Mississippian Plants from the Parnaíba Basin

Iannuzzi Roberto, Willian Mikio Kurita Matsumura, and
Mercedes Di Pasquo

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Abstract

The Poti Formation Flora represents the unique record of Mississippian age in Brazil. However, it is not so diverse bearing ten taxa represented by a dwarf lycopsid, shrubby sphenopsids, a putative fern (i.e., *Paulophyton sommeri*, *Paulophyton* sp. 1), a microsporangiate fructification (i.e., *Kegelidium lamegoi*), a cupule, and mainly distinct pteridosperm foliages. Among the pteridosperm

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I. Roberto (✉)
Department of Palaeontology and Stratigraphy, Federal University of Rio Grande do Sul, Porto Alegre, RS, Brazil
e-mail: roberto.iannuzzi@ufrgs.br

W. M. K. Matsumura
Department of Biology, Federal University of Piauí, Teresina, PI, Brazil
e-mail: willian.matsumura@ufpi.edu.br

M. Di Pasquo
CICyTTP (CONICET-ER-UADER), Laboratorio de Palinoestratigrafía y Paleobotánica, Diamante, Entre Ríos, Argentina
e-mail: medipa@cicyttp.org.ar

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foliages, the presence of *Diplothmema gothanica*, *Notorhacopteris* cf. *N. kellaybelenensis* and *Fedekurtzia* cf. *F. argentina* is significant. The Poti Flora was considered as part of the warm-temperate Paraca floral realm, a wide belt (approximately 30° to 60° South) extending from the west (South America) up to the east of Gondwana (Australia) during late Mississippian times (late Visean-earliest Serpukhovian). This realm represents a frost-free climate zone that existed in a short warming (greenhouse) interval directly before the onset of the major episode of the Carboniferous (Pennsylvanian) glaciations. It is fundamental to understanding the floristic evolution of taxa in Western Gondwana and even in the world due to a mixture of elements of Euramerican and Gondwanan affinities are present. This flora offers us a rare chance to contribute to the knowledge of ferns with psilophytic habits and non-synangiate microsporangiate fructifications, as well as the first seeds of pteridosperm affinity and the process of terrestrialization in different groups of plants.

Glossary of Terms/List of Abbreviations, Symbols and Acronyms

Amerosinian (Euramerican) Floral Realm. A broad pantropical biogeographic realm for Carboniferous (Pennsylvanian)–Permian terrestrial vegetation. It occupied the paleoequatorial belt that extended from North and Central America and parts of northern South America and North Africa through Europe into Central Asia and China.

Angaran Floral Realm. A north-temperate terrestrial vegetation dominated by a lycopsid-rich flora during Early Carboniferous and seed ferns and cordaiteans during Late Carboniferous–Permian. This realm occupied the northern paleolatitudes at Siberia and Kazakhstan paleocontinents.

ANM. National (=Brazilian) Mining Agency.

CICyTTP. Centro de Investigaciones Científicas y Transferencia Tecnológica a la Producción (from Argentina).

Cladoxylopsids. A geologically short-lived (Middle Devonian to Mississippian), fern-like group of plants bearing an intricate morphological and anatomical pattern, and including the Pseudosporochnales and Iridopteridales orders. They are characterized by a sequence of branching patterns that display a hierarchical architecture, with the production of a single type of lateral branch at each node; in other records of this group, the branching is less well organized around a central trunk. This group was spore-bearing, reproducing through sporangia on ultimate tips. Still, little is known about the gametophyte phase of this group.

Deep time. Deep time is the concept of geological time developed in the eighteenth century by the Scottish geologist James Hutton (1726–1797). A system of chronologic measurement relating the succession of rocks to time to describe the timing and relationships between events that have occurred during the history of the Earth.

Dehiscence mechanism. Mode of splitting (opening) at maturity of a fruit capsule, anther or sporangia, along a built-in line of weakness in a plant structure to release the contents.

DNPM. National (=Brazilian) Department of Mineral Production.

Enation. A projection or outgrowth from the surface of an organ or structure.

Endemic. Native or having a restricted distribution not naturally found elsewhere, such as being confined to a single locality, country, or region.

Epiphyte. Life habit of growing on other plants, usually on the trunk or branches of a shrub or tree.

Exine. The outer wall of a pollen grain (compared to the intine – the inner wall), the sculpture, and internal layering of the exine usually provide useful taxonomic characters.

Frond. A large, usually divided leaf of a fern, cycad, or palm; in the past, other extinct groups bearing this type of compound foliage.

Geniculate. With abrupt knee-like bends and joints.

Gondwanan Floral Realm. The largest land area of any floristic region during the Paleozoic. It includes South America, Antarctica, Africa, India, Australia, Madagascar, Arabia, New Zealand, and the smaller, peripheral Tibetan, Iranian, and Turkish Plates, showing a great range of climatic variations. During the Carboniferous and Permian, the northern-most parts of Gondwana (northern South America and North Africa) were in the tropics, and fossil assemblages from these areas are distinctive from Gondwanan ones. All other parts of the continent were in the South Temperate Zone and characterized by progymnosperms and pteridosperms.

Greenhouse conditions or intervals. It is a concept of the Natural Greenhouse effect, where the presence of certain gases in the atmosphere allow solar radiation to warm the Earth and then prevent some of the heat from escaping, which keeps the planet warm enough for maintaining life as we know it. It is often used in contrast to Ice House conditions.

GSSP. Global Boundary Stratotype Section and Point.

Heteromorphism. With variation in normal structure or with organs differing in length, size, or shape in a single plant species.

Icehouse. Term coined by Scotese et al. (1999) identifying those times when one or both of the Earth’s polar regions are covered by permanent ice.

IGc. Geosciences Institute of the University of São Paulo.

Integument. It is the covering of an organ or the outer cell layer(s) of an ovule which will become the seed coat.

Lagenostome. A pre-pollination pollen chamber formed at the apex of the megasporangium wall (nucellus) of the pre-ovule.

Lianas. A vine or woody climbing plant supported by other vegetation.

Lignophytes. A clade of vascular plants that consists of seed plants and progymnosperms that have, by definition, a real woody stem (formed from secondary xylem).

LPIA. Late Paleozoic Ice Age.

Micropyle. The opening in the integuments of the ovules.

Milankovitch cycles. The variation of the Earth's exposure to the sun's rays or insolation that results from variations in the orbit of the Earth and the tilt of its axis, and might affect climate, sea level, and sedimentation. Such variations are thought to occur in distinct time periods and intervals ranging from decades to thousands of years. Ice ages might be a consequence of Milankovitch cycles. Milutin Milankovitch (1879–1958) was a Yugoslavian mathematician and physicist specialized in studies of solar radiation and the orbit of the Earth.

Mother-plant. A plant that is the source of seeds (or ovules), seedlings, or vegetative propagules.

Nucellus. The part of the ovule just beneath the integuments and surrounding the female gametophyte.

Pinnule. The pinnate division of a pinna in a bipinnately compound leaf, or the ultimate divisions of a leaf which is more than twice pinnately compound; the terminal photosynthetically active unit of a compound leaf.

Presynangiates. Group of pteridophytes lacking fused sporangia in which the spores develop.

Progymnosperms. An extinct odd group (Middle Devonian to early Carboniferous) of spore-bearing, homosporous, and heterosporous plants with secondary growth attaining shrubby to arborescent habits that gave rise to a pycnoxylic, conifer-like wood, and represented by three orders: the Archaeopteridales, Aneurophytales, and Protopityales. Although poorly understood, progymnosperms provide the most convincing evidence of a lineage ancestral to the seed plants.

Propagules. Any vegetative or sexual structure (other than a seed) giving rise to a new plant.

Pseudomonopodial. A type of branching where the apical meristem appears to divide into two branches, one of which is dominant, resulting in an upright main axis with distinct side branches.

Pteridospermales. An extinct gymnosperm order which represented the earliest seed plants and flourished in the Carboniferous to Triassic. Their foliage was fern-like in appearance, but the fertile leaves bore seeds and pollen-producing organs.

Rachis. The main axis of a structure, such as a compound leaf.

Sphenopsids. A group of geologically long-lived (Late Devonian to Recent), vascular plants with jointed stems, small microphyllous leaves usually arranged in whorls at distinct stem nodes and sporangia carried by sporangiophores. Internodal regions are regularly spaced, bearing longitudinal ribs and furrows. Sphenopsids include three orders: Pseudoborniales, Sphenophyllales, and Equisetales.

Sympodial. Of a sympodium without a single main stem.

UFRGS. Federal University of Rio Grande do Sul.

USP. The University of São Paulo.

Zonobiome. A biome defined mostly by climatic than geographic conditions.

Introduction

Mississippian (early Carboniferous) floras from Gondwana are quite rare, and among the few known ones in South America (Sessarego and Césari 1989; Carrizo and Azcuy 1997; Iannuzzi et al. 1998), the flora from the Poti Formation is probably one of the least studied and understood. The geologic record of Mississippian floras is rare worldwide (Cleal 1991; DiMichele and Hook 1992). In addition, these occurrences generally contain very fragmented remains of plants with detached or separated segments one from each other (i.e., stems, leaves, reproductive structures, **propagules**), which makes it very difficult to reconstruct the plants themselves and to understand the plant communities. Anatomically preserved plant remains are also uncommon during this period, obscuring the systematic relationships and evolutionary grades of taxa (Cleal 1991; DiMichele and Hook 1992).

