mentioned from which exact specimen(s) they were recovered, and is somewhat unclear what the cushion type that yielded such cuticles looked like. Fossils from Vereeniging are typically preserved as impressions, lacking cuticles (Anderson and Anderson, 1985).

The presence of a ligule in *Lycopodiopsis* remains somewhat problematic. No convincing evidence has been found so far in the other sub- to arborescent taxa from the *Glossopteris flora,* such as *Brasilodendron* Chaloner et al., and *Cyclodendron* Kräusel (Kräusel, 1961; Chaloner et al., 1979; Spiekermann et al., 2018). *Bumbudendron*, also reported in South American Permian beds, lacks evidence of this structure too (Cariglino et al., 2012). However, the evidence for ligule pit reported here no longer supports the presumed eligulate nature of *Azaniadendron*. Ligules can be obscured by several factors, such as ontogeny, taphonomy, fracture plane, and quality of preservation (e.g., Meyen, 1972; Gensel and Pigg, 2010), and are not preserved in every single *Azaniadendron* leaf cushion. In many cases, even well-preserved impressions and compressions of undoubtedly ligulate taxa such as *Lepidodendron* Sternberg and *Sigillaria* Brongniart often lack clear evidence of ligule (Chaloner, 1968). Our evidence in support of the presence of a ligule helps to hypothesise the systematic position of *Azaniadendron* at an ordinal level, showing that it was not an unusual heterosporous, presumed eligulate lycopsid.

4.5. Azaniadendron in space and time

To date, *Azaniadendron fertile* is the only described species of its genus. Convincing evidence of macrofossils belonging to the taxon is known only from South Africa. All the specimens included in the synonymy list come from South Africa, and seem to have been collected from Vryheid Formation beds at the quarries studied here or nearby areas within the current territory of the Gauteng Province (e.g., Anderson and Anderson, 1985; Lemoigne and Brown, 1980a, 1980b). According to the available data, the strata from the studied quarries are assigned to the Guadalupian. Little can be said about the autecology of *A. fertile*, as taphonomical and sedimentological information from the quarries where specimens were collected is limited. By analogy with other Palaeozoic heterosporous lycopsids (e.g., Phillips, 1979), it seems likely that the plant lived in or adjacent to wet areas within the fluvio-deltaic and peat-forming system, postulated for the Vryheid Formation and its equivalents.

Data availability

All fossils used in this investigation are stored and available for studies in the Fossil Herbarium of the Evolutionary Studies Institute at the University of the Witwatersrand, Johannesburg, South Africa.

Declaration of Competing Interest

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

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Publication 3

Small but not trivial: Nothostigma sepeensis sp. nov., a lycopsid from the Cisuralian (early Permian) of the Paraná Basin, Brazil

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R. Spiekermann: author position, 1; scientific ideas, 85%; data generation 70%; analysis and interpretation, 90%; paper writing, 90%.
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Small but not trivial: *Nothostigma sepeensis* sp. nov., a lycopsid from the Cisuralian (early Permian) of the Paraná Basin, Brazil

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ABSTRACT

This study deals with lycopsid axes from Cisuralian strata of the São Sepé outcrop in southern Brazil, belonging to the *Glossopteris* flora. Their gross morphology is described using standard palaeobotanical techniques. They lack cuticles, but the description is complemented using vinyl polysiloxane replicas of their leaf cushions, which reveal imprints of their epidermal features under the scanning electron microscope. The specimens are distinct from other lycopsid fossil-taxa found so far in Permian post-glacial strata including elements of the *Glossopteris* flora. They resemble *Nothostigma* Doweld, a common fossil-genus of lycopsids that flourished in Gondwana during the Mississippian pre-glacial stage. Based on their morphology, we propose the new fossil-taxon *Nothostigma sepeensis* sp. nov., increasing the knowledge of the so far often neglected lycopsid diversity from the Permian of Gondwana.

1. Introduction

Once the southern ice sheets contracted during the Permo-Carboniferous (e.g., Griffis et al., 2019), lycopsids thrived in Permian post-glacial terrains from western Gondwana as part of the *Glossopteris* flora (e.g., Anderson and Anderson, 1985; Guerra-Sommer et al., 1995; Spiekermann et al., 2020). Their macrofossils are known from a fair number of Cisuralian and Guadalupian post-glacial assemblages, mainly from South Africa and South America (e.g., Kräusel, 1961; Rayner, 1986; Jasper and Guerra-Sommer, 1998; Cariglino et al., 2012; Manfroi et al., 2012; Spiekermann et al., 2018, 2020; Carvalho et al., 2022; Mottin et al., 2022). Most of them belonged to assumedly sub-arborescent to arborescent forms, which form the basis of fossil-genera such as *Lycopodiopsis* Renault (1890), *Cyclodendron* Kräusel (1928), *Brasilodendron* Chaloner et al. (1979), and *Azaniadendron* Rayner (1986). Reports of macrofossils interpreted as herbaceous lycopsids are rare in these strata in western Gondwana but include *Lycopodites riograndensis* Salvi et al. (2008), a fossil-species known only from a single locality in Brazil.

In India and Australia, once part of eastern Gondwana, lower Permian strata yielded few fragments of lycopsid axes and leaves lumped in *Cyclodendron* (e.g., Rigby, 1966; Chandra and Rigby, 1981; Beeston, 1990; Goswami et al., 2006). The lower Permian beds of Australia were also the source of the almost entirely preserved taxon *Selaginella harrisiana* Townrow (1968). More recently, macrofossils interpreted as herbaceous lycopsids were described from Guadalupian and Lopingian deposits of Antarctica. The Guadalupian specimens were placed in *Paurodendron* Fry (McLoughlin et al., 2015), and those from the Lopingian formed the basis of the fossil-genera *Collinsonites* Schwendemann et al. (2010) and *Collinsonostrobus* Ryberg et al. (2012).

Overall, lycopsid macrofossils are far less common in Permian strata from eastern than western Gondwana (McLoughlin et al., 2015). However, dispersed micro- and megaspores, potentially belonging to them, are common and relatively diversified in many Permian assemblages from both parts of the palaeocontinent, suggesting that the southern lycopsid macrofossil record of this period is somewhat biased (e.g., Cauduro and Zingano, 1965; Wilder, 1980; Glasspool, 2003a, 2003b; Tewari and Jha, 2007; Tewari, 2008). Here we describe in detail lycopsid axes from the Cisuralian strata from the São Sepé outcrop in southern Brazil. Their morphology is distinct from typical lycopsid fossil-genera described so far from Permian post-glacial deposits bearing

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remains of the *Glossopteris* flora. However, they resemble lycopsids that thrived in Gondwana during a much older, Mississippian pre-glacial stage. We place them in the fossil-genus *Nothostigma* Doweld (2017) and, based on their morphology, propose the new taxon *Nothostigma sepeensis* sp. nov.

2. Material and methods

Four fragments of plant axes form the basis of this study. They correspond to remains of casts (with leaf cushions standing in positive relief) and external moulds (with leaf cushions appearing in negative relief). The specimens come from the São Sepé outcrop (Fig. 1), situated in the municipality of São Sepé in the Rio Grande do Sul State, southern Brazil (Bortoluzzi and Veiga, 1981; Simões, 1992).

2.1. *Locality and source strata*

The São Sepé outcrop lies within the Paraná Basin (Fig. 1), a large Palaeozoic–Mesozoic basin located in the central-eastern part of South America (Milani et al., 1998). The outcrop rests unconformably on a granitic basement (Bortoluzzi and Veiga, 1981). Its strata include arcosic conglomerates, massive grey-coloured siltstones, and fine-grained sandstones with wavy, horizontal, or hummocky cross-bedding (Simões, 1992). Fine-grained coquinoid sandstones containing abundant bivalve shells also occur at the locality (Simões, 1992). The bivalves identified in the outcrop were assigned to marine taxa (Simões, 1992; Simões et al., 1998).

The studied specimens come from the grey-coloured siltstones of the outcrop, which are highly silicified and remarkably hard (Bortoluzzi and Veiga, 1981). They are associated with other lycopsid remains of hitherto uncertain generic affinities, impressions of *Noeggerathiopsis* Feistmantel and *Glossopteris* Brongniart leaves (Bortoluzzi and Veiga, 1981), as well as charcoalified wood fragments (*sensu* Scott, 2010), detected and figured here for the first time (Fig. 2a–d), indicating the occurrence of palaeo-wildfires. These siltstones also yielded a diversified palynological assemblage, including dispersed megaspores, miospores, and pollen grains (Cauduro and Zingano, 1965; Cauduro, 1970).

The outcrop was first assigned to the Rio Bonito Formation (Fig. 3) of the Paraná Basin (Zingano and Cauduro, 1959; as cited in Bortoluzzi and Veiga, 1981). After subsequent studies, its strata have been interpreted to belong to the Palermo Formation of the same basin, based on their palynological content and lithological correlations (Bortoluzzi and Veiga, 1981; Simões, 1992). Here we follow these latter studies, maintaining the interpretation that the São Sepé outcrop should be assigned to the Palermo Formation. This lithostratigraphic unit exhibits a transgressive trend, and its sediments have been deposited mainly in shallow marine settings (e.g., Milani et al., 2007; Holz et al., 2010). Except for isolated outcrops such as São Sepé, in other parts of the Paraná Basin, the Palermo strata (Fig. 3) lie below the Irati Formation and overlay conformably or interfinger laterally with the upper part of the Rio Bonito Formation (e.g., Milani et al., 2007; Holz et al., 2010).

In the Rio Grande do Sul State, the most recent U–Pb dating of a volcanic ash-fall layer from the upper Rio Bonito Formation yielded an age of 285.42 + 1.2/-2.1 Ma (Griffis et al., 2018). U–Pb dating of a volcanic ash-fall horizon from the upper member of the Irati Formation in the same Brazilian state resulted in an age of 275.75 ± 0.29 Ma (Cagliari et al., 2022). This constrains the Palermo Formation, at least in Rio Grande do Sul, within the Artinskian–Kungurian interval (Cohen et al., 2013; updated). To date, no radioisotopically datable horizons have been reported in the Palermo Formation.

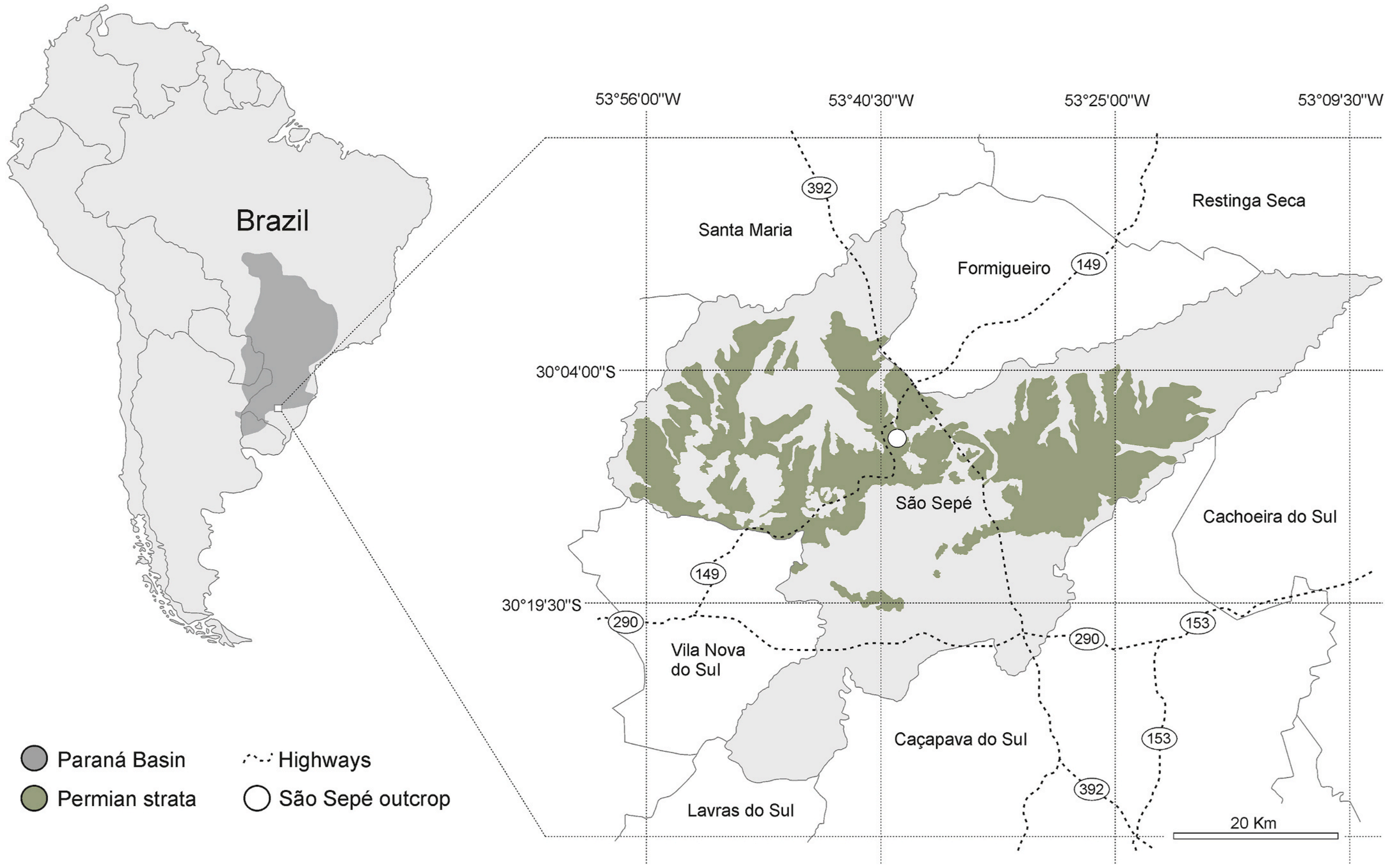


Fig. 1. Map of South America highlighting the Paraná Basin, and map of the municipality of São Sepé and its surroundings, indicating the location of the outcrop. Geographical extension of the Paraná Basin based on Milani et al. (1998). Map of São Sepé adapted from Terra et al. (2016).

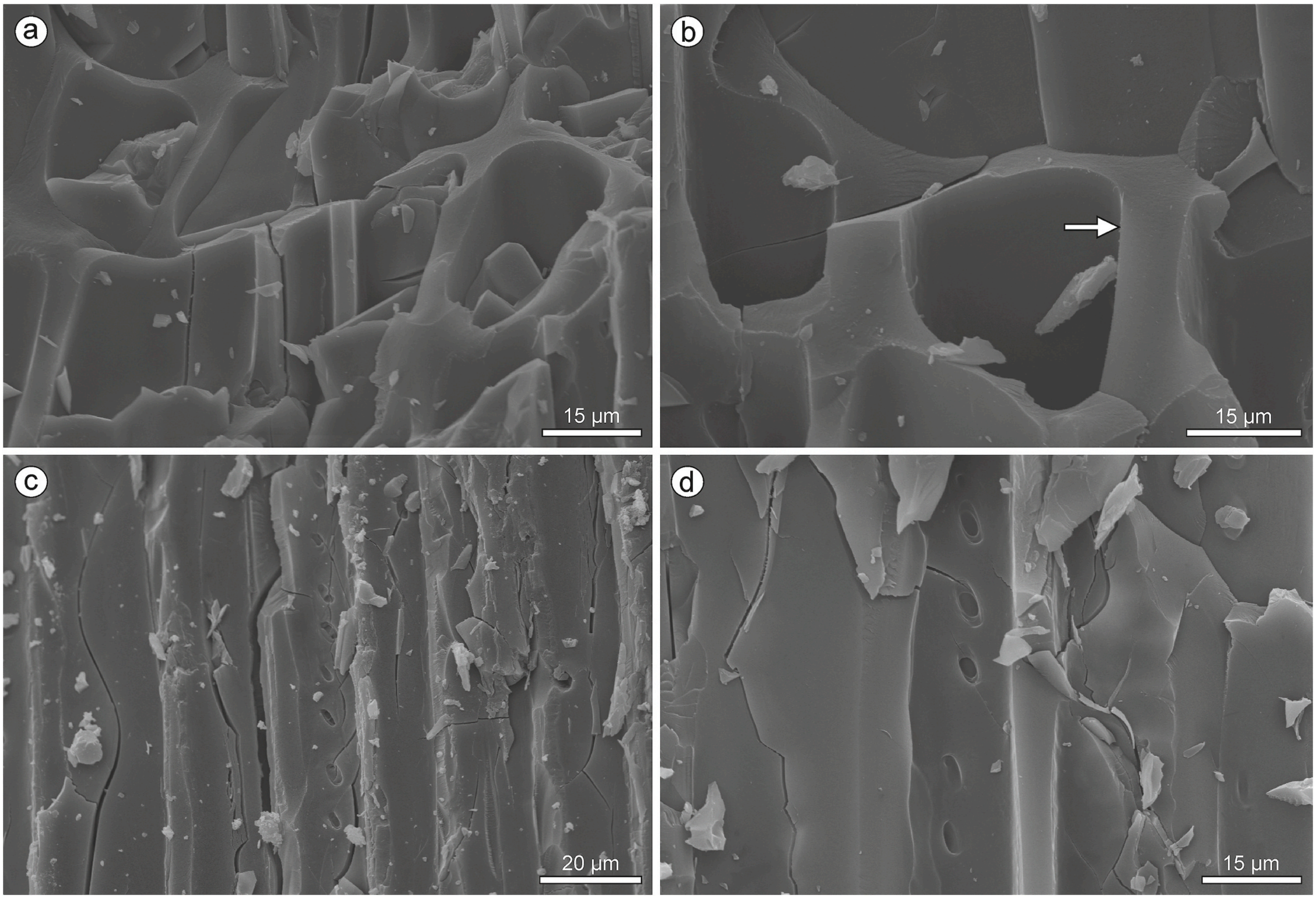
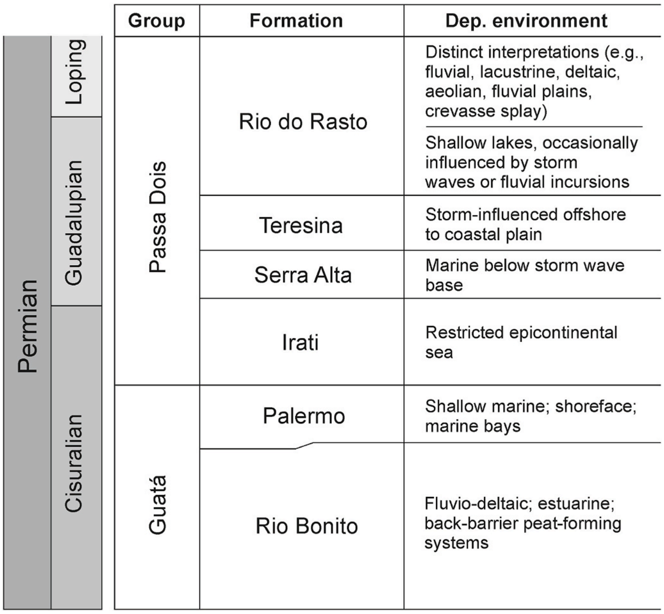


Fig. 2. Charcoalified wood fragments from the grey siltstones of the São Sepé outcrop. (a) Oblique cross section of fragment showing tracheids with homogenised cell walls, indicative for charcoal. Pb 1229stubA. (b) Detail of tracheids exhibiting homogenised cell walls (arrow). Pb 1229stubA. (c) Longitudinal section showing tracheids with uniseriate pitting. Pb 1229stubB. (d) Detail of uniseriate pitting. Pb 1229stubC. Material stored in the Palaeobotanical Collection of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.