This scarce information of Mississippian fossil plants impairs the proper understanding of the evolution of terrestrial vegetation since it is a crucial time interval for the differentiation and diversification of several groups of plants. Seed-producing plants had just emerged at the end of the previous Devonian period, and they radiate out into new groups during the Mississippian, spreading across all continents (Cleal 1991; DiMichele and Hook 1992). Many types of seeds are often disconnected from vegetative parts of their **mother plants** due to the fragmentary nature of the fossil associations, as mentioned above. However, these seeds themselves tell us an incredible story about the evolutionary steps that led to the emergence of modern gymnosperm groups in the following geological periods. Unlike the current seeds, the first seeds of the plants, from the late Devonian – Mississippian interval, did not have a **micropyle**, as their **integument** (coat seed) was not totally fused to the **nucellus** (= megasporangium + megagametophyte). The micropyle is the area on the seed surface formed by the fusion of the integument that aids in the reception and germination of microspores (pollen grains) produced by the male reproductive structure. Instead, these basal seeds have a structure called the **lagenostome** that rises from the wall (= megasporangium) at the top of the nucellus in the place of the micropyle is positioned in modern ones. It is thought that lagenostome performed a similar function to that of the micropyle in current seeds, helping to capture and germinate the microspores. Due to this significant anatomical difference of not having a micropyle but a lagenostome, some paleobotanists called these first seeds "preovules" or "pre-seeds" (see Fig. 1; Stewart and Rothwell 1993). Additionally, it is essential to note that the involucres (= **exines**) of the microspores that germinated on the pre-seeds were, at times, more similar to those found in spores than to those found in pollen grains and, therefore, they are called by paleopalynologists as "pre-pollen." Pollen grains with exines similar to the current ones appear along with the first modern seeds (containing micropyles) during the transition from Mississippian to Pennsylvanian, as a result of the coevolution between microspores and seeds to improve the pollination process (the fecundation of the egg = megagametophyte) in plants.

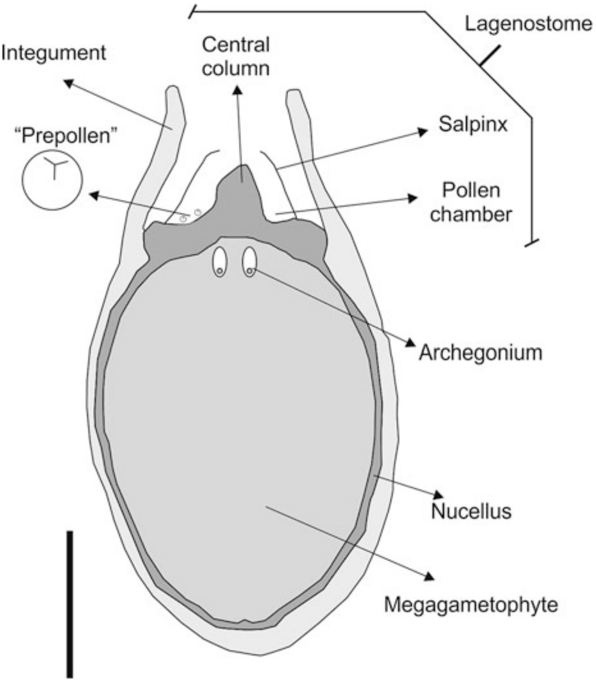

Fig. 1 Original schematic drawing of a preovule based on anatomical slides studied by Rothwell and Scott (1992, pl. III, Fig. 1). Note that integument (= seed coat) is open and lagenostome (consisting of central column, salpinx, and pollen chamber) is a projection of the nucellus (= megasporangium wall) adapted to receive and promote the germination of pre-pollen grains. Scale bar: 1 mm

Another process that was underway in the Mississippian was the structuring of the first forests as we know them today! Although already from the Middle Devonian some plants developed the arboreal habit (i.e., tree-fern like **cladoxylopsids**), it was only at the end of this period that the first woody trees appeared represented by the different species of *Archaeopteris*, from the group of **progymnosperms** (Meyer-Berthaud et al. 2010). From the Mississippian, woody shrubby and tree plants (= **lignophytes**) begin to diversify and expand across the globe, consisting of progymnosperms and seed plants – the latter mostly included in **Pteridospermales** (Meyer-Berthaud et al. 2010; Decombeix et al. 2011). Unfortunately, the fragmentary and dispersed way (parautochthonous to allochthonous associations) of plant fossils preservation in rocks of this period has prevented more precise reconstructions of plant communities. However, the occurrence of certain large-sized permineralized woods testifies that forest formations already existed in this period (DiMichele and Hook 1992; Decombeix et al. 2011). In addition, there is evidence that canopy stratification begins to develop and spatial heterogeneity in the distribution of taxa (i.e., species, genera, and other major taxonomic groups of plants), and **lianas** and putative **epiphytes** became part of the woods (DiMichele and Hook 1992). Indeed, these Mississippian forests were important precursors that enabled the emergence of the first tropical forests, similar in structure and diversity to the modern ones, and well-known in the following Pennsylvanian period.

Finally, the lamination process, i.e., the acquisition and development of leaves, reaches all groups of plants during the middle-to-late Devonian–Mississippian interval (Boyce and Knoll 2002). Apparently, parallel evolution of leaf lamination started at least four times independently, in progymnosperms, **sphenopsids**, seed plants, and ferns, during this time. The earliest known leaves in Middle Devonian ancestors of these four plant groups were highly dissected structures composed of terminal axes that were small, narrow, and with a single vein. From this, all the leaves evolved through planning and webbing the terminal axes that became frondose or entire organs, and typically laminates and containing more than one vein (unless secondarily reduced as in most conifers). These organs are traditionally termed “megaphylls” and considered homologous, unlike leaves of lycopsids that evolved much earlier in the early Devonian and are named “microphylls” because of their possible origin from **enations**. The parallel appearance of laminated “megaphylls” in these four plant lineages took place in the paleotropics and is linked to a significant drop in atmospheric CO_2 concentration through the Late Devonian (Beerling et al. 2001). This process continued in the Carboniferous and was normally identified as one of the causes of the long-term glacial phase that occurred in the medium-high latitudes south of Gondwana that cooled and dried up the Earth’s climate during the Carboniferous-Permian interval (Montañez et al. 2016). The appearance of laminate leaves is also related to the evolution of vascular systems competent to support high levels of evapotranspiration and other aspects of whole-plant function in increasingly stratified late Devonian and early Mississippian plant communities (Boyce and Knoll 2002). Therefore, environmental, ecological, and climate changes may well have stimulated an evolution of leaf lamination. It is interesting to note that in the Late Devonian, only the **progymnosperms** had broadly laminated, multiveined leaves. During the transition from the Devonian to Mississippian, a few sphenopsids (i.e., Sphenophyllales) had acquired leaves with a similar developmental stage, with relatively wide and multiveined laminae. In early-to-late Mississippian, on the other hand, seed plants and ferns still had frond-like leaves that supported small narrow-leaved leaflets and, often, with uni- to bi-veined end segments. This pattern is documented in the plant fossils of the Poti Formation that will be presented hereafter. Only at the end of the Mississippian, these two groups begin to show leaflets with comparatively wider and multiveined laminae, coinciding with the onset of glacial events in south hemisphere Gondwanan terrains. At the transition from the Mississippian to the Pennsylvanian, when glacial events become more intense, and the global CO_2 concentration has dropped as never before since the appearance of terrestrial plants (Montañez et al. 2016), the first large-sized leaves with whole and continuous laminae appear, such as those with parallel venation of the Cordaitales.

In conclusion, these Mississippian floras offer a rare opportunity to recognize how basal pre-seeds were, the early forest communities evolved, and how the process of lamination in different groups of plants, whether spore-producing or seed-producing, took place.

Carboniferous Period

The Carboniferous was established by Conybeare and Phillips (1822) to describe coal-bearing rocks in northern England and Wales. Phillips (1835) coined the term Carboniferous System for these deposits in North America and Europe. It is divided into Mississippian (older) and Pennsylvanian (younger) subsystems, and the former one into Lower Tournaisian, Middle Visean, and Upper Serpukhovian, and the latter include the Bashkirian, Moscovian, Kazimovian, and Gzhelian stages (Cohen et al. 2013; Ogg et al. 2016). Davydov et al. (2012) summarized the evolution and comparison among the various regional series/stage divisions of the Carboniferous chronostratigraphy in North America, Western and Eastern Europe. According to Davydov et al. (2012), Cohen et al. (2013), and Ogg et al. (2016), three major Carboniferous boundaries were accepted as Global Boundary Stratotype Section and Point (GSSP): (1) Devonian–Tournaisian boundary in France, (2) Base of the Visean Stage in China, and (3) Mississippian-Pennsylvanian boundary in the USA. The top of the Carboniferous is established by the GSSP for the base of the Permian.

Biostratigraphic zonations and regional to global correlations are based especially on ammonoids (Korn 1996, 2006), benthic foraminifera (especially fusulinids) and conodonts (Schmitz and Davydov 2012). The conodonts become the most reliable tool for calibration and geochronological boundary definition within the Carboniferous (Schmitz and Davydov 2012; Richards 2013; Nikolaeva et al. 2020). Other groups such as corals, radiolaria, ostracods, and crinoids have regional biostratigraphic importance, and they are also useful in providing paleoecological and paleoclimatic inferences (Ogg et al. 2016). Macroplants and miospores were groups firstly utilized for dating Carboniferous coal basins (Clayton et al. 1977; Wagner 1984; Cleal 1991; Archangelsky et al. 1995; Meyen et al. 1996). Macroplants evolved and diversified rapidly, yielding valuable data for biostratigraphic zonations (Clayton et al. 1977; Cleal 1991; Melo and Loboziak 2003; Playford et al. 2012; Di Pasquo and Iannuzzi 2014; Di Pasquo et al. 2019a) and the establishment of floristic successions in several regions along the equatorial to subtropical climatic belts (Wnuk 1996; Iannuzzi and Rösler 2000; Iannuzzi and Pfefferkorn 2002).

Paleobiogeography

During the Carboniferous, the majority of previously independent continents (Laurussia and Gondwana) merged to form the only Phanerozoic supercontinent, Pangea, at around 320 Ma, in the Bashkirian, and completed by the earliest Permian. Siberia, Amuria, and China terranes were also substantial continental and coal-bearing areas (Scotese and McKerrow 1990).

The formation of Pangea caused significant changes on the Earth's surface, including ocean circulation, fluctuations of atmospheric gases, global temperatures and sea levels, increased continental weathering rates, and storage of organic carbon as coal. These physical factors promoted biogeographic differentiation, diversification of land plants, the appearance of seed ferns (Decombeix et al. 2011), conifers (DiMichele et al. 2010) and reptiles (Clack 2002), making possible the occupation of drylands (Wnuk 1996; Davies and Gibling 2013). In the marine environment, the early Paleozoic biota such as stromatoporoids, tabulate corals, brachiopods (Raymond et al. 1990), trilobites, ostracods, and heavily armored fish were partial or fully succeeded by Foraminifera, ammonoids (Korn 1996, 2006), freshwater pelecypods, gastropods, sharks, and ray-finned fishes (Davydov et al. 2012).

The terrestrial environment saw one of the greatest animal evolutionary innovations, the amniotic egg, which allowed the ancestors of reptiles, birds, and mammals to avoid desiccation and breed their eggs on land. According to DiMichele and Hook (1992) and DiMichele and Bateman (1996), during the time from the Late Devonian to Early and Middle Mississippian, land plants experienced the second major radiation, with the establishment of the major lineages of vascular plants, such as sphenopsids, ferns, seed ferns, progymnosperms, and gymnosperms. This radiation led to the evolution of structurally stratified plant communities, consisting of the arborescent canopy and understory layers, including a herbaceous layer. The invasion of land plants in better-drained places promoted the peat formation in wetlands already existing by the Visean (Dunn et al. 2006).

Finally, there is an important response of plants on terrestrial invertebrates. The peat formation in wetland environments fixed the CO_2 as coal and reduced its levels from the atmosphere. In contrast, the atmospheric oxygen content had raised more than the modern level and influenced in their turn the breathing and gas exchange capabilities, increasing enormously the size of some terrestrial invertebrates, such as arthropleurids (ca. 2 m long) and dragonflies (ca. 60–70 cm wingspan) (Shear and Kukalova-Peck 1990).

Paleoclimate

According to Scotese et al. (1999), during the latest Devonian–Early Permian times, the Earth experienced the third episode of Ice House conditions or Late Paleozoic Ice Age (LPIA). The LPIA is generally formed by two significant glaciation periods (latest Devonian–earliest Carboniferous and Late Carboniferous–Early Permian) separated by a warmer period (Early Carboniferous). The first glaciation interval in the latest Devonian to earliest Carboniferous is based on diamictites and tillites found in Bolivia, northern Brazil, and Niger (Caputo et al. 2008). The warmer period or **greenhouse interval** is inferred by the late Visean Paraca Floral Realm through correlation with macrofloras, palynology, and comparison with numerical ages from Australia (Iannuzzi and Pfefferkorn 2002; Pfefferkorn et al. 2014), as well as by dispersion towards high-latitudes of marine invertebrate fauna from the equatorial belt (Raymond et al. 1990; Powell et al. 2009). According to Scotese et al. (1999), no tillites are reported from the Late Mississippian (Visean–Namurian A), corroborating the warmer conditions. Although, the occurrence of punctual short-term glacial episodes is not totally discarded for this time (Streel et al. 2012). Finally, the second global glaciation interval commenced in the early Pennsylvanian (Namurian B) and lasted until the Early Permian (Artinskian–Kungurian), maybe except in Australia, where alpine-type glaciation may have occurred up to the middle Permian. In Gondwana, the ice caps covered the southern half of South America, the southern two-thirds of Africa as far north as southernmost Saudi Arabia, India, Antarctica, and Australia (Scotese et al. 1999).

Geologic Setting, Age, and Material

Geology

The plant fossil material was collected from the Poti Formation in the Parnaíba Basin, NE Brazil (Fig. 2). The intracratonic Parnaíba Basin, formerly named as Maranhão Basin, covers an area of ca. 600,000 km^2 in the northeast and north-central Brazil, occupying the states of Ceará, Piauí, Maranhão, and Tocantins (Fig. 2). The basin is delimited by the Tocantins and Ferrer/Urbano Santos Highs in the north, and by the São Francisco High in the south. Vaz et al. (2007) subdivided the stratigraphic record of this basin into six second-order depositional super-sequences, ranging from the Early Silurian to the Early Cretaceous. The Mississippian is included in the Mesodevonian–Eocarboniferous Sequence and represented by upper Longá and Poti formations, Tournasian and Visean, respectively. These lithostratigraphic units are included in Canindé Group, and those sedimentary rocks recorded an epicontinental sea to fluvial, deltaic system influenced by tectonic events and eustatic sea-level fluctuations (Vaz et al. 2007).

The Poti Formation (Paiva and Miranda 1937) is divided into lower and upper members, and represents part of the first transgressive-regressive megacycle proposed by Mesner and Wooldrige (1964). Medium to coarse sandstones with sparse light gray siltstones compose the lower Poti Formation interpreted as deposits of shallow marine settings. The fossil content is represented by invertebrates of Bivalvia (Kegel 1954) and fish vertebrates such as chondrichthyans and sarcopterygians (Figueroa et al. 2016; Figueroa and Machado 2018), besides

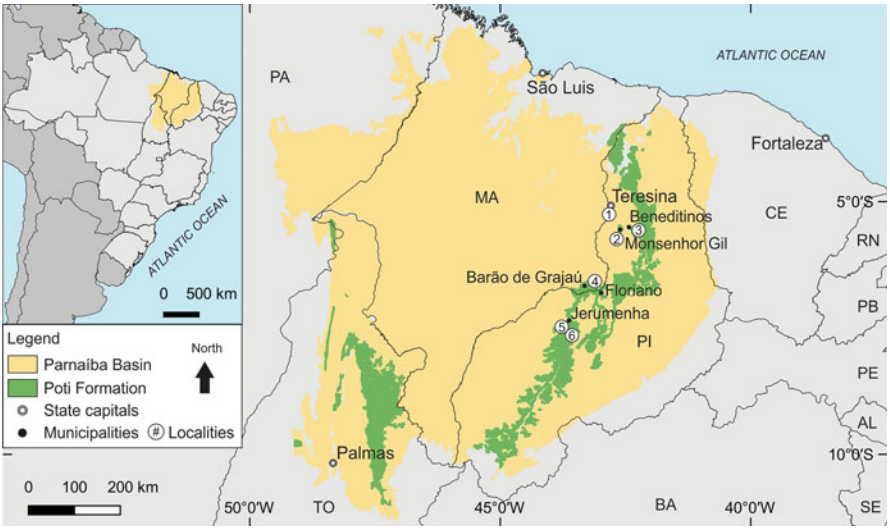

Fig. 2 Location map of Mississippian deposits of the Poti Formation in the Parnaíba Basin and sites bearing plant fossils (white circles) are as follows: borehole no 125 (1) in Teresina; Curral de Pedra Farm (2), in Monsenhor Gil; Beneditinos borehole (3), in Beneditinos; road cut at BR 230 (4), in Barão do Grajaú; Roncador creek (5–6), Salto de Pedra district, in Jerumenha

paleoniscids (Santos and Salgado 1970). The upper Poti Formation contains fine to coarse sandstones with interbedded organic carbon-rich siltstones and mudstones interpreted as fluvial–deltaic settings near the coastline (Schobbenhaus et al. 1984; Santos and Carvalho 2009). The plant material (see section "Historical Overview of the Poti Formation Flora") is restricted to the upper member mainly studied by Dolianiti (1954), Iannuzzi and Rösler (2000), Iannuzzi and Pfefferkorn (2002), and Iannuzzi et al. (2006).

Age

The earlier age assignment of the Poti Formation was Mississippian from palynological evidence (Müller in Mesner and Wooldridge 1964). Later, Daemon (1974) and Loboziak et al. (1992) proposed a Tournaisian–Visean interval still based on palynological associations recovered in drilling cores. Presently, a late Visean age is supported by additional palynological studies (Melo and Loboziak 2000, 2003; Di Pasquo and Iannuzzi 2014; see Fig. 3). Macroscopic plant remains are concentrated and more abundant in the upper part of the Poti Formation and were used to determine the age of this lithostratigraphic unit as well. Initially, Oliveira (1934, 1935), who analyzed only the sphenopterid fronds, considered this floral record as Westphalian in age. Later, Dolianiti (1954) assigned it to the Mississippian based on a much larger collection of plant fossils. In 1969, Rigby proposed a more precise age within the Mississippian, Visean, for this flora considering correlations with other Gondwanan Carboniferous floras. After that, some authors (Rocha-Campos and Archangelsky 1985; Sessarego and Césari 1989) proposed slightly younger ages for this flora that ranged from the late Mississippian to early Pennsylvanian based on