		Group	Formation	Dep. environment
Permian	Loping	Passa Dois	Rio do Rasto	Distinct interpretations (e.g., fluvial, lacustrine, deltaic, aeolian, fluvial plains, crevasse splay)
	Guadalupian			Shallow lakes, occasionally influenced by storm waves or fluvial incursions
			Teresina	Storm-influenced offshore to coastal plain
			Serra Alta	Marine below storm wave base
	Cisuralian		Irati	Restricted epicontinental sea
		Guatá	Palermo	Shallow marine; shoreface; marine bays
			Rio Bonito	Fluvio-deltaic; estuarine; back-barrier peat-forming systems

Fig. 3. Simplified chart of the Permian lithostratigraphic units of the Paraná Basin in the Rio Grande do Sul State, Brazil. Based on Holz et al. (2010).

2.2. *Methodology and repositories*

We examined and photographed the fossils using a Zeiss SteREO Discovery V.12 stereomicroscope equipped with a Zeiss AxioCam 506 Color digital camera. The fossils lack cuticles, but imprints of epidermal features remain preserved on their leaf cushions. To study these minute features and to get a detailed view of leaf cushion morphology, we made synthetic replicas of two selected specimens based on the method described by Moisan (2012). We made the replicas using 3 M™ Express™ XT Light Body, a detail reproduction product based on vinyl polysiloxane (VPS). The VPS replicas were mounted on stubs, coated with gold, and examined with a JEOL JSM 6490 LV scanning electron microscope (SEM) at the Senckenberg Research Institute and Natural History Museum Frankfurt, Germany. Measurements were taken from calibrated images using the software ImageJ-NIH (Schneider et al., 2012). The fossils are stored in the Palaeobotanical Collection of the Universidade Federal do Rio Grande do Sul in Porto Alegre, Brazil. They are available under the accession numbers Pb 1229A, Pb 1229B, Pb 1229C, and Pb 1229D. VPS replicas originated from specimens Pb 1229A and Pb 1229C. These replicas are stored in the same collection under the accession numbers Pb 1229Are and Pb 1229Cre.

3. Taxonomic palaeobotany

Class: Lycopodiopsida Bartling, 1830.
Order and family: *Incertae sedis*.

Fossil-genus: *Nothostigma* Doweld, 2017.

Type species: *Nothostigma pacificum* (Steinmann) Doweld (2017).

Nothostigma sepeensis Spiekermann, Jasper, Guerra-Sommer et D. Uhl sp. nov.

1981 Unnamed lycopsid; Bortoluzzi and Veiga, Pesqui. Geociênc. 14 (14), pl. I, b.

1995 Unnamed lycopsid; Guerra-Sommer et al., Pesqui. Geociênc. 22 (1–2), pl. 2, 3.

Etymology: After the São Sepé locality, from where the fossils were collected.

Holotype: *Hic designatus*, specimen Pb 1229A (Fig. 4a).

Paratype: *Hic designatus*, specimen Pb 1229B (Fig. 4b).

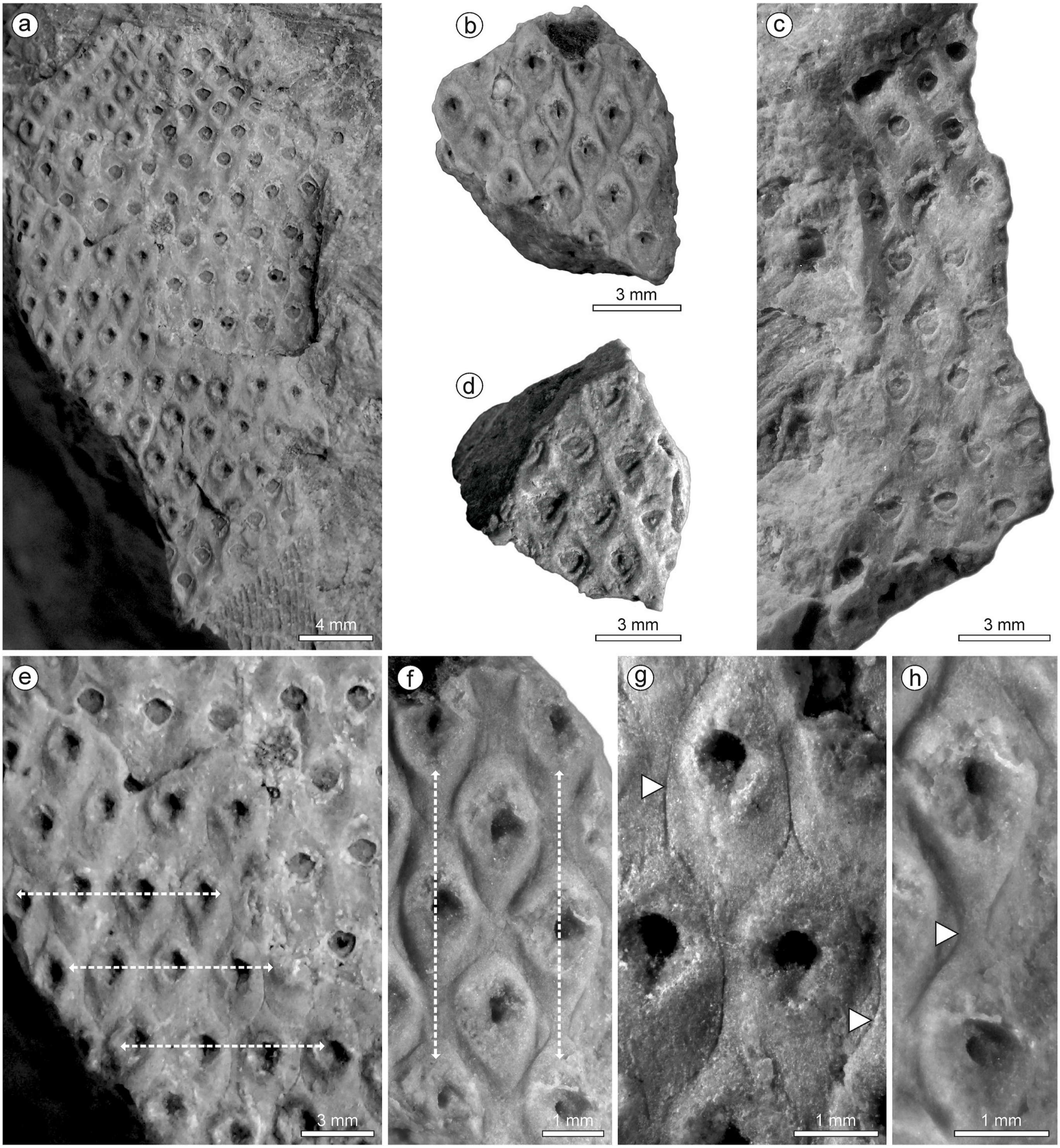


Fig. 4. *Nothostigma sepeensis* sp. nov. (a) Axis with leaf cushions projected either in positive or negative relief. Pb 1229A; holotype. (b) Small piece exhibiting cushions preserved exclusively in positive relief. Pb 1229B; paratype. (c) Axis with cushions preserved only in negative relief as external moulds. Pb 1229C. (d) Small piece with cushions preserved only in negative relief as external moulds; Pb 1229D. (e) Leaf cushions arranged side by side in a pseudowhorled pattern (dashed lines). Pb 1229A; holotype. (f) Detail of evident orthostichies (dashed lines). Pb 1229B; paratype. (g) Extremely narrow interareas (arrowheads), resembling delicate, sharp ingrown lines. Pb 1229A; holotype. (h) Open connection (arrowhead) between succeeding cushion fields in an orthostichy. Pb 1229B; paratype.

Additional material: Specimens Pb 1229C and Pb 1229D, plus replicas Pb 1229Are and Pb 1229Cre.

Type locality: São Sepé outcrop (30°09′S; 53°40′W), municipality of São Sepé, Rio Grande do Sul State, Brazil.

Type stratum and age: Grey and remarkably hard siltstones from the São Sepé outcrop, Palermo Formation, Artinskian–Kungurian, Cisuralian, early Permian.

Repository: Palaeobotanical Collection of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul State, Brazil.

Diagnosis: Axes covered in minute leaf cushions, exhibiting rhomboidal outline or swollen spindle shape usually with acuminate apex. Leaf cushions arranged side by side in pseudowhorled pattern, and orthostichies sometimes evident. Extremely narrow leaf cushion interareas, resembling thin, delicate, sharp ingrown lines, occasionally leading to an open connection between the succeeding cushion fields in an orthostichy. Leaf scar in the central or superomedial part of the cushion, with rhomboidal to curvilinear triangle outline when well-delineated. Leaf cushion epidermis composed of polygonal-shaped cells.

Description: Four small fragments of axes, lacking attached leaves, evidence of branching, rooting system, and reproductive structures (Fig. 4a–d). They are broken at both upper and lower ends and lateral margins, precluding the determination of their original widths. The specimen Pb 1229A, designated as the holotype, is about 18 mm wide and 33.5 mm long (Fig. 4a). The samples Pb 1229B, Pb 1229C, and Pb 1229D are smaller, ranging from circa 7–8.5 mm in width and 9.0–22.5 mm in length (Fig. 4b–d).

The axes are covered in minute but well-defined leaf cushions, which are somewhat prominent when preserved in positive relief (Fig. 4e–f). The fragmented nature of the fossils makes interpretation regarding phyllotaxis difficult. Noteworthy, however, is that in Pb 1229A, the cushions are arranged in horizontal rows in a pseudowhorled pattern (Fig. 4e), whereas in Pb 1229B, orthostichies are evident (Fig. 4f). The leaf cushions are separated by extremely narrow interareas, resembling thin, delicate, sharp ingrown lines (Fig. 4g). Occasionally, these interareas lead to an open connection between the succeeding leaf cushion fields in an orthostichy, giving a vertically fused-like appearance to the cushions (Fig. 4h).

The specimen Pb 1229A exhibits leaf cushions projected either in positive or negative relief (Fig. 5a–f). The cushions in negative relief correspond to external moulds (Fig. 5a, d), and VPS casting reveals that their morphology is identical to those standing in positive relief (Fig. 6a–b, d–e). In this particular specimen, the outline and size of the leaf cushions are variable. At its top, the cushions have a rhomboidal-like geometry (Fig. 5a–b; Fig. 6a–c) and are 1.5–2.5 mm high and 1–2 mm wide (Fig. 7). From the base to its superomedial part, the cushions exhibit a swollen spindle-like shape (Fig. 5c–f; Fig. 6d–e). The apex of these spindle-shaped cushions usually has an acuminate aspect (Fig. 5f), and they are 2.5–4 mm high and 1.5–2 mm wide (Fig. 7), with the broadest part generally (but not always) situated near their centre.

The specimen Pb 1229B exhibits leaf cushions preserved exclusively in positive relief (Fig. 4b; Fig. 8a). In contrast, Pb 1229C and Pb 1229D have cushions preserved only as negative relief moulds (Fig. 4c–d; Fig. 8b, d). Their leaf cushions are 2.5–3.5 mm high and 1.5–2 mm wide. VPS replicas of Pb 1229C reveal the appearance of its cushions in positive relief (Fig. 8c). The morphology of the leaf cushions in these three specimens (Fig. 4b–d; Fig. 8a–c), despite not so well-preserved in the two external moulds, is essentially similar to the spindle-shaped ones occurring from the base to the superomedial part of the specimen Pb 1229A.

The leaf cushion's upper and lower fields are unornamented. They are not keeled, lack the so-called infrafoliar bladders, and there is no convincing evidence of a ligule (Fig. 5a–f; Fig. 8f–g). There is a conspicuous leaf scar on the cushions. This scar is situated in the centre of the rhomboidal-like cushions (Fig. 5b) and in the medial or superomedial part of the spindle-shaped ones (Fig. 5c, e–f; Fig. 8f–g). In the leaf cushions in positive relief, the scars exhibit either a well-delineated or more or less irregular broken-like rim (Fig. 8e–g). The scars are circa 0.7–1.0 mm high and 0.5–1.0 mm wide in the cushions in positive relief. They generally have a rounded rhomboidal to curvilinear triangle-like shape when their outline is well-defined (Fig. 8f–g).

The "scars" visible in the central to superomedial part of the leaf cushions preserved as external moulds have a well-defined rounded rhomboidal but mostly curvilinear triangular outline (Fig. 8b, h–i). They are nearly identical in size to those leaf scars of the cushions in positive relief and circa 0.5–1.0 mm high and 0.5–1.0 mm wide. VPS casting of the cushions preserved as external moulds shows in detail the outline of such scars too (Fig. 6a–b, d–e; Fig. 8c; Fig. 9e). The leaves were vascularized by a single vascular bundle (Fig. 8h–i). There is no evidence of foliar and infrafoliar parichnos.

SEM examination of the VPS replicas revealed anatomical details preserved on the leaf cushion surfaces. The cushions standing in positive relief are covered by imprints of polygonal-shaped epidermal cells (Fig. 9a–d), with a diameter of 11–28 μm × 13–27.5 μm (n = 50). We did not detect any evidence of stomata among these cells. The micromorphology of the cushions preserved as external moulds is completely different from those standing in positive relief. The surface of the latter is covered by longitudinal striations, sometimes showing a reticulate-like pattern (Fig. 8c; Fig. 9e–f).

Remarks: We interpret that the four described specimens represent the same fossil-taxon based on the similar morphology and size of their leaf cushions. The cushions standing in positive relief on the holotype probably did not experience significant decay and decortication as their epidermal tissue is still impressed on their surfaces. There is no evidence of significant shape distortion on these cushions, and they may emulate how the original external surface of the plant could have more or less been. In contrast, the external moulds seem to provide an inside view, showing the inner side of the leaf cushions. The reticulate-like striations visible on such cushions in negative relief probably correspond to a sub-epidermal cortical tissue. The absence of any evidence for stomata among the cushion epidermal cells suggests that such structures may have never been there, as it is known that the VPS casting technique used here has the potential to replicate stomata (Moisan, 2012).

The leaf scars indicate approximately the point from which the leaf laminae departed from the cushions. Defining whether such scars correspond to false or true ontogenetic leaf abscission scars remains challenging. In the leaf cushions in positive relief, there are scars with irregular broken-like borders. This suggests that they may have resulted from taphonomical or mechanical *post-mortem* detachment of the leaves rather than natural leaf abscission (= false leaf scar). Alternatively, the splitting of the host rock, revealing the fossil surface, could have pulled off parts of the borders of true leaf scars, giving them a broken-like appearance. What leads us to such doubts is that there are cushions in positive relief exhibiting scars with a well-delineated outline, suggesting that these may have been formed after natural leaf abscission (= true leaf scar). If leaf abscission occurred during the ontogenetic development of the plant, then those scars with a defined rhomboidal or curvilinear triangle shape most likely represent true leaf scars. In the leaf cushions preserved as negative relief moulds, the scars are always well-defined, but as mentioned, these moulds seem to provide a view of the inner surface of the cushion. The scars visible on them likely represent an inside view of the proximal part of the leaf laminae in cross section rather than a leaf detachment scar.