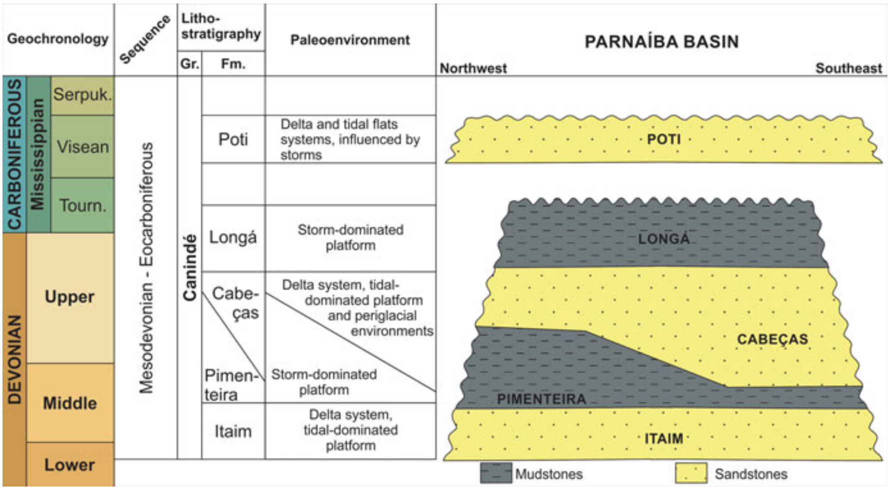

Fig. 3 Chronostratigraphic chart of the Canindé Group, including the Devonian–Mississippian units from the Parnaíba Basin: Itaim, Pimenteira, Cabeças, Longá, and Poti formations. Note the Visean age attributed to the Poti Formation (based on the Vaz et al. 2007, Melo and Loboziak 2000, 2003). Legend: Tourn. = Tournaisian; Serpuk. = Serpukhovian; Gr. = Group; Fm. = Formation

synonyms established with taxa found in the Carboniferous deposits from Argentina. Finally, Iannuzzi and Pfefferkorn (2002) ratified a Mississippian age, probably late Visean, from the reevaluation of plant taxa and sporomorphs and correlations with other equivalent plant associations distributed throughout Gondwana, some of them dated by radiometric methods, such as Australian floras (see Playford and Melo 2012).

Material

Most of the specimens recovered from Poti Formation come from well no. 125 (Paiva and Miranda 1937), drilled in the municipality of Teresina (Fig. 2), Piauí state, collected at a depth of 225–226 m according to Dolianiti (1954). The other significant specimens, except for one, were collected at the locality referred to by Dolianiti (1954) as "Curral de Pedra" (= Stone Pen). This locality corresponds to an outcrop situated at the "Curral de Pedra Farm," in the municipality of Monsenhor Gil, 63 km south of Teresina on the BR 316 highway, in the Piauí State (Fig. 2). The Roncador Creek outcrop, located in the municipality of Jerumenha, in the state of Piauí, represents the last location that provided important specimens for this unit. The specimens from "Curral de Pedra" are preserved as impressions and/or adpressions and casts in a yellowish fine sandstone matrix, whereas the others from the well no. 125 are found as compressed material in organic-rich muddy siltstone of the core samples, and those from Roncador Creek are prints preserved in a yellowish fine-silty sandstone. Paleobotanical material is housed at following institutions: (a) the Museum of Earth Sciences (Museu de Ciências da Terra – MCT), National Mining Agency (ANM; ex-Departamento Nacional de Produção Mineral – DNPM), Rio de Janeiro, labelled under the prefix DGM; (b) the Paleontological collection of Department of Sedimentary and Environmental Geology (DGSA), Geosciences Institute (IGc), University of São Paulo (USP), São Paulo, labelled under the prefix GP/3 T. Palynologic materials are stored at the following laboratories: (a) the Paleopalynology and Paleobotany at the CICYTTP, Diamante, Entre Ríos, Argentina, under the prefix CICYTTP-Pl; (b) the Palynology "Marleni Marques Toigo," Institute of Geosciences (IGeo), Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, Brazil, under the prefix MP-P. The illustrated palynomorph specimens are presented with prefixes and numbers of the respective collection followed by the England Finder reference, as for instance, MP-P 9743 Y12/2.

Poti Formation Flora

The assemblages are relatively poor in the number of taxa presented in the studied material. Over ten taxa, many of which need revision as they were erected a long time ago, are listed in Table 1. Main taxa published by Iannuzzi and Pfefferkorn (2002, see also Di Pasquo and Iannuzzi 2014) are revised and illustrated below. Fragmentary and incomplete specimens are not included (e.g., dwarf lycopsid, ?*Archaeocalamites* sp., ?*Sphenopteridium* sp., ?*Fryopsis* sp., and *Aneimites* sp.).

Table 1 Different taxonomic names proposed for the floral elements of the Poti Formation already described in the literature. On the left, the original classifications; in the center, the various other proposals made over time; and on the right, the taxonomy adopted in this contribution

Original classification	Other proposals over time	This work
Sphenopteris/*Palmatopteris furcata* (in Oliveira 1934)	*Sphenopteris furcata* (Oliveira 1935); *Adiantites gothanica* (Dolianiti 1954); *Adiantites paracasica* (Rigby 1969); *Diplothmema bodenbenderi* (Césari 1986, 1987); *Diplothmema gothanica* (Iannuzzi and Pfefferkorn 2002, Iannuzzi et al. 2006).	*Diplothmema gothanica*
Sphenopteris obtusiloba (in Oliveira 1935)	*Eusphenopteris sanjuanina* (Césari 1986); *Aneimites* sp. (Iannuzzi and Pfefferkorn 2002).	*Aneimites* sp.
Cardiocarpon sp. (in Oliveira 1935)	*Cordaicarpus* sp. (Millan 1965).	Cupulate organ?
Adiantites oliveiranus (in Dolianiti 1954)	*Sphenopteris oliveiranus* (Rigby 1969); *Diplothmema gothanica* (Iannuzzi et al. 2006).	*Diplothmema gothanica*
Adiantites santosi (in Dolianiti 1954)	*Sphenopteris santosi* (Rigby 1969); *Diplothmema gothanica* (Iannuzzi et al. 2006).	*Diplothmema gothanica*
Kegelidium lamegoi (in Dolianiti 1954)	*Paulophyton sommeri* (Leguizamón and Archangelsky 1981); *Kegelidium lamegoi* (Iannuzzi and Pfefferkorn 2002, 2014).	*Kegelidium lamegoi*
Paulophyton sommeri (in Dolianiti 1954)	*Paulophyton sommeri* (Iannuzzi and Pfefferkorn 2002, Iannuzzi et al. 2015).	*Paulophyton sommeri*
Rhodea sp. (in Dolianiti 1954)	*Paulophyton sommeri* (Leguizamón and Archangelsky 1981, Iannuzzi and Pfefferkorn 2002).	*Paulophyton sommeri*
Cardiopteridium sp. (in Dolianiti 1954)	*Botrychiopsis weissiana* (Rocha-Campos and Archangelsky 1985);? *Fryopsis* sp. (Iannuzzi and Pfefferkorn 2002).	?*Fryopsis* sp.
Sphenopteridium sp. (in Dolianiti 1954)	*Sphenopteris*? sp. (Rigby 1969);? *Sphenopteridium* sp. (Iannuzzi and Pfefferkorn 2002).	?*Sphenopteridium* sp.
Lepidodendropsis sp. (in Dolianiti 1954)	"*Lepidodendropsis*" sp. (Iannuzzi and Pfefferkorn 2002).	Dwarf lycopsid
Cyclostigma brasiliensis (in Dolianiti 1962)	Not discussed herein.	Taxon removed
Rhacopteris sp. (in Dolianiti 1980)	*Nothorhacopteris argentinica* (Sessarego and Césari 1989); *Notorhacopteris* cf. *N. kellaybelenensis* (Iannuzzi and Pfefferkorn 2002, Di Pasquo and Iannuzzi 2014).	*Notorhacopteris* cf. *N. Kellaybelenensis*

(continued)

Table 1 (continued)

Original classification	Other proposals over time	This work
Triphyllopteris alvaro-albertoi (in Dolianiti 1980)	*Fedekurtzia argentina* (Césari 1986, Sessarego and Césari 1989); *Triphyllopteris alvaro-albertoi* (Iannuzzi and Pfefferkorn 2002); *Fedekurtzia* cf. *F. argentina* (Di Pasquo and Iannuzzi 2014)	*Fedekurtzia* cf. *F. argentina*
?*Stamnostoma* sp. (in Iannuzzi and Pfefferkorn 2002)	No other records.	*Lagenospermum* sp.
Archaeocalamites sp. (in Iannuzzi and Pfefferkorn 2002)	No other records.	Cf. *Archaeocalamites* sp.
Paulophyton sp. 1 (Iannuzzi 1996)	*Paulophyton* sp. 1 (in Iannuzzi and Pfefferkorn 2002)	*Paulophyton* sp. 1
Diplothmema cf. *D. bodenbenderi* (in Iannuzzi and Pfefferkorn 2002)	No other records.	*Diplothmema* cf. *D. Bodenbenderi*

Historical Overview of the Poti Formation Flora

The first report of plant fossils from the Poti Formation (Oliveira 1934, 1935) was based on specimens found in core samples of the well no. 125 (Paiva and Miranda 1937). Oliveira (1934, 1935) described and classified the first floral elements as *Sphenopteris* (*Palmatopteris*) *furcata*, *S. obtusiloba*, and *Cardiocarpon* sp. Later, Dolianiti (1954) presented a more detailed study of this flora based on the reexamination of Oliveira's material and analyzed new specimens collected by W. Kegel at the "Curral de Pedra" outcrop, and one recovered from a core sample in the Beneditinos borehole (Kegel 1952). From well no. 125, Dolianiti (1954) identified samples using appropriate descriptions and illustrations, and mentioned the following taxa: *Adiantites gothanica*, *A. oliveiranus*, *A. santosi*, *A. alvaro-albertoi*, *Sphenopteridium* sp., *Cardiopteridium* sp., *Rhodea* sp., *Kegelidium lamegoi*, and *Paulophyton sommeri*. Also, he included *A. alvaro-albertoi*, *Rhodea* sp., *K. lamegoi*, and *P. sommeri* based on some specimens recovered from the "Curral de Pedra" outcrop. *Lepidodendropsis* sp. was added from the sample obtained in the Beneditinos borehole. Dolianiti (1954) described and classified almost all floral elements known even today. Subsequently, Dolianiti (1962) described the new lycoposid *Cyclostigma brasiliensis* found in two new localities from the Maranhão (banks of the Manoel Alves River) and Pará (Municipality of Cinzeiro) states, far from the places where the materials he described previously came from. Although Dolianiti made no mention of the presence of any seed in his extensive work of 1954, Millan (1965) suggested a new combination for the form originally identified as *Cardiocarpon* sp. by Oliveira (1935), transferring it to the genus *Cordaicarpus*.

After that, Rigby (1969) made the first revision of the floral elements of the Poti Formation, a more general study in which he sought to reassess all the plant taxa already described in the literature for the Carboniferous floras of Gondwana. He suggested three new combinations for some taxa identified by Dolianiti (1954): *Adiantites oliveiranus* passed to *Sphenopteris oliveirianus*, *A. santosi* to *Sphenopteris santosi*, and *A. alvaro-albertoi* to *Triphyllopteris alvaro-albertoi*. In addition, he suggested synonymizing *A. gothanica* in *Adiantites paracasica* Gothan, a taxon documented in the Ambo Formation of Paraca, Peru, invalidating Dolianiti's species. Besides, Rigby suggested that *Cardiopteridium* sp. could represent a pinnule of fronds attributed to the genus *Botrychiopsis*, foliage widely distributed among Carboniferous strata of Gondwana.

In his last contribution to the knowledge about this flora, Dolianiti (1980) added new specimens based on the material from a locality on the banks of the Roncador creek in Jerumenha municipality, Piauí. He described some bipinnate fronds attributed to *Triphyllopteris alvaro-albertoi* a taxon previously proposed by Rigby (1969) and *Rhacopteris* sp. Soon after that, Leguizamón and Archangelsky (1981) suggested recombining *Kegelidium lamegoi* into *Paulophyton sommeri*. In an abstract, Rösler and Ciguel (1985) reported the collection of new material from 63 km of the Teresina–Picos highway in Piauí, in which specimens with Devonian affinities, i.e., *Paulophyton sommeri*, were recognized. For the first time, sphenopsid stems have been found, hitherto not mentioned among the elements of this flora. However, Rösler and Ciguel (1985) did not describe nor illustrate them. In the same year, Rocha-Campos and Archangelsky (1985) suggested the combination of *Cardiopteridium* sp. Dolianiti (1954) with *Botrychiopsis weissiana* Kurtz, as recommended by Rigby in 1969. Also, during that decade, several paleobotanists revised and proposed new synonymies of these species with others documented in the Carboniferous of central-western Argentina. Among them, Césari (1986) indicated the presence of *Eusphenopteris sanjuanina* (= *A. alvaro-albertoi* in Dolianiti 1954) and *Fedekurtzia argentina* (= *T. alvaro-albertoi* in Dolianiti 1980), and also Césari (1987) recognized *Adiantites gothanica* as a synonym of *Diplothmema bodenbenderi*. Finally, Sessarego and Césari (1989) indicated the presence of *Nothorhacopteris argentinica* (= *Rhacopteris* sp. in Dolianiti 1980) and *Fedekurtzia argentina* (= *T. alvaro-albertoi* in Dolianiti 1980).

Iannuzzi (1994) revised Dolianiti's material and the so far unstudied collection of O. Rösler (Rösler and Ciguel 1985) and own material collected at different localities for his Master thesis. Later, Iannuzzi and Scherer (2001) removed the lycoposid *Cyclostigma brasiliensis* from the Poti flora since the outcrops bearing specimens of this species belong to the Permian Pedra-de-Fogo Formation as recently ratified by Iannuzzi et al. (2018). Iannuzzi and Pfefferkorn (2002) revised Iannuzzi's collection and indicated the occurrence of the following taxa: *"Lepidodendropsis"* sp., *Archaeocalamites* sp., *Nothorhacopteris* cf. *N. kellaybelenensis*, *Triphyllopteris alvaro-albertoi*, ?*Sphenopteridium* sp., ?*Fryopsis* sp., *Paulophyton sommeri*, *Paulophyton* sp. 1, *Kegelidium lamegoi, Aneimites* sp., *Diplothmema gothanica*, *Diplothmema* cf. *D. bodenbenderi*, and ?*Stamnostoma* sp. After that, Iannuzzi et al. (2006) considered that *A. oliveiranus* and *A. santosi* were synonyms of *Diplothmema gothanica.* Di Pasquo and Iannuzzi (2014) also accepted the presence of

Notorhacopteris cf. *N. kellaybelenensis* (= *Rhacopteris* sp. in Dolianiti 1980) and *Fedekurtzia* cf. *F. argentina* (= *T. alvaro-albertoi* in Dolianiti 1980) as proposed by some previous authors.

From this history, numerous taxonomic changes were proposed, mostly from the pictures published without any examination of the specimens. This was stimulated by the necessity of the establishment of an adequate stratigraphic correlation of the Poti Formation with other units of South American basins. The difficulties in achieving a proper taxonomic designation of specimens are due to the poorly preserved, fragmented specimens of these collections. Moreover, those specimens were compared (Oliveira 1934, 1935) with taxa from the Carboniferous deposits of Euramerica (northern alliance). From the work of Dolianiti (1954), the endemic character of the flora was emphasized with the creation of new and exclusive genera such as *Paulophyton* and *Kegelidium*, and species such as *A. gothanica*, *A. oliveiranus*, *A. santosi*, and *A. alvaro-albertoi*. After that, several paleobotanists compared the specimens with the Gondwanan taxa to establish relationships with other floras, especially from South America (Rigby 1969; Rocha-Campos and Archangelsky 1985; Césari 1986, 1987; Sessarego and Césari 1989). Nowadays, in this flora, elements are recognized from both Euramerica and Gondwana. Nevertheless, the accentuated endemism found in this flora due to its paleogeographic position is addressed below. Finally, we highlight the earliest records of some typical taxa, well-represented and more widely distributed in South America at the beginning of the Pennsylvanian but documented in the Mississippian flora of the Poti Formation.

Plant Systematics

Class FILICOPSIDA

Family *incertae sedis*

Genus *Paulophyton* Dolianiti emend. Leguizamón et Archangelsky, 1981

Emended generic diagnosis: *"Herbaceous plant composed of a main axis or rachis that support second-order rachis, which are repeatedly dichotomized into three-dimensional systems. Sporangia terminal, pyriform, arranged singly or in groups, straight or bent, with or without dehiscence mark, containing spores smooth or slightly ornate triletes"* [Translated from the original text in Spanish published by Leguizamón and Archangelsky 1981, p. 104].

Diagnostic features: Leafless axes repeatedly dichotomized into a three-dimensional **pseudomonopodial** branching system, small sporangia terminal, pyriform, arranged singly or in groups, straight or bent, apparently without dehiscence marks.

Comments: Due to its three-dimensional branching system consisting of leafless axes terminally bearing small clusters of sporangia, Dolianiti (1954) considered that *Paulophyton* could represent a form related to the group of Devonian psilophytes *s.l.* which survived until the Carboniferous, representing a relictual taxon. Also, Leguizamón and Archangelsky (1981), by emending the diagnosis of *Paulophyton* based on Argentinean material, include these forms in the Primofilices Class, the former name used for the plant group related to psilophytes *s.l. Paulophyton*'s overall appearance reminds us of a Devonian plant of the Order Trimerophytales, more specifically of the forms attributed to *Psilophyton* (Iannuzzi 1994). However, Iannuzzi (1994) made a comparative analysis between *Paulophyton* and *Psilophyton* and concluded the following differences:

(a) *Paulophyton* is exclusive of the Carboniferous and has a Gondwanan (South American) distribution, while *Psilophyton* is restricted to the Early-to-Middle Devonian of Euramerica.
(b) *Paulophyton* is distinguished by its tiny sporangia without an evident **dehiscence mechanism**. In *Psilophyton,* the sporangia are larger and have a longitudinal dehiscence mechanism.
(c) In *Paulophyton,* the fertile branches are slender and fragile, always located laterally to the main axes, first and second order branches, and terminally they carry a small number of sporangia (from 8 to 16), while in *Psilophyton*, the fertile branches are shortened and robust, being positioned closer to the main axes of the plant and show large concentrations of terminal sporangia forming clusters;
(d) *Paulophyton* has an exclusively **pseudomonopodial** arrangement, where the lateral branches alternate in pairs from the main axis. In *Psilophyton,* this arrangement ranges from preferably dichotomous (**sympodial**?) to slightly pseudomonopodial. The arrangement of the lateral branches is generally alternate but not regular from the main axis.

Paulophyton species generally appear to present a strictly pseudomonopodial branching system more regular than the *Psilophyton* forms, thus representing a more advanced vegetative branching system. However, in contrast, the *Paulophyton* forms appear to have reproductive systems and organs more primitive than *Psilophyton* ones, resembling those of the basal forms of rhyniophytes, in which any dehiscence mechanism lack. These aspects suggest that *Paulophyton* evolved from an independent lineage, in which some characters became quite advanced while others hardly evolved.

Finally, Leguizamón and Archangelsky (1981) and Iannuzzi et al. (2015) also stressed the similarity of *Paulophyton* with some representatives of the orders Protopteridales, Cladoxylales (e.g., *Pseudosporochnus*), and Psilophytales (e.g., *Psilophyton*). However, the lack of petrified or permineralized material that would allow the recognition of anatomical structures precluded a more accurate systematic classification. In many respects, *Paulophyton* shows the closest morphological similarities with Trimerophytes and Cladoxylaleans of the Devonian. However, sporangia of *Paulophyton* are small, only up to 1 mm long, and nobody has found one of these sporangia open as one might expect if a real mechanism of dehiscence existed in this plant. Short parts of axes are always attached to the sporangia, even if the material is very incomplete. Leguizamón and Archangelsky (1981) were able to macerate sporangia of Argentinean material but did not see any dehiscence line. Nevertheless, it seems that only anatomical studies could elucidate the possible phylogenetic relationships of these forms of psilophytic habit in South America.