Comparison and justification: The studied fossils differ from late Palaeozoic Euramerican leaf-cushion bearing lepidodendrids in lacking evidence of ligule and parichnos (e.g., DiMichele and Bateman, 1996). They also differ from known leaf cushion-bearing lycopsids belonging to the *Glossopteris* flora, such as *Azaniadendron*, *Brasilodendron*, and *Lycopodiopsis*. *Azaniadendron* was a ligulate plant, and its cushions exhibit a distinctive narrow, elongated, vertically-oriented structure in their centre (Rayner, 1986; Spiekermann et al., 2022). *Brasilodendron* lacks convincing evidence of ligule and has spindle-shaped fusiform leaf cushions, but these cushions have a subdued upper field, exhibit slightly

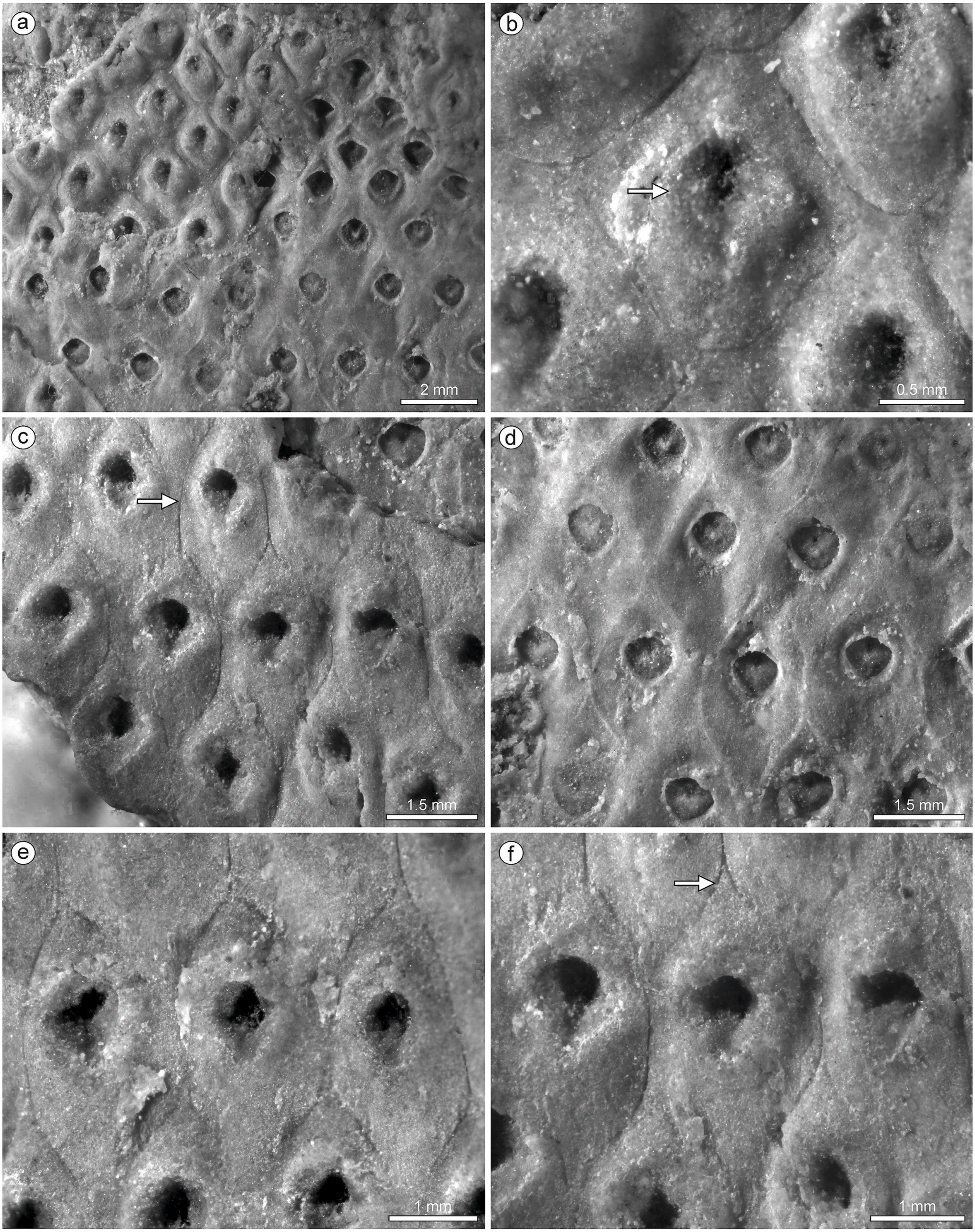


Fig. 5. *Nothostigma sepeensis* sp. nov. (a) Detail of the upper part of the holotype. (b) Detail of rhomboidal leaf cushion. Arrow indicates scar formed after leaf detachment. (c) Spindle-shaped cushions from the medial to lower part of the holotype preserved in positive relief. Arrow indicates the line-like interareas. (d) Spindle-shaped cushions preserved as negative relief moulds. (e) Detail of spindle-shaped cushions. (f) Detail of spindle-shaped cushion with acuminate apex (arrow). All images from Pb 1229A; holotype.

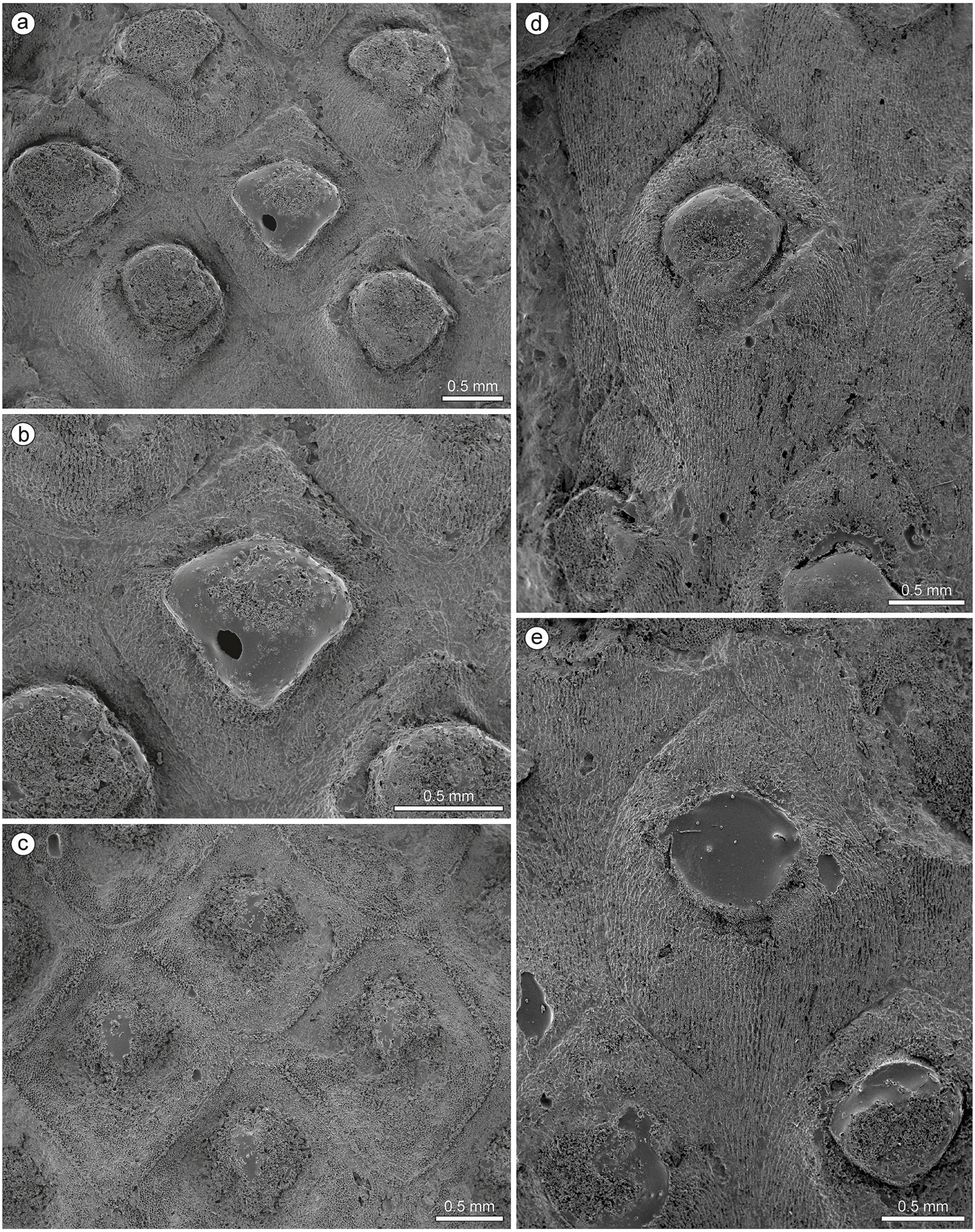


Fig. 6. SEM-images of VPS replicas of *Nothostigma sepeensis* sp. nov. (a) Replica of rhomboidal leaf cushions preserved as external moulds. (b) Detail of rhomboidal cushion. (c) Replica of rhomboidal cushions preserved in positive relief. (d) Replica of spindle-shaped cushion preserved as external mould. (e) Replica of spindle-shaped cushion preserved as external mould. VPS replica made from the holotype; Pb 1229Are.

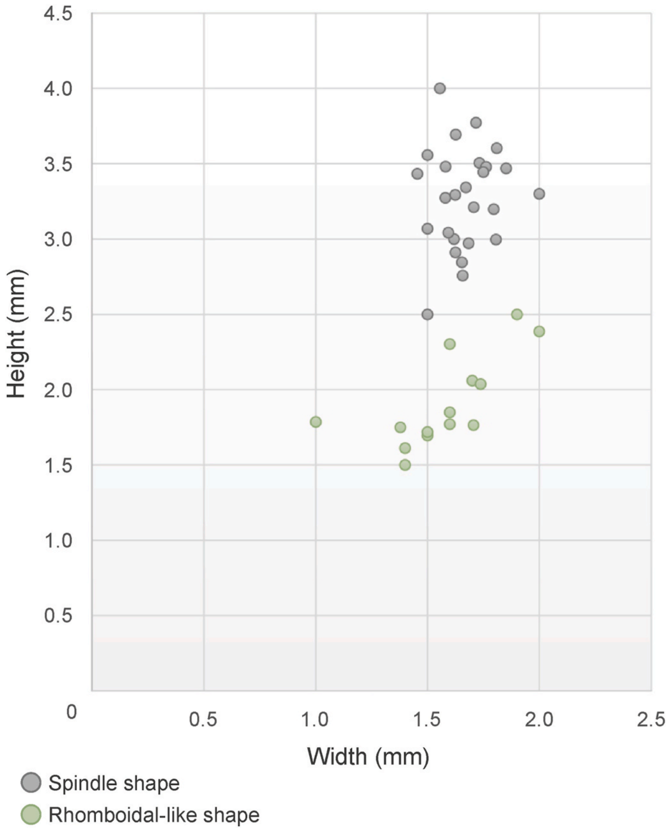


Fig. 7. Scattered diagram showing the width × height of the holotype leaf cushions. Pb 1229A; n = 40.

sigmoid extensions in their upper and lower ends, and lack any evidence of leaf detachment scar comparable with those seen in the studied specimens (Chaloner et al., 1979; Spiekermann et al., 2018). Whether *Lycopodiopsis* was ligulate or eligulate remains problematic (Spiekermann et al., 2022), and at first glance, the rhomboidal cushions visible at the top of the holotype (Pb 1229A) resemble those of some fossils assigned to that fossil-genus (Steinmann, 1924; Kräusel, 1961; Faria et al., 2009). However, the spindle-shaped cushions, usually with acuminate apexes, that dominate the surface of the studied fossils are distinct from those falling within the concept of *Lycopodiopsis* (Renault, 1890; Steinmann, 1924; Kräusel, 1961; Faria et al., 2009). Further, the specimen's cushion interareas, resembling very thin, delicate, sharp ingrown lines are distinct from those of *Azaniadendron, Brasilodendron,* and *Lycopodiopsis* and have never been reported in specimens assigned to these fossil-genera (e.g., Renault, 1890; Steinmann, 1924; Kräusel, 1961; Chaloner et al., 1979; Faria et al., 2009; Spiekermann et al., 2018, 2022).

Well-defined decurrent leaf cushions, such as the spindle-shaped ones of the studied material, go beyond the formal generic definition of *Cyclodendron*, another lycopsid from the *Glossopteris* flora (cf. Kräusel, 1928, 1961; Rayner, 1985). Rayner (1985), who analysed the type material and described many additional *Cyclodendron* specimens, providing details of their epidermis and reproductive structures, claimed that their defoliated axes are covered only in leaf scars and lack leaf cushions. *Bumbudendron* Archangelsky et al. (1981), reported mainly from Carboniferous but also Permian strata of South America (Cariglino et al., 2012), differs from the described material in having infrafoliar bladders. A shared aspect is that fossils of both *Cyclodendron* and *Bumbudendron* lack convincing evidence of ligule, such as the specimens studied here (e.g., Kräusel, 1961; Archangelsky et al., 1981; Rayner, 1985). The absence of evidence for a ligule distinguishes them from common leaf cushion-bearing fossil-taxa of the Angaran Carboniferous flora, such as *Angarodendron* Zalessky (1918), *Tomiodendron* Radczenko (1956), and the also known from European deposits *Eskdalia* Kidston (1903), all of which have been interpreted as ligulate (Meyen, 1972). *Angarophloios* Meyen (1972) lacks convincing evidence of ligule but exhibits infrafoliar bladders.

Among late Palaeozoic fossils, the morphology of the studied specimens closely resembles that of some Mississippian lycopsid axes from Peru, once placed in *Cyclostigma* Haughton by Jongmans (1954, pl. 17, figs. 6–6a). As such material lacks evidence of parichnos, Archangelsky et al. (1981) stated, on what we fully agree, that they did not belong to *Cyclostigma* but could represent a new genus. After revising the nomenclature of *Cyclostigma*, Doweld (2017) included many late Palaeozoic species from Gondwana, first assigned to that fossil-genus, into the new generic name *Nothostigma* Doweld. Such as, in what is now *Nothostigma*, the leaf cushions of the studied fossils are somewhat prominent, lack evidence of ligule, parichnos, and any distinctive ornamentation in their upper and lower fields, and are separated by narrow interareas, resembling fine, delicate, sharp ingrown lines (cf. Jongmans, 1954). At least in one specimen, these line-like interareas lead to an open connection between the succeeding cushion fields within an orthostichy, a typical feature of that fossil-genus (Jongmans, 1954; Doweld, 2017). Further, the position of the leaf scars and their outlines when well-defined, as well as the overall shape of the cushions, are similar to those of specimens assigned to *Nothostigma*'s type species (cf. Jongmans, 1954, pl. 17, figs. 6–6a). Unfortunately, leaf cushion epidermal details of previously proposed *Nothostigma* species remain unknown, precluding comparisons with the material described here in this aspect.

Aware of the lack of epidermal data on other *Nothostigma* fossils, but considering all shared characters between the latter and the studied material, we tentatively place the São Sepé specimens into that fossil-genus. This decision also relies on the absence of any conspicuous character in the available material that would justify the proposal of a new generic name. Doweld (2017) proposed six new *Nothostigma* combinations. The latter consist of small fragmented axes, which reproductive structures remain unknown (e.g., Jongmans and Koopmans, 1940; Jongmans, 1954; Pal, 1978). Among these, *Nothostigma zafrense* (Jongmans) Doweld from the Mississippian of Zafra in Spain is covered in irregularly arranged scars and may merely correspond to stigmarian remains (Wagner and Álvarez-Vázquez, 2010). *Nothostigma brasiliense* (Dolianiti) Doweld, reported from strata of north-northeastern Brazil now placed in the Permian (Iannuzzi et al., 2018), is described as lacking leaf cushions and having potential parichnos (Dolianiti, 1962). Whether this Brazilian fossil-species should be placed in *Nothostigma* seems to require a re-examination of its fossils.

The other *Nothostigma* taxa comprise *N. pacificum* (Steinman) Doweld, *N. indicum* (Pal) Doweld, *N. aegypticum* (Jongmans) Doweld, and *N. sinaicum* (Jongmans) Doweld. Among these, the studied material closely resembles *Nothostigma pacificum* (cf. Jongmans, 1954, pl. 17, figs. 6–6a). The latter, based on fragmented axes from the Mississippian strata of Peru, represents the type species of the genus (Doweld, 2017). The narrow and delicate line-like interareas, so conspicuous in the studied material, are virtually identical to those of the type species. However, Jongmans (1954) mentions that in *Nothostigma pacificum* such line-like interareas always lead to a vertical "open communication" between succeeding cushions fields, an aspect that occurs only occasionally in the São Sepé specimens.

Further similarities between the studied fossils and *Nothostigma pacificum* include the presence of swollen spindle-shaped cushions (cf. Jongmans, 1954, pl. 17, fig. 6a). In the type species, however, some well-preserved spindle cushions tend to show a more sinuous shape (cf. Jongmans, 1954, pl. 17, fig. 6a). *Nothostigma pacificum* and the São Sepé fossils exhibit leaf scars either with an irregular broken-like rim or well-delineated outline. The position of these leaf scars is the same in both, but in the type species, well-defined scars tend to exhibit raised borders (cf. Jongmans, 1954, pl. 17, fig. 6a). Focusing on the São Sepé

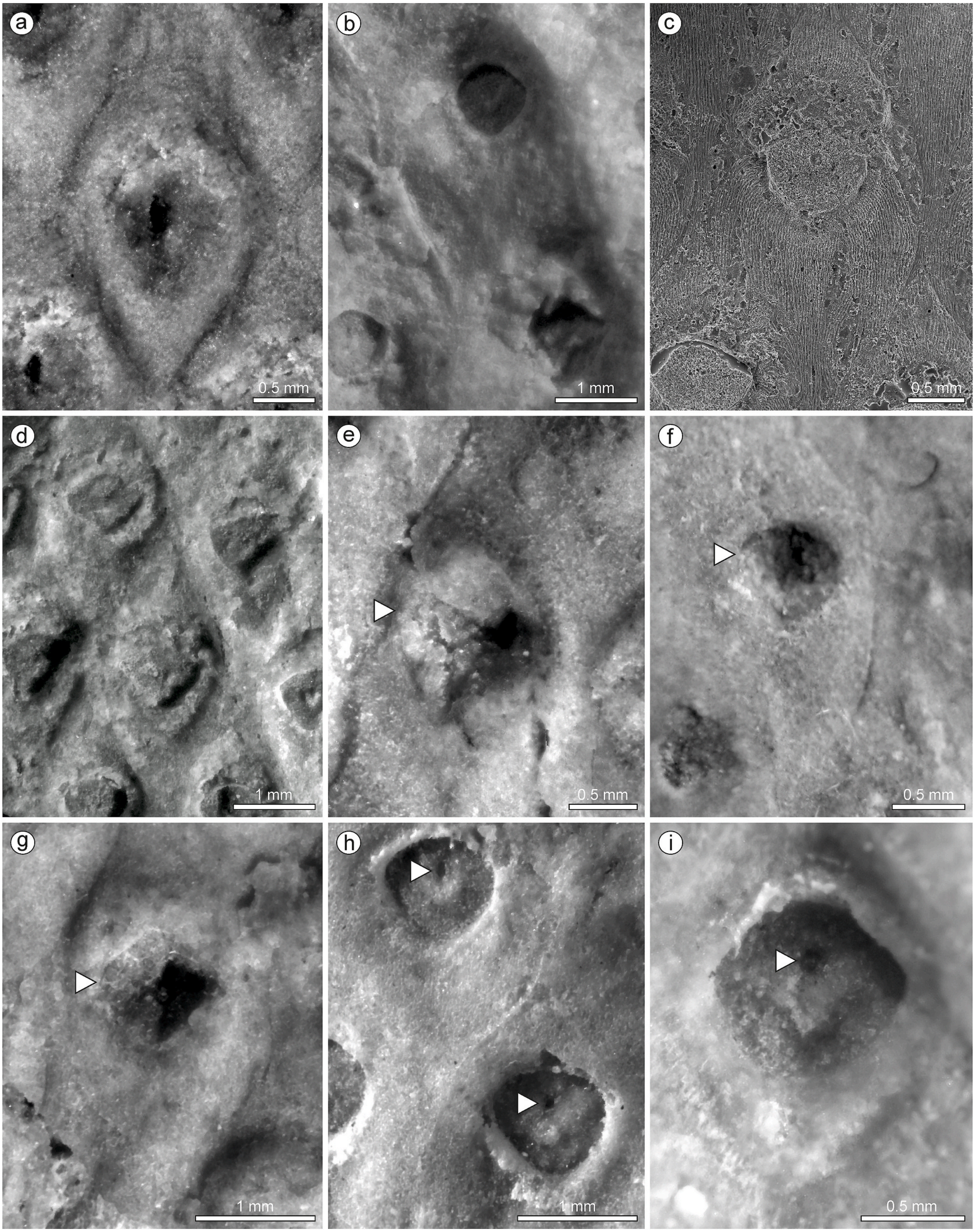


Fig. 8. *Nothostigma sepeensis* sp. nov. (a) Leaf cushion preserved in positive relief. Pb 1229B; paratype. (b) Cushion preserved as negative relief mould. Pb 1229C. (c) SEM-image of VPS replica of cushion preserved as negative relief mould. Pb 1229Cre. (d) Cushions preserved as negative relief moulds. Pb 1229D. (e) Detail of leaf cushion in positive relief, exhibiting leaf scar with irregular rim (arrowhead). Pb 1229A; holotype. (f) Cushion in positive relief showing leaf scar with a well-defined curvilinear triangle-like shape (arrowhead). Pb 1229A; holotype. (g) Cushion in positive relief showing leaf scar with a well-defined rhomboidal-like shape (arrowhead). Pb 1229A; holotype. (h) Detail of cushions preserved as external moulds showing an inside view of the leaves in cross section and single vascular bundle scars (arrowhead). Pb 1229A; holotype. (i) Detail of external mould showing the single vascular bundle (arrowhead). Pb 1229C.