Apparently, *Paulophyton* aroused in northeastern Argentina, represented by species *P. argentinus*, during the earliest Mississippian (Tournaisian) (Carrizo and Azcuy 2015). In the late Visean, the genus was dispersed northward, occupying areas of Peru, Bolivia, and northern Brazil, which resulted in the species *P. sommeri* (Dolianiti 1954, Iannuzzi et al. 1999, 2015). Towards the end of the Mississippian (early-to-late Serpukhovian), the genus dispersed once more, now toward the tropics, recorded in Germany by the species *P. jongmansi* (Kräusel 1957). After this late Mississippian glacial interval, *Paulophyton* returned to appear in northeastern Argentina and diversified into two species, e.g., *P. cuyanum* and *P. llanensis,* during the early Pennsylvanian (Leguizamón and Archangelsky 1981). These are the last known records of this unusual Carboniferous plant.

Type-species *Paulophyton sommeri* Dolianiti 1954
(Fig. 4; Table 1)

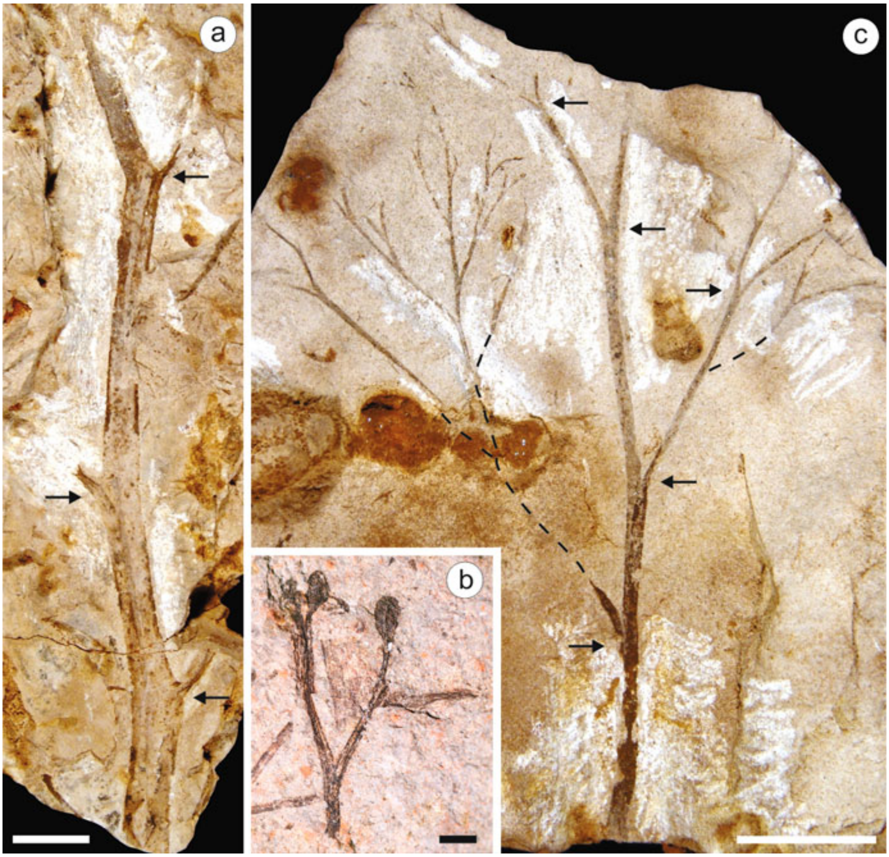

Fig. 4 *Paulophyton sommeri* Dolianiti 1954. (**a**) GP-3E 4489. Main axis showing the pseudomonopodial branching system; (**b**) DGM 672. Cluster of four-paired terminal sporangia; (**c**) GP-3E 4460. Main axis bearing alternately secondary dichotomous axes. Note the terete terminal axes and psilophytic aspect of the branching system. Scale bars: (**a** and **c**) = 1 cm; (**b**) = 1 mm

Original specific diagnosis: *"Terminal sporangia, globular to pear-shape disposed in singly or in pairs. They measures from 1 to 1.25 mm. long. External structure of epidermis with rhomboidal and elongated cells and clearly visible in all sporangia. In some of specimens there is observed a longitudinal ridge that does not reach the apical region, and which may be interpreted as an area of dehiscence. The sporangia are see gathered to dichotomous branchlets, which are very slender, measuring from 0.25 to 0.50 mm and which a very fine central vein."* [English version of the original diagnosis as published by Dolianiti 1954, p. 48].

Diagnostic features: Small terminal sporangia inserted into erect and slender branches.

Comments: This form represents the type-species, and accordingly, it is used as a reference for the other forms of *Paulophyton* later discovered in different parts of South America. There are five species of *Paulophyton*: *P. argentinus*, from the early Mississippian (Tournaisian-to-Visean) of Argentina (Carrizo and Azcuy 2015), *P. sommeri* from the late Mississippian (Visean-to-Serpukhovian) of Peru, Bolivia, and northern Brazil (Dolianiti 1954, Iannuzzi et al. 1999, 2015), *P. jongmansi* from the latest Mississippian (early-to-late Serpukhovian) of Germany (Kräusel 1957), and *P. cuyanum* and *P. llanensis* from the early Pennsylvanian (Bashkirian-to-Moscovian) of Argentina (Leguizamón and Archangelsky 1981). *P. sommeri* differs from the other species of the genus by the erect orientation of sporangia, the alternate arrangement in pairs, probably spiral, of secondary axes and the division pattern alternating between pseudomonopodial and sympodial of terminal axes.

Holotype. DGM 572.

Paratypes. DGM 672, 1002.

Other specimens. GP/3E 4460, 4489.

Collections. Museum of Earth Sciences, ANM (ex-DNPM), Rio de Janeiro; Depto. Sedimentary and Environmental Geology, IGc, USP, São Paulo.

Paulophyton sp. 1 in Iannuzzi 1994, 1996
(Figs. 5 and 6; Table 1)

Description: Terminal sporangia, oval, 0.6–0.9 mm long and 0.4–0.5 mm wide; arranged in pairs on shortened dichotomous stalks loosely coiled on themselves from the apex toward their base; clusters of at least eight sporangia per terminal axis. [English version of the original description by Iannuzzi 1994, p. 101].

Diagnostic features: Small terminal sporangia inserted into circinate branches.

Comments: This form represents a presumable new species as suggested by Iannuzzi (1994, 1996), but has not yet been formally proposed. Therefore, it is designated here as *Paulophyton* sp. 1. This form is distinguished from all other species by its small sporangia, comparable only to *P. cuyanum* and mainly by its coiled terminal fertile axes (Iannuzzi et al. 2015).

Study material. GP/3E 5698, 5752.

Collection. Depto. Sedimentary and Environmental Geology, IGc, USP, São Paulo.

Fig. 5 *Paulophyton* sp. GP-3E 5698. Main axis bearing alternately secondary and tertiary dichotomous axes. Note coiled terminal fertile axes and psilophytic aspect of the branching system. Scale bar: 1 cm

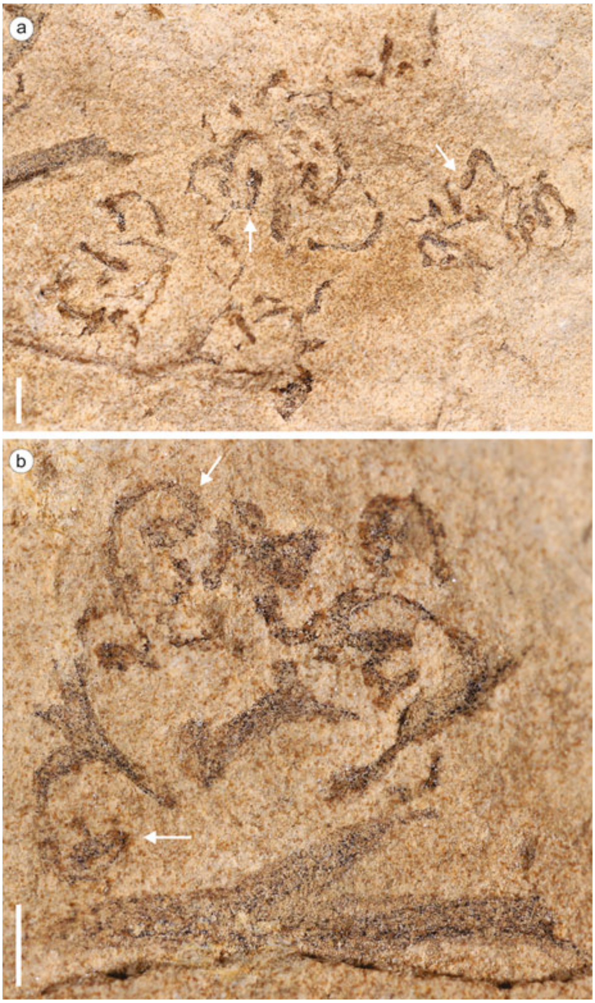

Fig. 6 *Paulophyton* sp. GP-3E 5698. (**a**–**b**) Details of the coiled terminal fertile axes (arrows). Note the oval-elliptic small sporangia inserted at the end of coiled axes. Scale bars: 1 mm

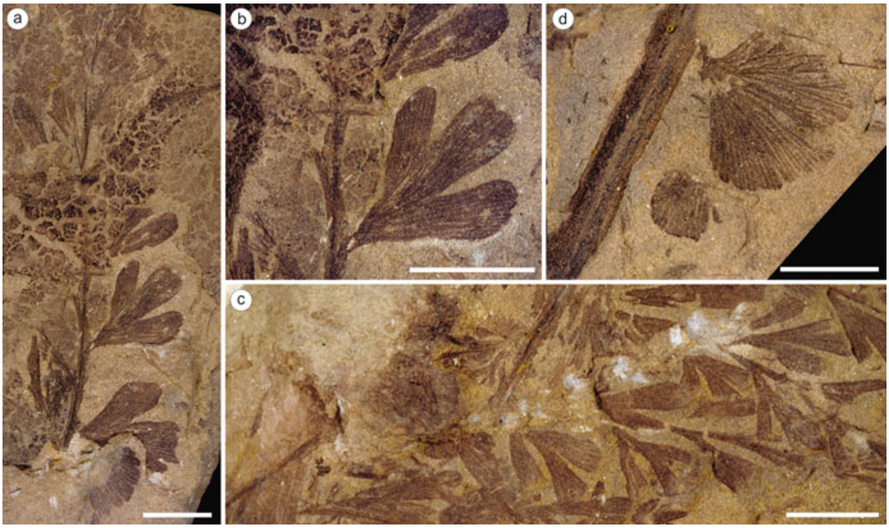

Fig. 7 *Fedekurtzia* cf. *F. argentina* (Kurtz) Archangelsky emend. Coturel et Césari, 2017. (**a**–**b**) DGM 1682. (**a**) Pinna bearing trilobed pinnules; (**b**) Detail of a trilobed pinnule showing the narrower base and fan-shaped dichotomous venation; (**c**) DGM 1681. Bipinnate frond bearing trilobed pinnules. *Notorhacopteris* cf. *N. kellaybelenensis* Azcuy and Suárez Soruco emend. Azcuy, Carrizo et Iannuzzi 2011. (**d**) DGM 1680. Detail of a cuneiform pinnule attached to a robust rachis, showing distal margin lobed and incised with fan-shaped dichotomous venation. Scale bars: 1 cm

Class PTERIDOSPERMOPSIDA
Order PTERIDOSPERMALES
Family Austrocalyxaceae Vega et Archangelsky, 2001
Genus *Fedekurtzia* (Archangelsky) emend. Coturel et Césari, 2017
Type-species *F. argentina* (Kurtz) Archangelsky emend. Coturel et Césari, 2017
Fedekurtzia cf. *F. argentina*
(Fig. 7; Table 1)

Description: It has its pinnules attached to a stem that we could consider a secondary rachis, allowing for a glimpse disposition in which the pinnules are inserted alternately on a relatively thin stem and with spacing in a range from 10 to 13 mm. The insertion of the pinnae in the main rachis is about 45 degrees. [English version of the original description of Dolianiti 1980, p. 167 and 168].

Diagnostic features: Bipinnate fronds bearing trilobed pinnules with narrower bases and fan-shaped, uniform, dichotomous venation.

Comments: Dolianiti (1980) attributed these bipinnate fronds to *Triphyllopteris alvaro-albertoi*, a taxon already described by him as *Adiantites alvaro-albertoi*, in 1954, and recombined by Rigby (1969) in the genus *Triphyllopteris*. Later, Césari (1986) and Sessarego and Césari (1989) included these specimens in *Fedekurtzia argentina*. Recently, Di Pasquo and Iannuzzi (2014) also accepted the inclusion of these specimens in *Fedekurtzia* but as cf. species *F. argentina*.

In 1981, Archangelsky combined the species *Archaeopteris argentina*, previously described by Kurtz (1921), into the new genus *Fedekurtzia*, in which he included specimens originally referred to *Sphenopteris*, *Eremopteris*, *Archaeopteris*, *Rhacopteris*, *Sphenopteridium*, *Adiantites*, or *Triphyllopteris* from Argentina, Peru, and Australia. They correspond to bipinnate foliages with significant variation in the morphology of the pinnules and pinnae throughout the fronds. This **heteromorphism** created serious difficulties to include fragmentary material in *Fedekurtzia argentina*, once it was not clear the limit of this variation. Only afterwards, the description of more complete material, such as shown by Césari (1986) and Coturel and Césari (2017), this taxon became better circumscribed. Recently, male and female structures have been added to the diagnosis of *Fedekurtzia argentina*, making it a more natural taxon with better established botanical affinities (Coturel and Césari 2017).

The specimens initially analyzed by Dolianiti represent specimens in a regular state of preservation. Perhaps this is why Dolianiti included them in *Adiantites alvaro-albertoi*, a species erected by him in 1954. However, upon looking at the specimens illustrated for *A. alvaro-albertoi* by Dolianiti (1954, Plate VI), we find that they differ from those presented here in that they have very small rounded-spatulate pinnules, ranging from simple to slightly lobed, inserted terminally in slender, weak and loose stalks. On the one hand, they have sufficient features to relate them to *Fedekurtzia*. On the other, they do not clearly show the morphological variation in the shape of the pinnules typical of the species *F. argentina*, even due to their incompleteness and incomplete state. The pinnules range from simple (apical) to bi- or trilobed (basal to medium portions of the pinnae). In addition, only a portion of the frond appears to be preserved, preventing the recognition of pinnular variation from the base to the top of this foliage. Therefore, we refer these specimens as to *Fedekurtzia* cf. *F. argentina* for now, until a formal study is published in the near future.

Study material. DGM 1680, 1681, 1682.

Collection. Museum of Earth Sciences, ANM (ex- DNPM), Rio de Janeiro.

Genus *Notorhacopteris* Archangelsky emend. Azcuy, Carrizo et Iannuzzi, 2011

Type-species *N. argentinica* (Geinitz) Archangelsky emend. Azcuy, Carrizo et Iannuzzi, 2011

Notorhacopteris cf. *N. kellaybelenensis*

(Fig. 7; Table 1)

Description: *Rhacopteris*-type pinnule isolated, apparently non-petiolate and attached to a robust rachis, 16 mm long and 18 wide and lacerate on its edge. [English version of the original description adapted from the text of Dolianiti 1980, p. 166 and 167].

Diagnostic features: Cuneiform pinnules, with distal margin lobed and incised.

Comments: Initially, this specimen was introduced by Dolianiti (1980) as *Rhacopteris* sp. Later, Sessarego and Césari (1989) reinterpreted it as *Nothorhacopteris argentinica*. On the other hand, Iannuzzi (1994) and Iannuzzi and Scherer (1996) reassigned it only as *Nothorhacopteris* sp. 1. More recently, Iannuzzi and

Pfefferkorn (2002) and Di Pasquo and Iannuzzi (2014) referred this specimen to *Notorhacopteris* cf. *N. kellaybelenensis*.

Nothorhacopteris was a genus erected by Archangelsky (1983) for similar monopinnate fronds occurring in Gondwana and gathered under various generic names (*Otopteris*, *Aneimites*, *Rhacopteris*, and *Pseudorhacopteris*). These forms, due to their entire pinnules, generally cuneiform to subcircular, were comparable to those of European *Anisopteris* in the sense that proposed by Oberste-Brink and Hirmer (according to Hirmer and Guthörl 1940). Archangelsky (1983) pointed out the distinctive characters that justified the inclusion of Gondwanan forms in a new genus: pinnules symmetrical to almost symmetrical, sessile, or shortly petiolate at least from the basal and middle portions of the frond. Thick leafy limb or mesophyll with uniform dichotomous venation that radiates from the base and fine intervening striations. Despite its incompleteness, the specimen described herein shows an almost complete symmetrical pinnule that appears relatively thick and can therefore be attributed to the genus *Nothorhacopteris*. There are currently three species recognized and well established for the genus, according to the criteria proposed by Azcuy et al. (2011), regarding the shape and degree of segmentation of the pinnules, as well as details of their distal margins. Pinnules in *N. kellaybelenensis* are cuneiform, composed of sharp segments, lobed and incised distal margins. In *N. argentinica,* they are flabelliform consisting of delicate segments in greater numbers and distal margins gently undulated. In *N. chubutiana,* they are subcircular, showing wide fibrous (darker) areas between limb segments and almost entire distal margins. Based on those specific delimitations, our specimen resembles *N. kellaybelenensis*. However, the fragmentary and preservational state of the specimen prevents us from including this material in a particular species. Because of this, the proposals of Iannuzzi and Pfefferkorn (2002) and Di Pasquo and Iannuzzi (2014) are herein accepted with a slight modification regarding the generic designation that has changed the spelling of the name, with the removal of the first letter "h," from *Nothorhacopteris* to *Notorhacopteris*, as suggested by Azcuy et al. (2011, 2014).

Study material. DGM 1680.

Collection. Museum of Earth Sciences, ANM (ex- DNPM), Rio de Janeiro.

Family Lyginopteridaceae?
Genus *Lagenospermum* Nathorst, 1914
Type-species *Lagenospermum sinclairi* (Arber) Nathorst, 1914
Lagenospermum sp.
(Fig. 8; Table 1)

Description: Oblong-shape cupules, over 8.5 mm long and up to 3.1 mm wide, consisting of at least three lobes each, 1.3 mm wide, 3.2–4.5 mm long, dividing once, separate from basal third, and apex acute; apparently supporting only one seed borne at the tips of dichotomous branchlets, 1 mm wide. [Modified English version of the original description by Iannuzzi 1994, p. 147].

Diagnostic features: Terminal lobed cupules inserted in dichotomous branchlets.