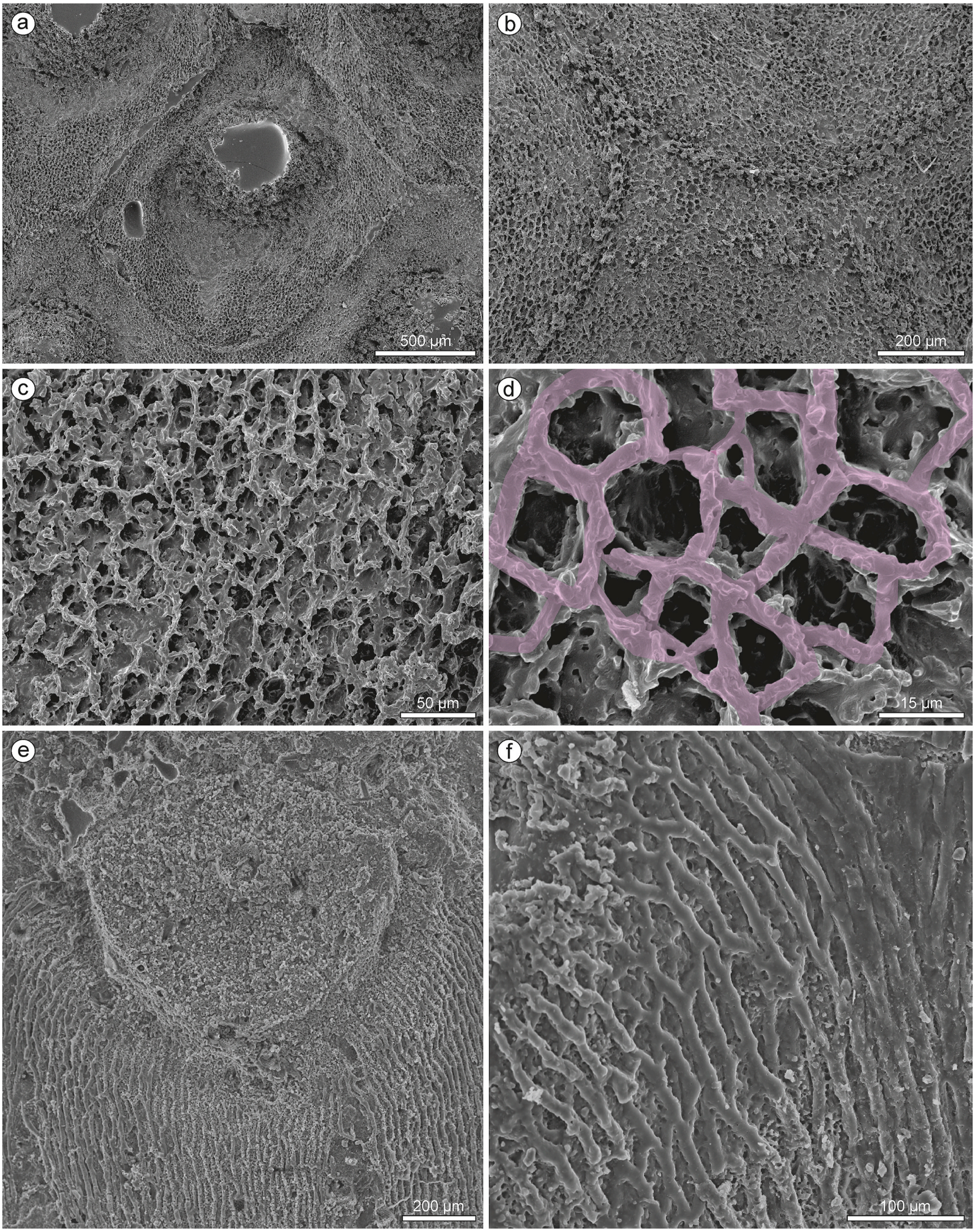


Fig. 9. SEM-images of VPS casts of *Nothostigma sepeensis* sp. nov. (a) Replica of rhomboidal cushion preserved in positive relief showing an overview of the epidermal tissue. Pb 1229Are. (b) Detail of cushion epidermal tissue. Pb 1229Are. (c) Detail of cushion epidermal tissue. Pb 1229Are. (d) Detail of epidermal tissue highlighting (purple) the shape of the cells. (d) Replica of cushion preserved as external mould exhibiting longitudinal reticulate-like striations. Pb 1229Cre. (f) Detail of structures visible in cushions preserved as external moulds. Pb 1229Cre.

fossil designated as the holotype, its most distinctive feature in comparison with *Nothostigma pacificum* is the well-organized side by side arrangement of its leaf cushions, forming nearly horizontal rows, which gives them a pseudowhorled-like appearance. Pseudowhorls also occur in Mississippian leaf cushion-bearing fossil-taxa such as *Prelepidodendron* Danzé-Corsin (1960) and the worldwide distributed *Lepidodendropsis* Lutz (1933). However, Chaloner and Boureau (1967) mention the presence of a ligule pit for *Prelepidodendron*. *Lepidodendropsis* lacks convincing evidence of ligule but has leaves attached to the uppermost part of the cushion and shows no sign of leaf detachment scars comparable with those seen in the studied fossils (Lutz, 1933; Thomas and Meyen, 1984).

Together with leaf cushion shape, the pseudowhorled pattern of the São Sepé holotype distinguishes it from *Nothostigma aegypticum,* a fossil-taxon based on Mississippian fossils from the Sinai Peninsula, Egypt (cf. Jongmans and Koopmans, 1940, pl. III, figs. 5a–5b; Jongmans and van der Heide, 1955, pl. 11, figs. 8c–f). From the same region and coeval strata, the specimen Doweld (2017) elected as the holotype of *Nothostigma sinaicum* seems to have had leaves borne at the upper part of the cushions and does not show any character that closely resembles the fossils studied here (cf. Jongmans and Koopmans, 1940, pl. I, figs. 1–1bis). *Nothostigma indicum* is based on branched axes from the Mississippian strata of Kashmir Himalaya (Pal, 1978). Its type specimen is poorly-preserved (cf. Pal, 1978, pl. 4, figs. 14–15), making comparisons with the São Sepé specimens difficult. The cushions and leaf scars in *Nothostigma indicum* appear to have been arranged more irregularly than in the studied material.

Considering the differences mentioned, we think we are dealing with a new fossil-species. Rather than maintain the material in an unnamed limbo, hiding the morphological diversity of fossils from the *Glossopteris* flora, we propose *Nothostigma sepeensis* sp. nov. This taxonomical decision is in accordance with Art. 1.2. of the ICBN (Turland et al., 2018).

4. Final remarks

Despite being small, and having been outside the scope of research for years, the fossils described here are far from trivial. The specimens exhibit well-preserved morphological characters, including epidermal details of their leaf cushions. They introduce a new element for the *Glossopteris* flora, helping to unveil the lycopsid morphological diversity from the Permian post-glacial terrains of Gondwana. Interestingly, they resemble *Nothostigma*, a fossil-genus of lycopsids that were common in Gondwana during a Mississippian pre-glacial stage, before the beginning of the late Palaeozoic major glacial event (Iannuzzi and Pfefferkorn, 2002).

Due to the small size and the depositional environment, which indicates an allochthonous deposition, nothing can be stated about the original habitat of the new taxon. The co-occurrence of charcoal in the same siltstone layer indicates that wildfire(s), which were widespread in the Permian on Gondwana (e.g., Jasper et al., 2021), occurred in an unknown kind of vegetation which was contemporary with the lycopsids, but it is not possible to decide whether this was the actual habitat of the lycopsids or not.

CRediT authorship contribution statement

Rafael Spiekermann: Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **André Jasper:** Writing – review & editing, Investigation. **Ândrea Pozzebon-Silva:** Methodology, Investigation. **Júlia Siqueira Carniere:** Methodology, Investigation. **José Rafael W. Benício:** Methodology, Investigation. **Margot Guerra-Sommer:** Writing – review & editing, Investigation. **Dieter Uhl:** Writing – review & editing, Supervision, Investigation.

Declaration of competing interest

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

Data availability

All fossils used in this investigation are stored and available for studies in the Palaeobotanical Collection of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

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Publication 4

Not a lycopsid but a cycad-like plant: Iratinia australis gen. nov. et sp. nov. from the Irati Formation, Kungurian of the Paraná Basin, Brazil

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R. Spiekermann: author position, 1; scientific ideas, 90%; data generation 60%; analysis and interpretation, 90%; paper writing, 90%.
A. Jasper: author position, 2; scientific ideas, 2%; data generation 5%; analysis and interpretation, 2%; paper writing, 3%.
A.M. Siegloch: author position, 3; scientific ideas, 2%; data generation 20%; analysis and interpretation, 2%; paper writing, 2%.
M. Guerra-Sommer: author position, 4; scientific ideas, 3%; data generation 10%; analysis and interpretation, 2%; paper writing, 2%.
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Not a lycopsid but a cycad-like plant: *Iratinia australis* gen. nov. et sp. nov. from the Irati Formation, Kungurian of the Paraná Basin, Brazil

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ABSTRACT

A new fossil taxon, *Iratinia australis* gen. nov. et. sp. nov., is proposed based on a monoxylic anatomically preserved axis from the Irati Formation, Kungurian of the Paraná Basin, Brazil. This specimen was initially interpreted as a lycopsid, but its set of morpho-anatomical characteristics indicate that it has systematic affinity with Cycadales. *Iratinia australis* is the oldest known anatomically preserved vegetative axis bearing affinities with this particular botanical order. It indicates that the general anatomy of cycad monoxylic axes, as well as the armour of leaf bases and the girdling leaf traces characteristic for Cycadales, were already established in the Kungurian. This fossil is the first record of an anatomically preserved cycad axis from the Permian of Gondwana, suggesting that during the Cisularian Cycadales or their direct ancestors were already widely/worldwide distributed.

1. Introduction

The Kungurian Irati Formation of the Paraná Basin, South America, has been the source of a large number of three-dimensionally preserved, silicified plant axes, which usually preserve details of the pith as well as primary and secondary vascular tissues (Mussa, 1982; Faria et al., 2018). Most of the so far described specimens belong to gymnosperms (Kräusel and Dolianiti, 1958; Mussa, 1982, 1986; Merlotti and Kurzawe, 2011; Faria et al., 2018), but one axis was interpreted as a lycopsid and informally assigned to Sigillariaceae (Guerra-Sommer, 1981). A recent study on the late Palaeozoic lycopsids from the Paraná Basin questioned this interpretation and suggested that this specimen could be related to gymnosperms (Spiekermann et al., 2020). The botanical affinity of this plant fossil, however, remains obscure as it has not been studied in detail yet.

Here we provide a detailed analysis of this particular specimen initially interpreted as an arborescent lycopsid. The anatomical pattern of this plant fossil suggests that it has a botanical affinity with Cycadales and that it is not related to lycopsids at all. We compared the specimen with extant and extinct anatomically preserved members of Cycadales; based on its unique set of characteristics we propose the new taxon *Iratinia australis* gen. nov. et sp. nov. This Kungurian fossil is the oldest known anatomically preserved axis exhibiting affinities with this botanical order, and provides noteworthy information about the evolution of cycad-like plants and their biogeographical distribution during the Permian.

2. Geological background

The Paraná Basin extends over an area of approximately 1,500,000 km^2, covering the south-central part of Brazil and parts of Uruguay, Paraguay, and Argentina (Milani et al., 2007). Its stratigraphical record comprises six depositional supersequences, deposited from the Ordovician up to the Cretaceous, and separated by basin-wide unconformities (Milani et al., 1998). The late Palaeozoic strata of the basin are included in the Gondwana I Supersequence, which is divided into three groups (Fig. 1) and represents a complete transgressive–regressive cycle of the Panthalassa Ocean (Milani et al., 2007).

The Irati Formation, from which the specimen studied here originates, is the lowermost unit of the Passa Dois Group. It is divided from the base to the top into the Taquaral and Assistência members (Fig. 1). The former is predominantly composed of non-bituminous shales, whereas the latter comprises mainly black bituminous shales interbedded with limestones (Hachiro, 1996; Holz et al., 2010). The intercalation between the limestone and black shales has remarkable rhythmicity in the northern part of the Paraná Basin (Amaral, 1971; Hachiro, 1996). These rhythmites were interpreted as formed by climate alternations linked to Milankovitch cycles (Hachiro, 1996).

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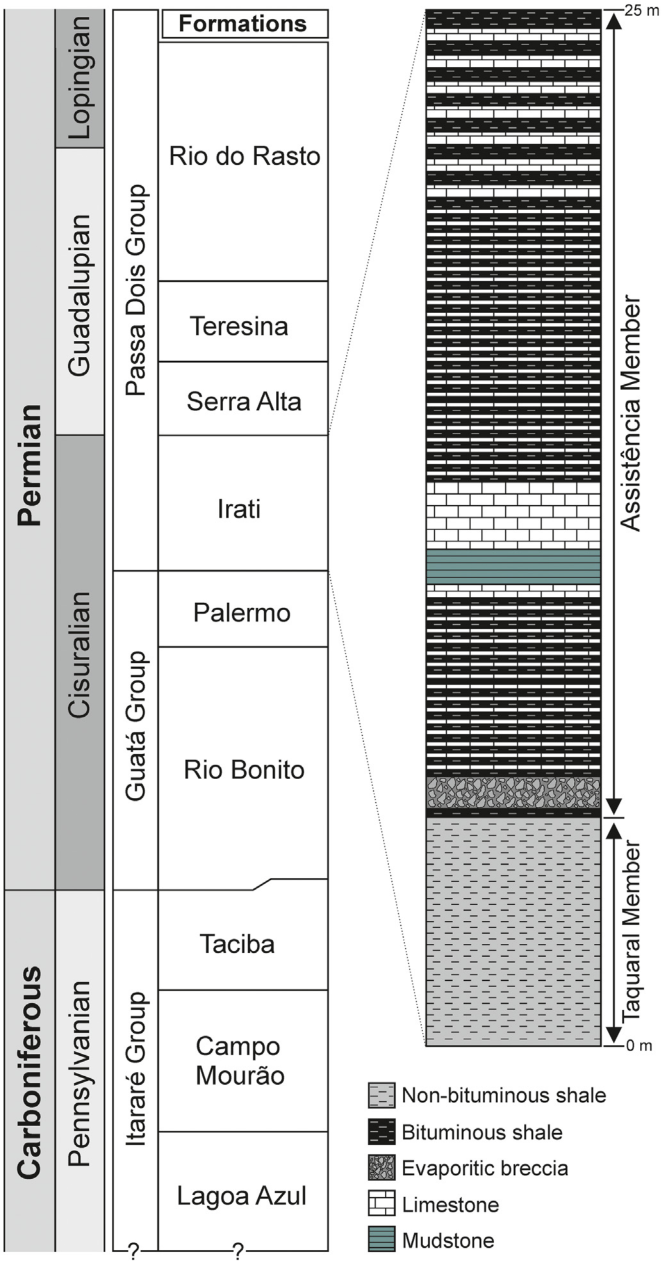


Fig. 1. Simplified chart of the late Palaeozoic units of the Gondwana I Supersequence, and overview of the Irati Formation lithology in São Paulo State, northeastern part of the Paraná Basin, Brazil. Chart adapted from Milani et al. (2007), and lithological column based on Hachiro (1991, 1996).

According to Holz et al. (2010), the Irati Formation was deposited over almost the entire Paraná Basin. Strata considered equivalent to this unit have also been reported from Namibia, South Africa, and the Falkland Islands (e.g. Oelofsen, 1987; Horsthemke et al., 1990; Faure and Cole, 1999). The depositional system of this formation is interpreted as a large inland sea with restricted connection to the Panthalassa Ocean (e.g. Holz et al., 2010; Xavier et al., 2018). Comparing the Taquaral and Assistência members, more restricted water circulation conditions probably existed during the deposition of the latter, allowing the formation of the black bituminous shales (Schneider et al., 1974; Holz et al., 2010).

U–Pb zircon dating of an ash fall layer interbedded between the black shales of the Assistência Member provided ages ranging from 279.9 ± 4.8 to 280.0 ± 3.0 Ma (Rocha-Campos et al., 2019). This places the upper part of the Irati Formation into the Kungurian according to the current International Stratigraphic Chart (Cohen et al., 2013, updated; Gradstein et al., 2020). Based on palynological data, the base of the unit (Taquaral Member) was recently included in the Kungurian as well (Rocha et al., 2020).

3. Material and methods

The material described here comprises a single vegetative axis, bearing both external morphological characteristics and internal anatomical details preserved. The fossil is permineralised by silica according to a previous study (Guerra-Sommer, 1981). It has been extracted from the Irati Formation strata at the district of Assistência (Fig. 2), municipality of Rio Claro, São Paulo State, Brazil (Guerra-Sommer, 1981). The exact location of the fossil-bearing outcrop in this district and details about the stratigraphic position of the specimen within the Irati Formation are not known. However, it most likely comes from the Assistência Member, since silicified gymnosperm axes are common in the limestones of this member at the municipality of Rio Claro (Mussa, 1982; Faria et al., 2018). According to Faria et al. (2018), almost all of the known fossils come from outcrops in the upper part of the Assistência Member.

The specimen was thin sectioned along the three standards planes (tangential, radial, and cross section). Macroscopic photographs of the material were taken with a Canon EOS T3i camera with Sigma 70 mm

Fig. 2. Sketch map showing the location of the district of Assistência, municipality of Rio Claro, São Paulo State, Brazil. Based on Hachiro (1996).

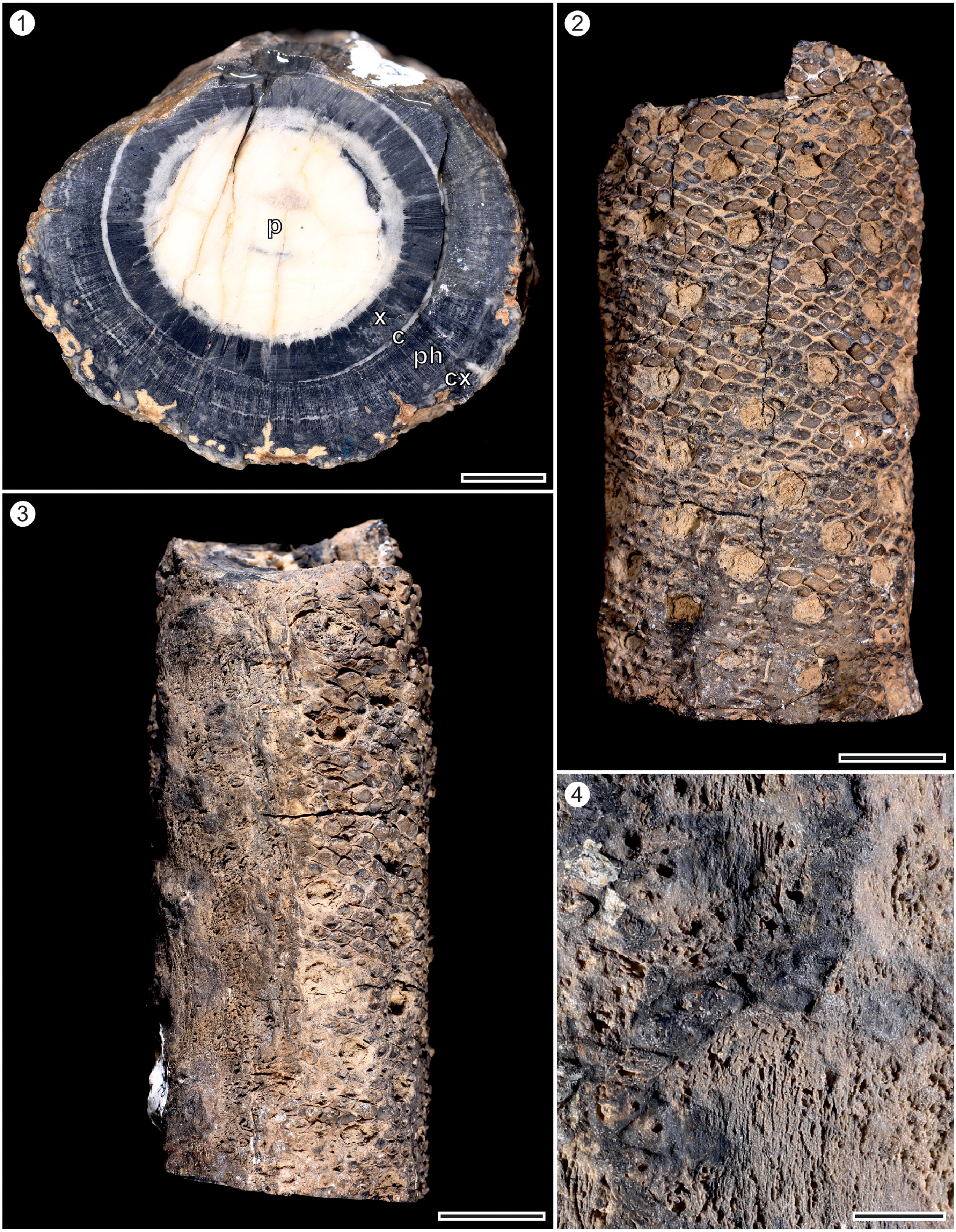


Plate I. *Iratinia australis* gen. nov. et sp. nov. Holotype, specimen MCT1487-PB. (1) Cross section showing the large pith (p), xylem ring (x), cambium (c), phloem (ph), and cortex (cx). Scale bar = 10 mm. (2) General view of the surface of the axis covered by leaf bases. Scale bar = 20 mm. (3) General view of the decorticated surface of the axis. Scale bar = 20 mm. (4) Detail of the decorticated surface showing remains of the leaf bases. Scale bar = 5 mm.

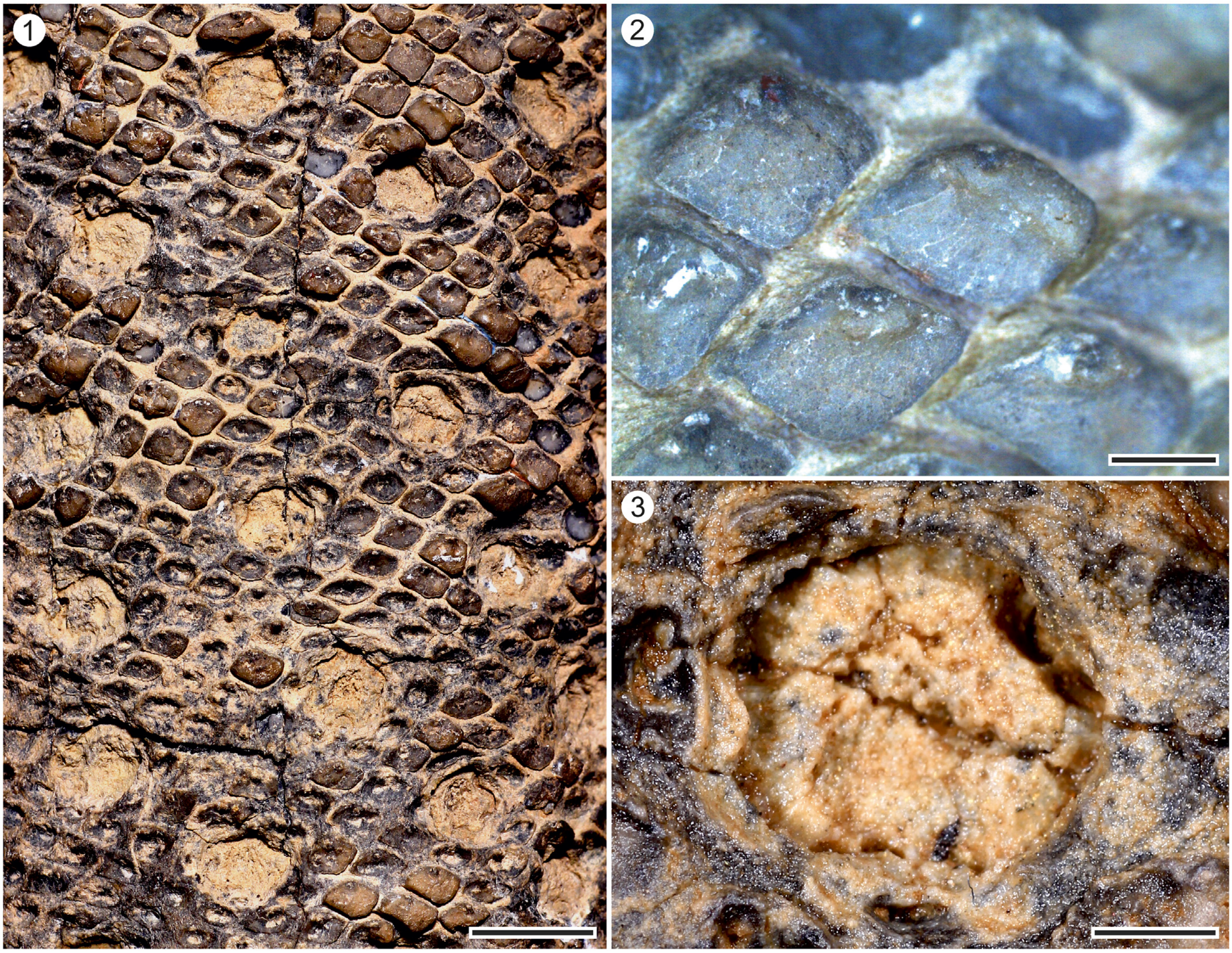


Plate II. *Iratinia australis* gen. nov. et sp. nov. Holotype, specimen MCT1487-PB. (1) Surface of the axis showing the helically arranged leaf bases and lateral outgrowth scars. Scale bar = 10 mm. (2) Detail of the leaf bases. Scale bar = 2 mm. (3) Detail of a lateral outgrowth scar. Scale bar = 5 mm.

DG macro lens. Observations and images of anatomical details were made with a Leica S8 APO stereomicroscope and a Zeiss Axio Scope A1 light microscope, both equipped with a digital camera system. Plates were composed with CorelDRAW® Graphics Suite 2018. Transformations made to the images include cropping and adjustment of brightness and contrast. Cells and tissues were measured using the software ImageJ – NIH (Schneider et al., 2012). Average dimensions were calculated from 25 measurements of each anatomical character; the average is mentioned first and the minimum and maximum values are given in parentheses. The specimen is housed in the palaeobotanical collection of the Museu de Ciências da Terra (Serviço Geológico do Brasil (CPRM), Rio de Janeiro, Brazil) under the accession number MCT1487-PB. The analysed slides are housed in the same collection under the accession numbers MCT1487-PB-1 to MCT1487-PB-5.

4. Systematic palaeobotany

Order: Cycadales Dumortier, 1829

Family: Incertae Sedis

Genus: **Iratinia** Spiekermann, Jasper, Siegloch, Guerra-Sommer et D. Uhl gen. nov.

Type species: *Iratinia australis* Spiekermann, Jasper, Siegloch, Guerra-Sommer et D. Uhl gen. nov. et sp. nov.

Etymology: After the Irati Formation, from which the type material has been discovered.

Diagnosis: Monoxylic and manoxylic axis covered by an armour of helically arranged rhomboidal leaf bases. Large pith and narrow centrifugal xylem ring. Primary xylem arranged in numerous strands distributed around the pith. Secondary xylem well-developed and relatively dense. Tracheids of the secondary xylem with araucarioid pitting. Phloem well-developed with abundant fibres. Radial system composed of numerous medullary and secondary rays. Rays parenchymatous and uni- to multiseriate. Wide medullary rays with vascular bundles. Leaf traces forming a girdling meshwork in the cortex before entering leaf bases. Cortex parenchymatous with mucilage cavities.

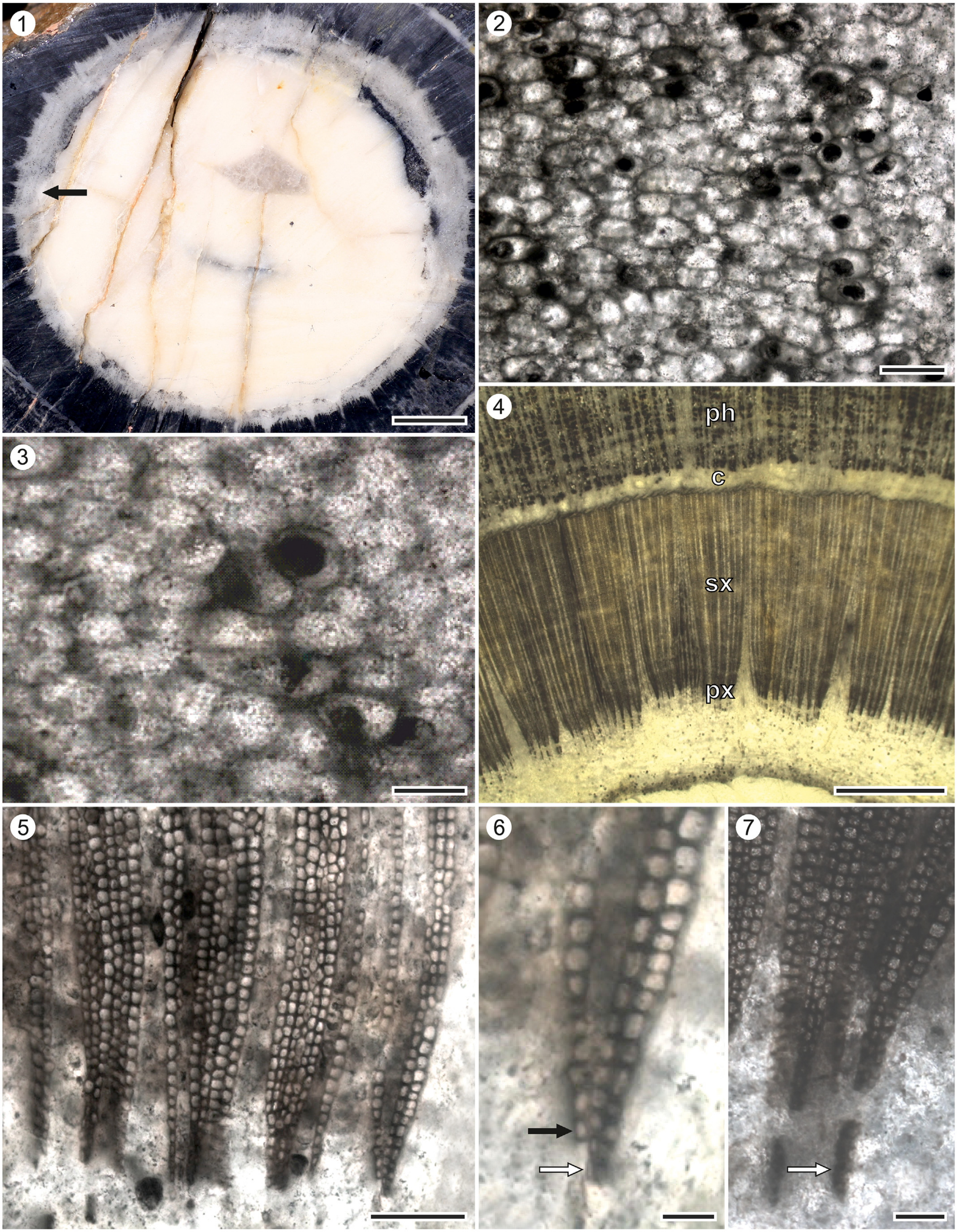
Species: *Iratinia australis* Spiekermann, Jasper, Siegloch, Guerra-Sommer et D. Uhl sp. nov.

Holotype: Specimen MCT1487-PB, and slides MCT1487-PB-1, MCT1487-PB-2, MCT1487-PB-3, MCT1487-PB-4, MCT1487-PB-5 (Plates I–VI).

Repository: Museu de Ciências da Terra, Serviço Geológico do Brasil (CPRM), Rio de Janeiro, Brazil.

Type locality: District of Assistência, municipality of Rio Claro, São Paulo State, Brazil.

Stratigraphic horizon and age: Irati Formation, Kungurian, Cisuralian, Permian.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Etymology: Specific epithet referring to the southern provenance of the specimen.

Diagnosis: Numerous lateral outgrowth scars inserted among the leaf bases and distributed along the axis in an apparent but not well-defined helical arrangement. Central pith with parenchymatous cells and idioblasts bearing dark content. Xylem ring centrifugal and narrow. Secondary xylem well-developed and relatively dense, with tracheids bearing 1–2 seriate araucarioid pitting and helical thickenings. Phloem broader than xylem, composed of abundant thick-walled fibres grouped in nests, and smaller and thinner-walled cells. Radial system with numerous medullary and secondary rays. Cortex relatively narrow.

Description: *General aspects*. The permineralized axis has a preserved length of 133 mm, and is elliptical in cross section (Plate I, 1), with a diameter of 53.2 mm × 64.7 mm. In general, the internal structure consists of a large central pith, surrounded by a monoxylic vascular cylinder, which is followed by the cortex (Plate I, 1). One side of its external surface is covered by an armour of persistent leaf bases (Plate I, 2), whereas the other side is decorticated (Plate I, 3). However, some leaf base remains can still be seen in this decorticated area (Plate I, 4), suggesting that this part of the specimen was originally covered by leaf bases as well, which have been eroded post-diagenetically.

The leaf bases are helically arranged along the axis and do not touch each other (Plate II, 1, 2). They are 2.8 mm (2.3–3.5) high and 4.4 mm (3.8–5.1) wide and generally rhomboidal in outline (Plate II, 2). There are numerous scars of lateral outgrowths distributed among the leaf bases in an apparent (but not well-defined) helical arrangement (Plate II, 1). These scars are more or less circular in outline (Plate II, 3) and have a diameter of 4.9 mm (3.7–7) × 5.4 mm (4.1–8.6). There is no evidence of cataphylls (Plate II, 1, 2).

Pith. The pith is large and located in the central part of the axis. It is slightly elliptical in cross section (Plate III, 1) and has a diameter of 29.2 mm × 32.5 mm. The centre of the pith is highly mineralized, and anatomical details are only preserved in its peripheral part (Plate III, 1). This preserved part is composed of parenchyma cells and numerous idioblasts bearing dark content (Plate III, 2, 3). The parenchyma cells are thin-walled and more or less polyhedral (Plate III, 2, 3), with a diameter of 61.9 μm (45.8–81.2) × 91.6 μm (66.6–117.8) in cross section and 67.7 μm (49.4–88.3) × 105.7 μm (73.1–164.5) in radial section. The idioblasts are similar to the fundamental parenchyma cells in shape (Plate III, 2, 3) and have a diameter of 86.2 μm (59.8–114.6) × 109.1 μm (84.7–132.4) in cross section and 71 μm (55.6–97.3) × 113.6 μm (79.1–158.3) in radial section. There is no evidence of medullary vascular bundles and mucilage canals in the preserved part of the pith (Plate III, 2).

Vascular cylinder. The vascular cylinder comprises a single xylem and phloem ring arranged in a collateral plan (Plate III, 4). Both vascular tissues are separated by a fascicular cambium (Plate III, 4), which is up to 0.7 mm wide and forms a continuous ring between them. Details of the cellular structure of the cambium are, however, not preserved.

The xylem ring is centrifugal, narrow and about 5 mm wide (Plate III, 4). Primary xylem tracheids are oval, polygonal or irregularly polygonal in cross section (Plate III, 5, 6). They are arranged in numerous strands, separated from each other by medullary rays, and distributed around the periphery of the pith, forming a typical eustele (Plate III, 4, 5). Protoxylem and metaxylem were tentatively distinguished by differences in the diameter of their tracheids in cross section (Plate III, 6). In the observed longitudinal sections, details of their tracheids are not preserved and it is not possible to differentiate both properly. The endarch protoxylem (Plate III, 5, 6) is composed of few and poorly preserved tracheids, which have a tangential diameter of 7 μm (5.1–9.6) and a radial diameter of 10.9 μm (8.3–14). Metaxylem tracheids have a tangential diameter of 15.2 μm (10.6–21.1) and a radial diameter of 19.7 μm (16.9–22.4). The primary xylem is generally in direct contact with the secondary xylem (Plate III, 5, 6), but some strands bearing poorly preserved tracheids occur isolated within the periphery of the pith (Plate III, 7).

Secondary xylem is well-developed and lacks evidence of growth rings. It is arranged in radial bands generally composed of 2–9 rows of tracheids (Plate IV, 1). These tracheid bands are separated from each other by parenchymatous medullary and secondary rays (Plate III, 4; Plate IV, 1). Except for the rays, there is no evidence of other parenchymatous tissue between the secondary xylem (Plate IV, 1, 2). The tracheids are generally polygonal in cross section (Plate IV, 2), with a tangential diameter of 25.3 μm (19.2–31.1) and a radial diameter of 27.8 μm (22.2–34.6). They exhibit 1–2 seriate pitting in their radial walls and helical thickenings are present (Plate IV, 3, 4). When 2 seriate, pits are alternately or suboppositely arranged (Plate IV, 3). The pits are bordered, contiguous, and araucarioid (Plate IV, 3), with a vertical diameter of 9.1 μm (6.5–12.5) and a horizontal diameter of 10.4 μm (7.5–14).

The phloem zone is broader than the xylem, and up to 6.5 mm wide. It contains a large number of fibres, and these are irregularly polygonal or more or less rectangular in cross section (Plate V, 1, 2), with a tangential width of 29.3 μm (15.9–43.8) and a radial length of 85.8 μm (52.1–113.4). They have thick walls, very narrow lumina, and are mostly grouped in nests (Plate V, 1, 2). The fibre nests are arranged in radial bands, and in these bands (Plate V, 1), they are alternating with layers of smaller and thinner-walled cells (Plate V, 2). These might be parenchyma and/or sieve cells, but they could not be observed and distinguished in longitudinal sections.

Radial system. The radial system transecting the vascular cylinder is composed of numerous medullary and secondary rays (Plate III, 4, 5, 6; Plate IV, 1; Plate V, 1, 3). The medullary rays are multiseriate and high to very high, commonly with more than 30 cells in height (Plate V, 3). The wide medullary rays contain vascular traces (Plate V, 3). There are also many smaller circular structures passing out through the rays (Plate V, 3), and these might be mucilage canals, but it is difficult to determinate that as they are not well-preserved. The secondary rays are rarely uniseriate and mostly biseriate (Plate V, 3, 4). The uniseriate ones are 5–15 cells high, whereas the biseriate ones may range from 10 to more than 30 cells in height (Plate V, 3, 4).

The rays are composed of parenchymatous cells. In the radial section of the xylem, ray cells are rectangular, have smooth vertical and horizontal walls (Plate IV, 5, 6), and are 40.2 μm (33.4–48.8) high and 114.1 μm (93.2–140.2) wide. Cross-field pitting could not be detected. In the radial section of the phloem, ray cells usually have an elongate hexagonal or rectangular shape with smooth vertical and horizontal walls (Plate V, 5, 6), and are 37.4 μm (27.1–47) high and 118.6 μm (85.5–140) long. The ray parenchymatous cells are polygonal, elliptical, and sometimes rectangular in outline in tangential section (Plate V, 4), with a vertical diameter of 34.9 μm (26.5–42.5) and a horizontal diameter of 47.6 μm (34.1–64.7).

Vascular traces. The vascular cylinder is segmented by numerous vascular traces departing from multiple sites around the stele. The traces originate from the primary and secondary xylem, pass out through the large multiseriate medullary rays in a horizontal path, and then curve upwards and extend into the cortex (Plate V, 3; Plate VI, 1, 2). In cross

Plate III. *Iratinia australis* gen. nov. et sp. nov. (1) General view of the pith showing its preserved part (arrow). Scale bar = 5 mm; specimen MCT1487-PB. (2) Parenchyma cells and idioblasts from the pith. Scale bar = 200 μm; slide MCT1487-PB-1. (3) Detail of the parenchyma cells and idioblasts from the pith. Scale bar = 100 μm; slide MCT1487-PB-1. (4) General view of the vascular cylinder showing the position of the primary xylem (px), secondary xylem (sx), cambium (c), and phloem (ph), and the numerous medullary and secondary rays. Scale bar = 2.5 mm; slide MCT1487-PB-2. (5) Detail of the primary xylem strands. Scale bar = 200 μm; slide MCT1487-PB-2. (6) Primary xylem strand with endarch maturation showing cells of the protoxylem (white arrow) and metaxylem (black arrow). Scale bar = 50 μm; MCT1487-PB-2. (7) Poorly preserved strand of tracheids isolated within the periphery of the pith (arrow). Scale bar = 100 μm; MCT1487-PB-2.

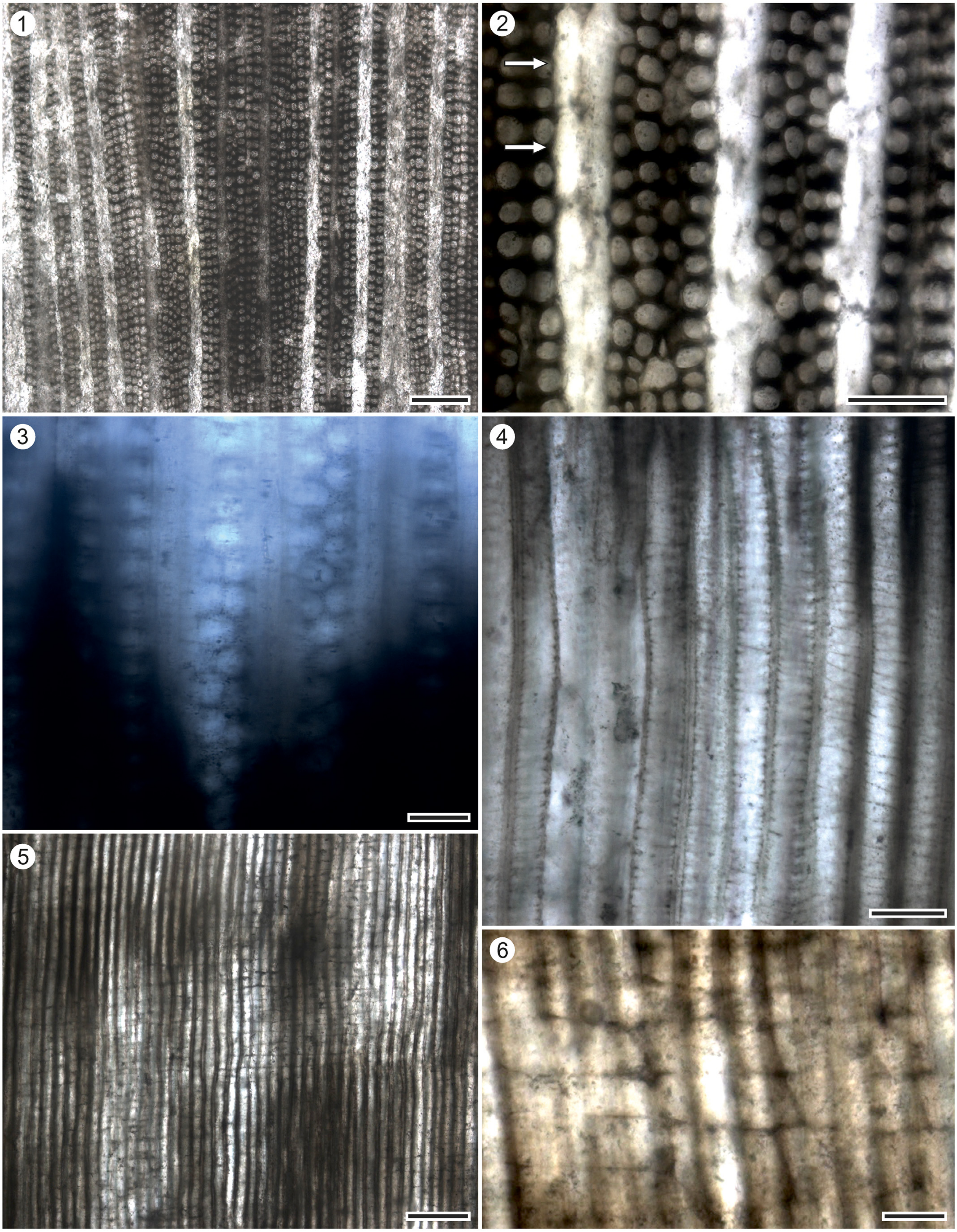
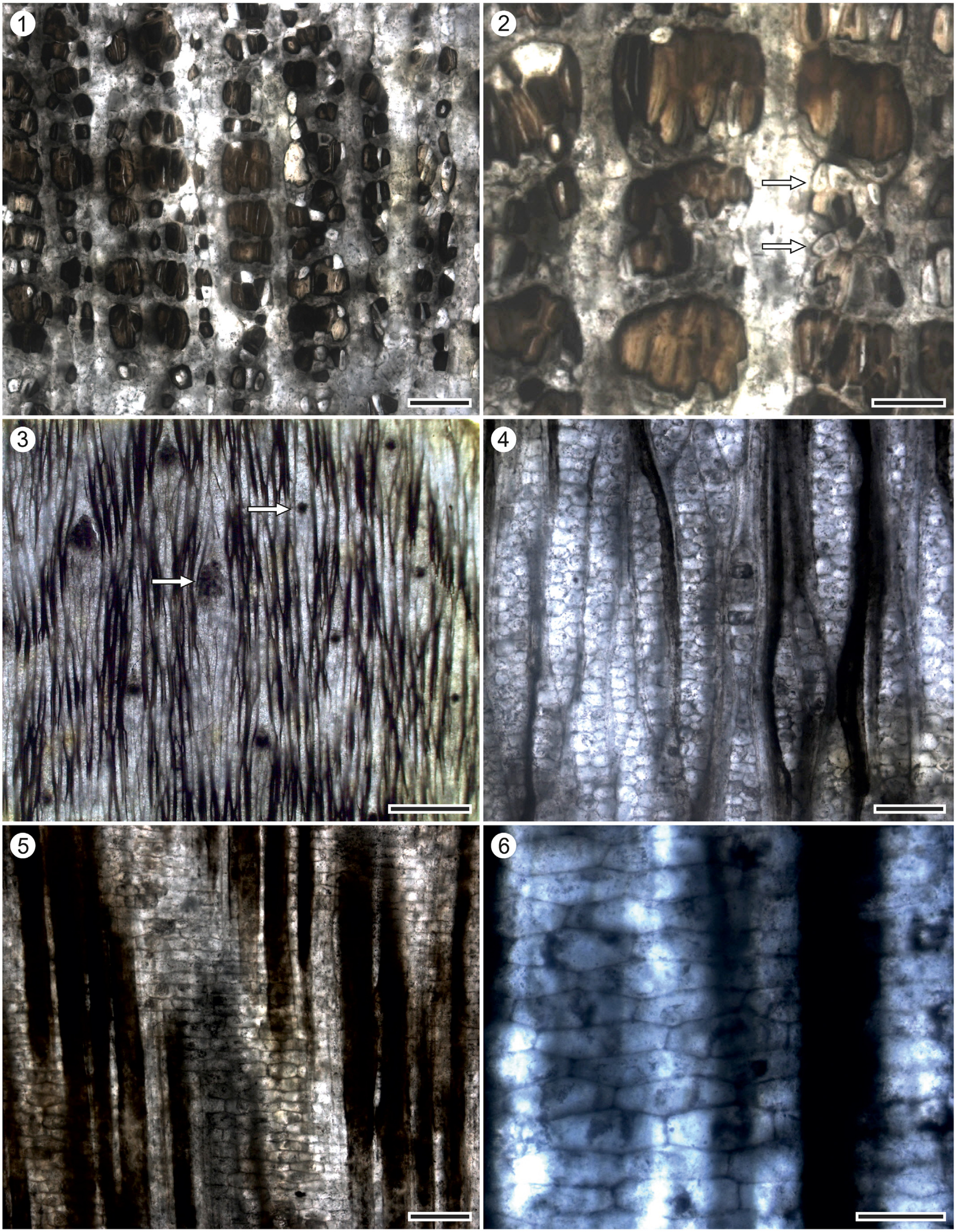


Plate IV. *Iratinia australis* gen. nov. et sp. nov. (1) Secondary xylem arranged in radial bands separated by medullary rays. Scale bar = 200 μm; slide MCT1487-PB-2. (2) Detail of the secondary xylem and ray cells in cross section (arrows). Scale bar = 100 μm; slide MCT1487-PB-2. (3) Tracheids of the secondary xylem exhibiting 1–2 seriate araucarioid pitting. Scale bar = 20 μm; slide MCT1487-PB-3. (4) Tracheids of the secondary xylem with helical thickenings. Scale bar = 50 μm; slide MCT1487-PB-3. (5) Rays of the xylem in radial section. Scale bar = 200 μm; slide MCT1487-PB-3. (6) Detail of the ray cells in the radial section of the secondary xylem. Scale bar = 50 μm; slide MCT1487-PB-3.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section, the traces of the larger lateral outgrowths apparently follow a straight path into the more or less circular scars visible on the surface of the specimen (Plate VI, 3), whereas the leaf traces turn and form a complex girdling meshwork in the cortex (Plate VI, 4, 5) before entering the leaf bases.

Cortex. The cortex is about 3.5 mm wide. It is composed of parenchymatous cells and irregularly or elliptical shaped structures bearing dark content (Plate VI, 6, 7). The latter are randomly distributed among the parenchymatous cells and seem to represent mucilage cavities rather than canals, as there is no evidence of canal-like structures in the longitudinal section of the cortex. The parenchyma cells are irregularly polygonal, elliptical, and sometimes laterally elongated in cross section (Plate VI, 7, 8), with a diameter of 58.6 μm (34.3–82.8) × 106 μm (71.1–152.2).

Comparisons: The presence of (1) a large pith with numerous idioblasts, (2) a narrow centrifugal xylem ring, (3) tracheids with araucarioid pitting, (4) numerous medullary and secondary rays, (5) multilacunar vascular traces passing out through large multiseriate rays, (6) leaf traces forming a girdling meshwork in the cortex, (7) parenchymatous cortex with mucilage-bearing structures, and (8) an external armour of persistent leaf bases, suggest that the specimen described herein has botanical affinities with Cycadales and is not related to lycopsids as previously suggested (Guerra-Sommer, 1981). These morpho-anatomical features typically occur in both living and extinct cycads, and the girdling leaf traces are considered a synapomorphy of this order of plants (e.g. Mettenius, 1861; Worsdell, 1898; Chamberlain, 1911, 1919, 1935; Gould, 1971; Smoot et al., 1985; Stevenson, 1990, 1992; Artabe et al., 2005; Wang et al., 2011; Martínez et al., 2012).

One of the most remarkable characteristics of the specimen is the large number of lateral outgrowth scars distributed among the leaf bases. At first glance, they may resemble the flower-like organ scars so conspicuous along the surface of some bennetitalean fossil stems. Vegetative axes of Bennettitales and Cycadales are anatomically very similar, but the former possess narrower rays and leaf traces that do not form the girdling pattern so characteristic of cycads and also present in the material described herein (e.g. Nishida et al., 1991; Taylor et al., 2009; Jud et al., 2010). It is unclear what type of organ developed at those lateral outgrowth scars visible on the surface of the specimen. One hypothesis is that they may represent adventitious buds scars, which are common in extant cycads (Stevenson, 2020) and occur in fossils ones as well (Martínez et al., 2012). An alternative interpretation is that they are scars of detached cones that remained along the axis during the plant lifespan. Most of the extant Cycadales have terminal cones, but some taxa such as *Macrozamia moorei* produce numerous laterally borne cones among the leaf bases (Chamberlain, 1913).

Extant cycads comprise 10 genera (Table 1), and these were divided into the families Cycadaceae, Stangeriaceae, and Zamiaceae in the last comprehensive systematic treatment of Cycadales (Stevenson, 1992). *Cycas* is considered as the only extant member of the family Cycadaceae (Stevenson, 1992) and has a polyxylic vascular cylinder, differing from the specimen described here (Greguss, 1968; Terrazas, 1991). The living *Stangeria* and *Bowenia* were placed in Stangeriaceae (Stevenson, 1992), but molecular-based phylogenies do not support their inclusion within the same family (Rai et al., 2003; Chaw et al., 2005; Salas-Leiva et al., 2013). Although monoxylic, both genera have subterraneous and tuberose stems with abundant parenchyma among the secondary xylem, differing from the material studied herein (e.g. Worsdell, 1900; Marsh, 1914; Chamberlain, 1916; Smoot et al., 1985).

Within Zamiaceae, the extant genera *Zamia*, *Microcycas*, *Ceratozamia*, and *Dioon* are monoxylic such as the specimen investigated in this paper (Artabe et al., 2005; Martínez et al., 2012). *Zamia*, *Microcycas*, and *Ceratozamia*, however, have cataphylls and abundant parenchyma among secondary xylem, differing from the material described herein (Artabe et al., 2005; Martínez et al., 2012). *Dioon* shares many characteristics with the specimen studied here. Both have a well-developed and relatively dense wood zone, helical thickenings on secondary xylem tracheids, and a persistent armour of helically arranged leaf bases (Chamberlain, 1911, 1935; Langdon, 1920; Greguss, 1968). However, *Dioon* has cataphylls, mucilage canals, and a narrower phloem zone and larger cortex than the fossil described herein. The latter has a relatively narrow cortex, whereas all extant cycads have a larger one. The comparison between the extant cycads and the specimen studied here are summarized in Table 1.

Before this report, a total of 18 fossil genera of anatomically preserved cycad axes were described from the late Permian up to the Palaeogene (Table 1). From those, *Antarcticycas*, *Charmorgia*, *Vladiloxylon, Michelilloa*, *Lyssoxylon* from the Triassic, and *Fascisvarioxylon*, and *Lioxylon* from the Jurassic have a single xylem ring such as the specimen described here (Jain, 1962; Archangelsky and Brett, 1963; Gould, 1971; Ash, 1985; Smoot et al., 1985; Lutz et al., 2003; Zhang et al., 2006). *Shuichengoxylon* from the late Permian and *Centricycas* from the Cretaceous are incompletely preserved (Cantrill, 2000; Wang et al., 2011). The former was interpreted as monoxylic (Wang et al., 2011), whereas it is difficult to decide whether the latter was monoxylic or polyxylic.

The fossil genera *Fascisvarioxylon* and *Lioxylon* develop centripetal and centrifugal xylem, differing from the material studied in this paper (Jain, 1962; Zhang et al., 2006). *Antarcticycas* has numerous mucilage canals, no persistent armour of leaf bases, and generally a greater amount of parenchyma within the xylem cylinder than in the specimen described herein (Smoot et al., 1985; Hermsen et al., 2009). However, some larger axes of *Antarcticycas* have a well-developed and continuous xylem cylinder, and in these specimens, the cortex is relatively narrow such as the material studied here (Hermsen et al., 2009). *Shuichengoxylon* is based on a single wood fragment and this taxon differs from the Irati specimen in having a much larger xylem cylinder (Wang et al., 2011). *Vladiloxylon* has a small pith, uniseriate and low rays, and a large cortex (Lutz et al., 2003), whereas *Centricycas* has a loose secondary xylem and up to 3 seriate pitting on the tracheid radial walls (Cantrill, 2000) and *Charmorgia* possesses cataphylls, abundant wood parenchyma, and a larger cortex than the specimen investigated herein (Ash, 1985; Martínez et al., 2012).

Michelilloa possesses a larger parenchymatous cortex (Archangelsky and Brett, 1963), and the fossil taxon that seems to share more anatomical characteristics with the specimen studied here is *Lyssoxylon*. The latter has a narrow cortex, phloem with abundant fibres, well-developed and relatively dense wood zone, secondary xylem tracheids with helical thickenings, and primary xylem arranged in strands and distributed around the pith such as the specimen described herein (Gould, 1971). However, *Lyssoxylon* has a narrower phloem zone and lacks the lateral outgrowth scars, as well as the well-defined and separated rhomboidal leaf bases so conspicuous in the material described in this study. The comparison between fossil cycad vegetative axes and the specimen studied here are summarized in Table 2.

Considering the differences between the specimen studied here and other cycad taxa, we propose the new fossil genus and species *Iratinia australis*. This taxon is anatomically most similar to the fossil genus *Lyssoxylon*. The latter was considered close to the living *Dioon* (Gould,

Plate V. *Iratinia australis* gen. nov. et sp. nov. (1) Phloem with abundant fibres arranged in radial bands and grouped in nests. Scale bar = 200 μm; slide MCT1487-PB-2. (2) Detail of the fibre nests and the smaller and thinner-walled cells of the phloem (arrows). Scale bar = 100 μm; slide MCT1487-PB-2. (3) Tangential section of the phloem showing the radial system with medullary and secondary rays. Note the vascular traces in the wide medullary rays (lower arrow) and mucilage canals? passing out through the rays (upper arrow). Scale bar = 2 mm; slide MCT1487-PB-4. (4) Detail of the secondary rays in the tangential section of the phloem. Scale bar = 200 μm; slide MCT1487-PB-4. (5) Radial section of the rays in the phloem. Scale bar = 100 μm; slide MCT1487-PB-5. (6) Detail of the ray cells in the radial section of the phloem. Scale bar = 100 μm; MCT1487-PB-5.

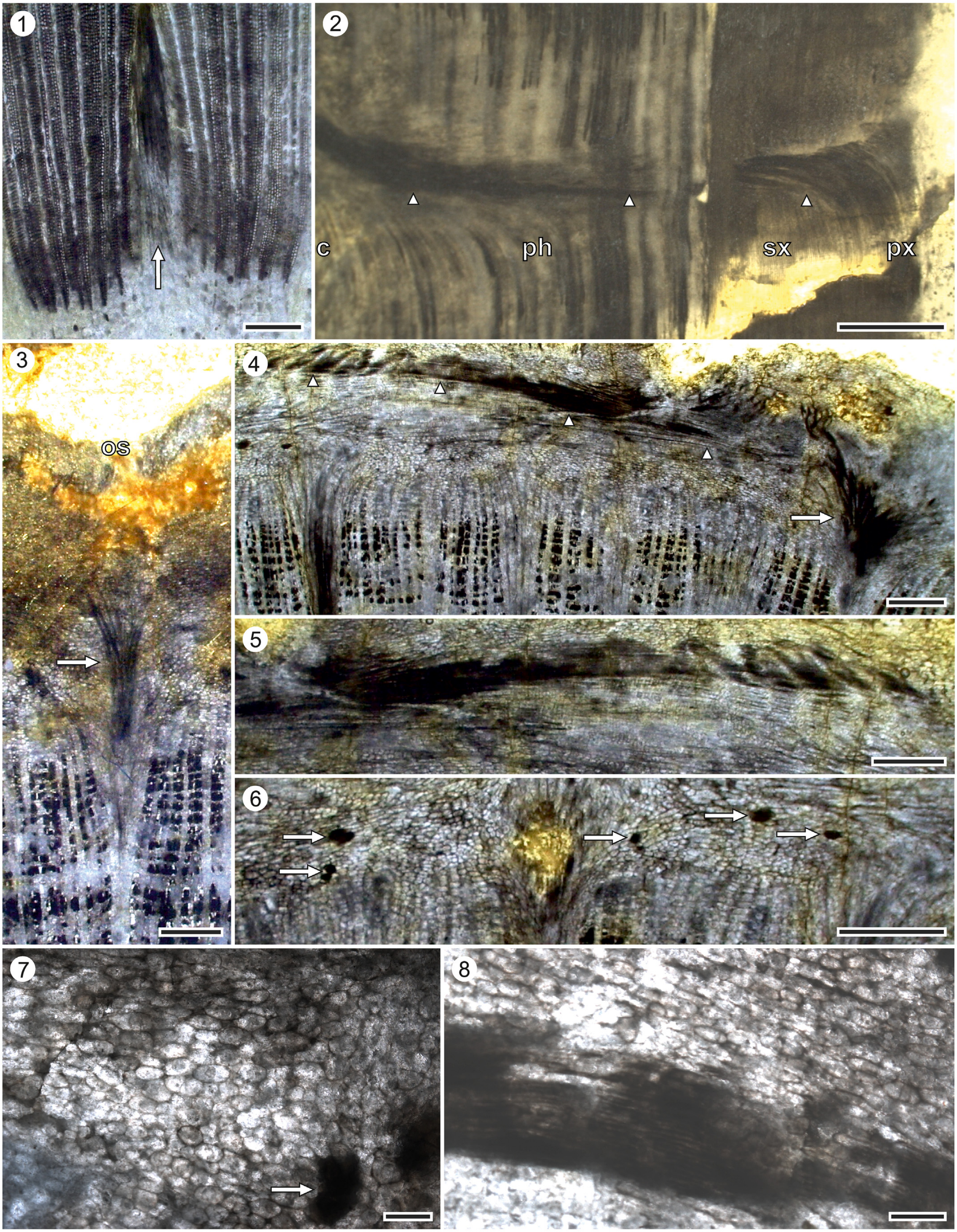
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Table 1

Comparison between *Iratinia* and vegetative axes of extant genera of Cycadales. Based on Artabe et al. (2005), and Martínez et al. (2012).

Genera	Mucilage system	Medullary bundles	Cone domes	Vascular cylinder	Xylem develop.	Wood parenchyma	Type of pitting	Bordered pitting seriation	Cortex
Iratinia gen. nov.	Cavities and possible radial canals	?	?	Monoxylic	Centrifugal	Scanty	Araucariod bordered	1–2 seriate	Narrow
Bowenia	Canals	Absent	Present	Monoxylic	Centrifugal	Abundant	Scalariform and araucariod bordered	Multiseriate	Well-developed
Ceratozamia	Canals	Absent	Present	Monoxylic	Centrifugal	Abundant	Scalariform and araucariod bordered	1–3 seriate	Well-developed
Cycas	Canals	Absent	Present	Polyxylic	Centrifugal, sporadically centripetal in some species	Abundant	Scalariform and araucariod bordered	Uni- to multiseriate	Well-developed
Dioon	Canals	Absent	Present	Monoxylic	Centrifugal	Scanty	Scalariform and araucariod bordered	1–3 seriate	Well-developed
Encephalartos	Canals	Present	Absent	Polyxylic	Centrifugal, sporadically centripetal in some species	Abundant	Scalariform and araucariod bordered	Uni- to multiseriate	Well-developed
Lepidozamia	Canals	Present	Absent	Polyxylic	Centrifugal, sporadically centripetal in some species	Abundant	Scalariform and araucariod bordered	1–3 seriate	Well-developed
Macrozamia	Canals	Present	Absent	Polyxylic	Centrifugal, sporadically centripetal in some species	Abundant	Scalariform and araucariod bordered	Uni- to multiseriate	Well-developed
Microcycas	Canals	Absent	Present	Monoxylic	Centrifugal	Abundant	Scalariform and araucariod bordered	1–3 seriate	Well-developed
Stangeria	Canals	Absent	Present	Monoxylic	Centrifugal	Abundant	Scalariform	–	Well-developed
Zamia	Canals	Absent	Present	Monoxylic	Centrifugal	Abundant	Scalariform, occasionally araucariod bordered	Multiseriate	Well-developed

1971), and was informally included in the family Zamiaceae, tribe Diooeae, based on the absence of centripetal xylem and medullary bundles (Artabe et al., 2005). *Iratinia* also shares aspects with *Dioon* and lacks centripetal xylem, but it is unknown whether the new taxon proposed here had medullary bundles or not, since details of a large part of its pith are not preserved. Considering this uncertainty, and as the families and tribes within Cycadales are based on phytochemistry and both reproductive and vegetative structures of extant genera (Stevenson, 1990, 1992), and that the phylogenetic relationship among the cycad genera is not completely resolved yet (e.g. Hill et al., 2003; Rai et al., 2003; Chaw et al., 2005; Salas-Leiva et al., 2013), we took a more cautious approach here and classify *Iratinia* as family *incertae sedis*.

5. Discussion

5.1. Remarks about growth structure

The narrow but well-developed secondary xylem indicates that the axis investigated here was part of an adult plant. Most of the extant cycads have aerial and arborescent axial vegetative structure (either short or several meters tall), but some genera develop exclusively subterranean and tuberous stems (Chamberlain, 1919). The subterranean stems are fleshy and exhibit a wrinkled surface and distorted vascular cylinder, occasioned by the contraction of the stem during the plant growth (Stevenson, 1980). There is no evidence of such a contraction on the specimen described herein, and based on its wood cylinder, non-tuberous structure, and armour of well-defined leaf bases, *Iratinia* can be interpreted as a plant that developed aerial and arborescent axial structure.

Cycadales are generally described as plants with unbranched stems, but vegetative branching is common in living taxa of the order (Stopes, 1910; Stevenson, 2020). Due to its incomplete preservation, it is difficult to determinate whether the axis described herein was a branch or part of the main stem of the plant. However, if one interprets it as the main stem of the plant based on the well-developed wood cylinder, *Iratinia* would have had a much more slender axial structure than those of most extant cycads. Some living taxa such as *Zamia obliqua* and *Cycas canalis* possess slender stems as well, and the Triassic cycad *Leptocycas*, which is based on compressed material, was reconstructed as a plant with slender growth habit (Delevoryas and Hope, 1971). Regardless of its position on the plant, the axis described herein seems to have had robust mechanical support provided by the wood cylinder, large phloem zone with abundant thick-walled fibres, and external armour of leaf bases.

5.2. Biogeographical and evolutionary significance

The oldest convincing cycad foliage comes from strata of China and South Korea, tentatively placed into the latest Pennsylvanian–Cisularian (Pott et al., 2010). However, the earliest undisputable cycad fossils are impressions and compressions of megasporophylls from China, which are very similar to those of the living *Cycas* (Gao and Thomas, 1989; Condamine et al., 2015). These reproductive structures were collected from the Shihhotse Formation and included in the fossil genus *Crossozamia* (Gao and Thomas, 1989). This formation was first interpreted as lower Permian, but a more recent biostratigraphic review placed its base into the Guadalupian (Wang, 2010). The specimen described herein as *Iratinia australis* is the oldest known and well-dated anatomically preserved vegetative axes bearing affinities with Cycadales. It indicates that the overall anatomy of monoxylic cycad axes, as well the armour of leaf bases and the girdling leaf traces characteristic for Cycadales, were already established in the Kungurian. The major difference is that *Iratinia* has a relatively thin cortex, whereas other cycads generally have a larger one. However, within fossil

Plate VI. *Iratinia australis* gen. nov. et sp. nov. (1) Detail of the xylem cylinder showing the origin of the vascular traces (arrow). Scale bar = 0.5 mm; slide MCT1487-PB-2. (2) Vascular trace (arrows) departing from the primary xylem (px), crossing the secondary xylem (sx) and phloem (ph), and curving upwards and extending into the cortex (c). Scale bar = 2.5 mm; slide MCT1487-PB-3. (3) Vascular trace (arrow) extending apparently in straight path until the lateral outgrowth scars (os). Scale bar = 1 mm; slide MCT1487-PB-2. (4) Leaf trace forming a complex girdling meshwork in the cortex (arrows). Scale bar = 1 mm; slide MCT1487-PB-2. (5) Girdling leaf trace in the cortex. Scale bar = 0.5 mm; slide MCT1487-PB-2. (6) General view of the cortex showing the parenchymatous cells and mucilage cavities (arrows). Scale bar = 1 mm; slide MCT1487-PB-2. (7) Detail of the cortex parenchyma cells and from a mucilage cavity (arrow). Scale bar = 200 μm; slide MCT1487-PB-2. (8) Detail of the cortex parenchyma cells showing a part of a girdling leaf trace. Scale bar = 200 μm; slide MCT1487-PB-2.

Table 2
Comparison between *Iratinia* and vegetative axes of extinct genera of Cycadales. Legend: Cisuralian (CI), Lopingian (LO), Lower Triassic (LT), Upper Triassic (UT), Middle Jurassic (MJ), Upper Jurassic (UJ), Lower Cretaceous (LC), Upper Cretaceous (UC), Palaeogene (PA). Based on Jain (1962), Archangelsky and Brett (1963), Gould (1971), Petriella (1969, 1972), Ash (1985), Smoot et al. (1985), Nishida et al. (1991), Cantrill (2000), Lutz et al. (2003), Artabe et al. (2004, 2005), Hermsen et al. (2009), Wang et al. (2011), Zhang et al. (2006, 2012) and Martínez et al. (2012); Martinez et al. (2017).

Genera	Age	Mucilage system	Medullary bundles	Cone domes	Vascular cylinder	Xylem develop.	Wood parenchyma	Type of pitting	Bordered pitting seriation	Cortex
Iratinia gen. nov.	CI	Cavities and possible radial canals	?	?	Monoxylic	Centrifugal	Scanty	Araucariod bordered	1–2 seriate	Narrow
Shuichengoxylon	LO	?	?	?	Monoxylic	Centrifugal	Scanty	Araucariod bordered	Mainly 2 seriate	?
Antarcticycas	LT	Canals	Absent	Present	Monoxylic	Centrifugal	Abundant, but scanty in some larger stems	Araucariod bordered	Multiseriate	Well-developed, but narrow in some larger stems
Charmorgia	UT	Canals	Present	Absent	Monoxylic	Centrifugal	Abundant	Araucariod bordered	1–3 seriate	Well-developed
Lyssoxylon	UT	Canals	Absent	Absent	Monoxylic	Centrifugal	Scanty	Araucariod bordered	1–3 seriate	Narrow
Michelilloa	UT	Canals	Absent	Absent	Monoxylic	Centrifugal	Scanty	Scalariform and araucariod bordered	1–3 seriate	Well-developed
Vladiloxylon	UT	Canals	Absent	Absent	Monoxylic	Centrifugal	Scanty	Araucariod bordered	?	Well-developed
Lioxylon	MJ	Cavities	Present	Absent	Monoxylic	Centrifugal and centripetal	Abundant	Araucariod bordered	1–3 seriate	Well-developed
Sinocycadoxylon	MJ	Canals	Present	Absent	Polyxylic	Centrifugal and centripetal	Scanty	Araucariod bordered	1–3 seriate	?
Fascisvarioxylon	UJ?	Cavities	Present	?	Monoxylic	Centrifugal and centripetal	Abundant	Araucariod bordered	1–3 seriate	Well-developed
Sanchucycas	LC	Cavities	Absent	Absent	Polyxylic	Centrifugal	Abundant	Araucariod bordered	1–2 seriate	?
Brunoa	UC	Cavities	Absent	Present	Polyxylic	Centrifugal	Scanty	Araucariod bordered	1–3 seriate	Well-developed
Centricycas	UC	Canals	Present	Absent	?	Centrifugal	Abundant	Araucariod bordered	1–3 seriate	?
Neochamberlainia	UC	Canals	Present	Absent	Polyxylic	Centrifugal and centripetal	Abundant	Araucariod bordered	1–3 seriate	Well-developed
Wintucyas	UC	Canals	Present	Absent	Polyxylic	Centrifugal and centripetal	Abundant	Araucariod bordered	1–2 seriate	Well-developed
Worsdellia	UC	Canals	Present	Absent	Polyxylic	Centrifugal and centripetal	Abundant	?	?	Well-developed
Zamuneria	UC	Canals	Present	Absent	Polyxylic	Centrifugal	Abundant	Araucariod bordered	1–3 seriate	Well-developed
Bororoa	PA	Canals	Absent	Present	Polyxylic	Centrifugal	Scanty	Araucariod bordered	Multiseriate	Well-developed
Menucoa	PA	Canals	Present	Absent	Polyxylic	Centrifugal and centripetal	Abundant	Araucariod bordered	Multiseriate	Well-developed

Cycadales, a narrow cortex is not an exclusivity of the new taxon described herein, since it also occurs in *Lyssoxylon* and large axes of *Antarcticycas*, both from the Triassic.

Iratinia is evidently monoxylic and supports the hypothesis that polyxyly is apomorphic within Cycadales (Crane, 1988; Stevenson, 1990). All the know Permian and Triassic anatomically preserved cycad axes are monoxylic (Artabe et al., 2004; Wang et al., 2011; Zhang et al., 2012), and the oldest polyxylic cycad taxon reported so far is *Sinocycadoxylon* from the Middle Jurassic of China (Zhang et al., 2012). Except for the medullary rays, there is no other evidence of parenchymatous tissue within the secondary xylem of *Iratinia*. Other early cycads, such as the late Permian *Shuichengoxylon*, and the Triassic *Vladiloxylon, Michelilloa*, and *Lyssoxylon* have a similar wood structure as well (Archangelsky and Brett, 1963; Gould, 1971; Lutz et al., 2003; Wang et al., 2011). The only exceptions are the Triassic *Charmorgia* and *Antarcticycas*, but in larger stems of the latter taxon, the wood zone is also relatively dense and well developed (Hermsen et al., 2009). In contrast, extant cycads have much more parenchymatous tissue among the secondary xylem and the only exception is *Dioon*. This may suggest that a relatively dense secondary xylem is plesiomorphic within Cycadales, supporting the hypothesis of a gradual reduction of secondary xylem and increase of parenchyma in the vegetative axes of this particular order of plants (Taylor et al., 2009).

The specimen described herein is the first record of an anatomically preserved cycad axis from the Permian of Gondwana, and indicates the presence of Cycadales in the Brazilian part of this palaeocontinent during the Kungurian. Before this report, the most compelling evidence of Cycadales fossils from similar (but not the same) age were fronds and reproductive structures from Cathaysia (Gao and Thomas, 1989; Pott et al., 2010; Wang et al., 2011). North American Pennsylvanian and Cisularian fossils first included into Cycadales are now considered part of a different group of plants (Anderson et al., 2007; Cleal and Thomas, 2019). All in all, the presence of this specimen in Western Gondwana may suggest that during the Cisularian, cycads or their direct ancestors were already widely/worldwide distributed.

Declaration of Competing Interest

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

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Outlook

Once the Permo-Carboniferous extreme icehouse conditions started to cease, sub- to arborescent lycopsids successfully thrived in Cisuralian to Guadalupian (early to middle Permian) post-glacial terrains of South America (south-west Gondwana) as elements of the *Glossopteris* flora (**Publication 1**). In the South African part of Gondwana, they flourished as components of that flora during the Guadalupian in localities such as the Leeukuil, Hammanskraal, and West Driefontein quarries (e.g., Anderson and Anderson, 1985; **Publication 2**). Most of the sub- to arborescent lycopsid macrofossils reported so far for the *Glossopteris* flora come from strata of the Paraná Basin in South America (**Publication 1**). At least in this basin, macrofossils of these plants disappeared from the record as arid conditions increased in the region towards the end of the Permian (**Publication 1**).

In contrast, lycopsid macroremains interpreted as herbaceous forms are rare in deposits including elements of the *Glossopteris* flora (e.g., McLoughlin et al., 2015; **Publications 1** and **3**, and citations therein). Among the few fossil-taxa of herbaceous forms so far described for the flora, most come from the Permian strata of the eastern Gondwanan sector, including the high palaeolatitudes of East Antarctica (McLoughlin et al., 2015; **Publications 1** and **3**, and citations therein). To date, evidence of sub- to arborescent lycopsids has still not been found in Permian beds from Antarctica. Overall, lycopsid macrofossils, regardless if belonging to herbaceous or sub- to arborescent plants, are rare in the Permian sedimentary successions from eastern Gondwana. Yet, such eastern deposits yielded abundant dispersed spores, including diversified megaspore assemblages, interpreted as potentially belonging to lycopsids (e.g., Glasspool, 2003; Tewari and Jha, 2007; Tewari, 2008). These lycopsid-like megaspores, at least theoretically, suggest the presence of a diversified array of heterosporous lycopsids of unknown growth habits, which are underrepresented in the macrofossil record (e.g., Glasspool, 2003; Tewari and Jha, 2007; Tewari, 2008).

The sub- to arborescent lycopsid macrofossils of the *Glossopteris* flora comprise incompletely preserved remains (e.g., **Publications 1** and **2**). The specimens collected so far and available in palaeobotanical collections lack one or more features with systematic significance, such as rooting system and evidence for the presence or absence of ligules, and reproductive structures are only known for two fossil-genera (e.g., Rao, 1940; Kräusel, 1961; Chaloner et al., 1979; Rayner, 1985; Spiekermann et al., 2018; **Publications 1** and **2**). These numerous missing characters have been precluding cladistic approaches on these plants, such as those conducted on selected Palaeozoic arborescent lycopsids from Euramerica (e.g., Bateman et al., 1992; DiMichele and Bateman, 1996; DiMichele and Bateman, 2020).

Among the recognised sub- to arborescent lycopsid fossil-genera from the flora, only the monotypic *Azaniadendron* from Guadalupian deposits of South Africa can be classified at an ordinal level with some degree of security (**Publication 2**). Considering its ligulate and heterosporous nature, plus the relatively broad size of some of its axes covered in leaf cushions, it can be assigned to the isoetalean clade (**Publication 2**). *Azaniadendron* differs from the most derived members of the isoetalean clade (i.e. the late Palaeozoic arborescent lycopsids belonging to the families Diaphorodendraceae, Lepidodendraceae and Sigillariaceae; DiMichele and Bateman, 1996) in having bisporangiate fertile areas rather than monosporangiate cones (**Publication 2**). However, it is not possible to place *Azaniadendron* soundly in an existing family of less derived isoetaleans (or propose a well-founded new family) due to the incomplete nature of its fossil remains, which lack structures of fundamental sub-ordinal systematic value, such as rooting system (**Publication 2**).

The systematic position of fossil-genera such as *Cyclodendron* remains unresolved, despite the reproductive structure of its type species *Cyclodendron leslii* (Seward) Kräusel being known (Kräusel, 1961; Rayner, 1985). Collected fossils of *Cyclodendron* lack convincing evidence of ligule (Kräusel, 1961; Rayner, 1985). After re-examining numerous specimens from the type locality (Leeukuil Quarries) in South Africa, I did not find convincing evidence of such a structure either. That is unusual because *Cyclodendron* is heterosporous, and it is well-known that lycopsids showing heterospory (Selaginellales and Isoetales) are typically ligulate (e.g., Meyen, 1987; Bateman and DiMichele, 1994; Kenrick and Crane, 1997; Taylor et al., 2009).

In the case of *Cyclodendron*, the following hypotheses can be postulated: (i) it evolved from a heterosporous lycopsid lineage but lost the ligule; (ii) heterospory evolved independently in eligulate forms as well; (iii) evidence of ligule is difficult to find or is not preserved in the known *Cyclodendron* specimens, which are represented mainly by impressions. These are significant open questions for understanding the lycopsid evolution in general, but unfortunately cannot be soundly resolved based on the available *Cyclodendron* fossils. Such as highlighted by Meyen (1972), the lack of evidence for a ligule does not necessarily mean that the plant was eligulate. Small structures like ligules can be obscured by a range of factors, including ontogeny, position on the plant (e.g., some taxa such as *Selaginella* have leaf-borne and not axillary-borne ligules), taphonomy, quality of preservation, as well as fracture plane of the fossil (e.g., Meyen, 1972; Gensel and Pigg, 2010; **Publication 2**). As mentioned by Chaloner (1968) as well, who undoubtedly examined many lycopsid fossils, in many cases, even well-preserved fossils of incontestably ligulate lycopsids, such as *Lepidodendron* and *Sigillaria*, lack convincing evidence of ligule or ligule pit.

While I remain doubtful whether *Cyclodendron* was eligulate or ligulate because ligules may just not have been preserved in the available fossils, *Azaniadendron* can no longer be considered eligulate (**Publication 2**). *Azaniadendron* and *Cyclodendron* co-occur in the Guadalupian deposits from the Hammanskraal and Leeukuil quarries in South Africa (e.g., Rayner, 1985; **Publication 2**). To date, they are the only sub- to arborescent lycopsid fossil-genera from the *Glossopteris* flora whose reproductive structures are known (Rayner, 1985, 1986; **Publication 2**). Interestingly, the reproductive parts of both were arranged in fertile areas or zones rather than compact cones (Kräusel, 1961; Rayner, 1985; **Publication 2**). Fertile areas rather than cones have also been reported in the few fertile lycopsid fossil-taxa known from the Carboniferous of Gondwana, such as *Lepidodendropsis devoogdi* Jongmans (1954) from Peru and *Bumbudendron paganzianum* Archangelsky et al. (1981) from Argentina. That may represent a more primitive evolutionary state (Chaloner and Boureau, 1967; Phillips, 1979).

In previous publications, *Azaniadendron* and *Cyclodendron*, as well as virtually all assumedly sub- to arborescent lycopsids from the *Glossopteris* flora (e.g., Rayner, 1985, 1986; Faria et al., 2009; Spiekermann et al., 2018; Carvalho et al., 2022), have been lumped in the family Lycopodiopsidaceae *sensu* Chaloner and Boureau (1967).

However, the fact is that the uncertainty about ligule, for instance, does not even allow a reliable ordinal classification for *Cyclodendron*. Besides, Lycopodiopsidaceae has little systematic meaning. It is based on deeply plesiomorphic characters, and fossil-genera lumped into the family, such as *Azaniadendron* and *Cyclodendron*, have substantial differences (**Publication 2**). In addition to the ambiguity about ligule, the fertile areas of *Cyclodendron* are interpreted as monosporangiate (Rayner, 1985), whereas those of *Azaniadendron* were bisporangiate (Rayner, 1986; **Publication 2**). Mono and bisporangiate reproductive structures are characters of systematic significance used to separate lycopsid families in cladistic studies (DiMichele and Bateman, 1996). The difference in reproductive characters between *Azaniadendron* and *Cyclodendron* suggests that the sub- to arborescent lycopsids from the *Glossopteris* flora may have been diversified not only at a generic but also at a suprageneric rank.

Another problem concerning *Cyclodendron* is the Gondwana-wide fragmented impressions of vegetative axes lumped in this fossil-genus. The vegetative axes of this fossil-taxon are covered in very simple leaf scars lacking parichnos and other distinctive characteristics (Kräusel, 1961; Rayner, 1985) and might be indistinguishable from poorly preserved or decorticated lycopsid axes of undetermined taxonomical affinities (e.g., Oliveira-Babinski and Rösler, 1984). Some fragmented vegetative axes from the Permian deposits of India assigned to *Cyclodendron leslii* are poorly preserved (cf. Surange, 1966, fig. 4, a–f; Chandra and Rigby, 1981, pl. 1, 3; Goswami et al., 2006, pl. 1, h–i), and in the absence of reproductive structures and epidermal information, taxonomical assignments of such type of fossils, should be interpreted with some reservation. The same applies to some *Cyclodendron leslii* samples from the Permian deposits of Australia (e.g., Rigby, 1966, pl. 30, 2). Other *Cyclodendron* fossil-species such as *C*. *golondrinensis* Cariglino et al. (2012) from the Cisuralian of Argentina and *C*. *andreisii* Herbst and Gutierrez (1995) are based on vegetative axes lacking information on epidermal features, which are known for the type species of this fossil-genus (Rayner, 1985). The technique used in **Publication 3,** based on Moisan (2012), may help to overcome problems concerning the lack of epidermal information in specimens, which lack cuticles, but still bear imprints of epidermal features preserved over their surface.

Other fossil-taxa from the *Glossopteris* flora, like *Brasilodendron* and *Lycopodiopsis*, continue far more problematic as their reproductive structures remain unknown (**Publication 1**). That also applies to the new fossil-species *Nothostigma sepeensis* Spiekermann et al. (**Publication 3**), as the reproductive structures of this fossil-genus remain obscure as well. The lack of detailed studies on long-ignored specimens such as those of *Nothostigma sepeensis* may have been obscuring the lycopsid morphological diversity of the *Glossopteris* flora. There may be, at least, some other new lycopsid fossil-taxa based on macrofossils waiting to be discovered and described, taking into account the morphological diversity of lycopsid-like spores documented in the Permian Gondwanan strata (e.g., Cauduro and Zingano, 1965; Wilder, 1980; Glasspool, 2003; Tewari and Jha, 2007; Tewari, 2008).

Brasilodendron includes the fossil-species *B*. *pedroanum* Chaloner et al. (1979) and *B*. *africanum* Lemoigne and Brown (1980). In Cisuralian strata from Brazil, nearly all lycopsid macrofossils exhibiting leaf cushions have been vigorously lumped into *Brasilodendron* or its type-species *B*. *pedroanum* (**Publication 1**). There is, however, a morphological and size disparity among Brazilian specimens assigned *B*. *pedroanum* (cf. Chaloner et al., 1979; Manfroi et al., 2012; Spiekermann et al., 2018; **Publication 1**). Some fossils assigned to it, for example, exhibit larger and nearly rhomboidal-like leaf cushions (cf. Manfroi et al., 2012, fig. 3, a–b). These are distinct from the typical fusiform cushions of *B*. *pedroanum* (cf. Chaloner et al., 1979, pl. I, 2). Other fossils, such as poorly preserved *in situ* stumps often cited as *B*. *pedroanum* in the literature (e.g., Jasper et al., 2006; Guerra-Sommer et al., 2008; Boardman et al., 2012), are much larger than the narrow and slender axes that form the basis of this fossil-species (Chaloner et al., 1979; Spiekermann et al., 2018). It is unknown whether these slender axes that characterise *B*. *pedroanum* correspond to stems of a small sub-arborescent plant or crown branches of a larger growth form (Spiekermann et al., 2018; **Publication 1**). To date, no fossil of *B*. *pedroanum* exhibiting evidence of branching has been discovered. Sound data that would justify connecting *B*. *pedroanum* with those large *in situ* stumps are still missing.

Brasilodendron africanum has been described based on three fragments of vegetative axes from the Guadalupian deposits of the Hammanskraal Quarry in South

Africa (Lemoigne and Brown, 1980). It is only known from this locality to date. I searched for its type material in the Evolutionary Studies Institute (former Bernard Price Institute for Palaeontological Research) in South Africa, where Lemoigne and Brown (1980) mentioned it was stored. Unfortunately, I could not locate the specimen. Therefore, our current knowledge of this fossil-species relies on the description and images published in Lemoigne and Brown (1980).

The fragmented state of the sub- to arborescent lycopsid macrofossils from the *Glossopteris* flora precludes sound reconstructions of their growth architectures. That also prevents cladistic analyses, which should primarily be based on whole reconstructed fossil plants (e.g., Bateman et al., 1992; DiMichele and Bateman, 1996; Cleal and Thomas, 2009). We do not know what exactly the Permian Gondwanan lycopsids looked like. We know that *Lycopodiopsis* and *Cyclodendron* exhibited dichotomous branching (e.g., Rayner, 1985; Faria et al., 2009), whereas all *Brasilodendron* and *Azaniadendron* fossils so far reported show no evidence of branching (Spiekermann et al., 2018; **Publications 1** and **2**). *In situ* stumps preserved in Cisuralian strata from South America, though exhibiting poorly preserved characters with generic taxonomical significance, indicate that at least some of these lycopsids could have been relatively large plants, with stem diameters reaching up to 75 cm (Cúneo and Andreis, 1993; Jasper and Guerra-Sommer, 1998; Mottin et al., 2022; **Publication 1**).

There is no convincing evidence of giant arborescent lycopsids in the *Glossopteris* flora deposits, such as the lepidodendrids from the Carboniferous of Euramerica, which could reach up to 2 m in diameter and about 45 m in height (e.g., Thomas and Cleal, 2018, and citations therein). Indeed, there is no convincing evidence of typical late Palaeozoic arborescent lycopsid fossil-genera from Euramerica in the *Glossopteris* flora. A fossil from the Kungurian of Brazil first interpreted as a Sigillariaceae is not a lycopsid but the oldest known anatomically preserved cycad (**Publication 4**). There is evidence of sigillarian lycopsids from presumed Permian-Carboniferous strata of the northern part of Gondwana (Seward, 1932). However, there is no evidence that such plants migrated southwards into the *Glossopteris* flora as the climate ameliorated in this region during the Permian.

The publications included in this cumulative thesis bring important novelties on the lycopsids from the *Glossopteris* flora and also about what was, for a long time, interpreted as a lycopsid but is not one. However, we are still far from understanding these plants due to the very fragmented and usually poorly preserved nature of their known fossils. Existing problems concerning the lycopsids from this flora, such as the systematic position of most fossil-genera and their growth architecture, can be solved only with extensive fieldwork to discover more completely preserved specimens. The reproductive structures of fossil-taxa such as *Brasilodendron* and *Lycopodiopsis*, for instance, must be preserved somewhere in an outcrop, considering the numerous vegetative fossils occurring in Permian strata from Brazil.

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