Comments: Originally, these cupules were not identified or described by Dolianiti (1954), although they are in the samples examined by him. Only Iannuzzi (1994) recognized these structures. Apparently, one of these poorly preserved

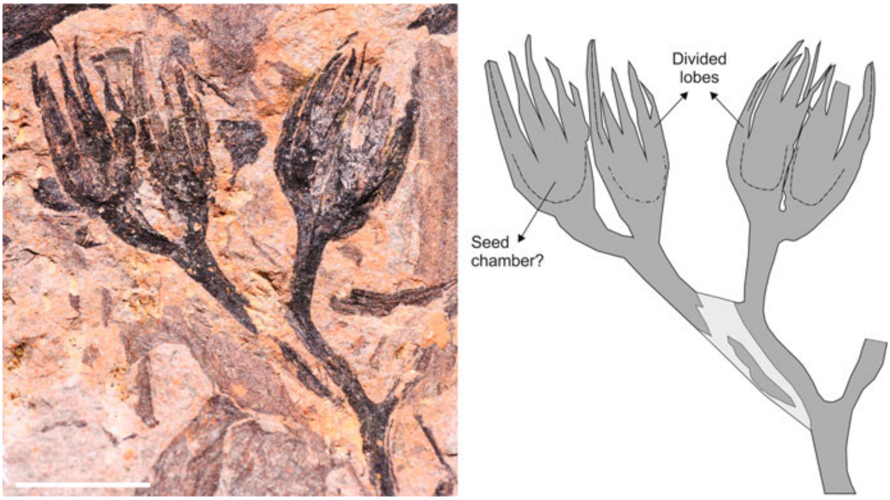

Fig. 8 *Lagenospermum* sp. DGM 1003. General view and schematic drawing of the terminal lobed (3) cupules inserted in dichotomous branchlets. Scale bar: 5 mm

structures was misidentified as a *Cardiocarpon*-type seed by Oliveira (1935). Therefore, they are first illustrated and published here but deserve a more detailed description and formal classification in a future contribution.

According to Iannuzzi (1994), these cupules, although fragmented and preserved only as compressions, are comparable to some registered cupules, mainly from the lower Carboniferous of Euramerica. Among the forms examined, *Geminitheca*, *Lagenospermum*, *Calathiops*, *Calymmatotheca*, *Calathospermum*, and *Stamnostoma* are the most similar in that they have approximately oblong-shaped cupules dissected into lobes and their sizes. However, all these genera differ in the occurrence of two ovules or more per cupule and the presence of emergences, hairs or glands on the cupules and hairs on the axes, except for *Lagenospermum* who has uniovulate cupules without any ornamentation. Among the *Lagenospermum* species, the form described here seems to be closer to *L. imparirameum* (Gensel and Skog 1977) because it has divided lobes that only join at the basal third of the cupules. Nonetheless, *L. imparirameum* differs by the larger dimensions of the cupules, which also have a larger number of lobes that divide one to several times over their entire lengths. Thus, they belong to distinct species, which will be clarified in upcoming publications. In South America, only one similar cupule-like structure has been designated by Cúneo (1990) for the Argentinean upper Carboniferous as *Calymmatotheca* sp. This single cupule was found in close association with *Sphenopteris* cf. *obtusiloba* foliage and differs from our form by the larger size, larger number of lobes which in turn are narrower and have middle veins.

Study material. DGM 1003.

Collection. Museum of Earth Sciences, ANM (ex- DNPM), Rio de Janeiro.

Family *incertae sedis*
Genus *Kegelidium* Dolianiti 1954
Type-species *K. lamegoi* Dolianiti 1954
(Figs. 9 and 10; Table 1)

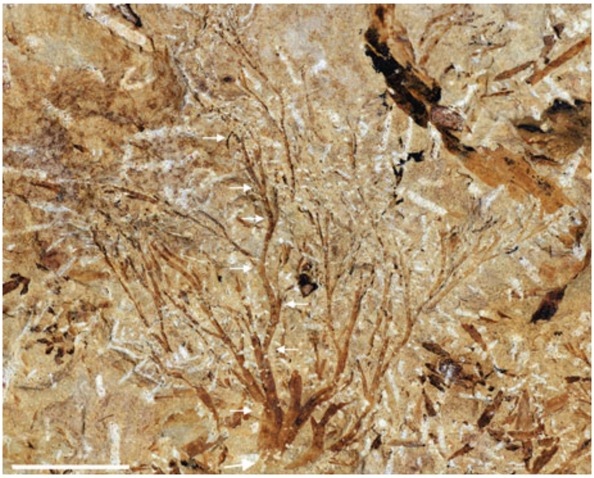

Fig. 9 *Kegelidium lamegoi* Dolianiti 1954. DGM 1012. Leafless slender axes repeatedly dichotomized (white arrows) into a three-dimensional branching system that bears terminal fusiform sporangia. Scale bar: 10 mm

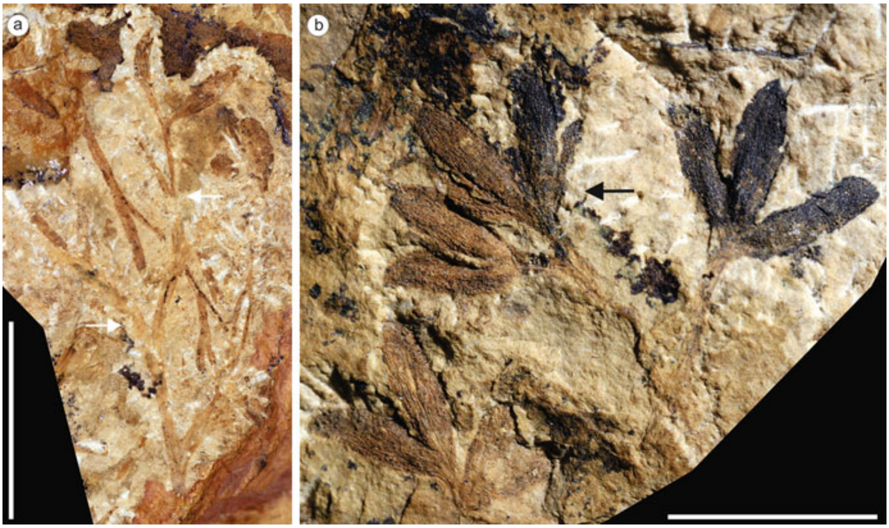

Fig. 10 *Kegelidium lamegoi* Dolianiti 1954. (**a**) DGM 1012. Distal leafless dichotomized axes (white arrows) bearing terminal fusiform (2) sporangia; (**b**) DGM 1028. Distal dichotomized axes bearing the terminal fusiform sporangia, arranged in pairs forming crowns with four erected sporangia (black arrow), apparently without dehiscence mechanism. Scale bars: (**a**) = 10 mm; (**b**) = 5 mm

Generic-specific diagnosis: *Terminal sporangia in slender dichotomous branches, disposed in pairs, oval-elongated to fusiform. Clusters with 2 to 4, rarely 6 sporangia. Externally the sporangia present a fine structure of cellular epidermal tissue, with longitudinally elongated rhomboidal meshes. The slender branches are dichotomous, without foliar element, with very fine longitudinal striae. The sporangia measure 4 to 6 mm. in length and 1 mm. width. The branches near the sporangia are 0.25 to 0.75 mm. No dehiscence or spores have been recognized in sporangia* [English version of the original diagnosis as published by Dolianiti 1954, p. 46 and 47].

Diagnostic features: Leafless slender axes repeatedly dichotomized into three-dimensional branching system, fusiform sporangia terminal, arranged in pairs forming crowns with four erected sporangia, apparently without dehiscence mechanism (see also Iannuzzi and Pfefferkorn 2014).

Comments: Dolianiti (1954) erected *Kegelidium lamegoi* to designate a microsporangiate fructification displaying terminal clusters of non-synangiate microsporangia. Later, Leguizamón and Archangelsky (1981) considered *K. lamegoi* to be so similar to *Paulophyton* spp. that they synonymized it with *Paulophyton sommeri*. However, as pointed out by Iannuzzi (1994) and Iannuzzi and Pfefferkorn (2014), these taxa show distinct morphological features. The sporangia-bearing branch system of *Kegelidium* arises from basal axes dichotomously branched, while *Paulophyton* exhibits a regular pseudomonopodial branch system. Sporangia of *Kegelidium* are slightly bigger than *Paulophyton* ones and fusiform, differing from the oval-shaped sporangia of *Paulophyton*. Finally, the terminal arrangement in a crown of two pairs of sporangia is not recognizable in *Paulophyton*. Because of these differences, Iannuzzi (1994) and Iannuzzi and Pfefferkorn (2014) rejected the synonymy proposed by Leguizamón and Archangelsky (1981) and considered *K. lamegoi* is a valid taxon.

As already noted by Dolianiti (1954), the sporangia-bearing branch system of *Kegelidium* resembles fertile structures found in distinct plant groups of the Middle–Late Devonian to Mississippian, such as trimerophytes, early ferns (Cladoxylales, Zygopteridales), **progymnosperms** (Aneurophytales, Protopityales), and early seed ferns (Lyginopteridaceae). *Kegelidium* seems to be morphologically closer to basal Mississippian pteridosperms related to Lyginopteridaceae (Iannuzzi and Pfefferkorn 2014). Taking into account the evolutionary sequence proposed by Millay and Taylor (1979) to the evolution of microsporangiate fructification in lyginopterid-like plants, *Kegelidium* could be considered as an intermediate step between non-synangiate forms, such as *Zimmermannitheca* and *Geminitheca*, and advanced synangiate ones as *Telangiopsis* and *Telangium*.

The sterile foliage of *Kegelidium* is unknown yet, but the specimens co-occur with at least three types of frond-like foliage: *Diplothmema*-like (sensu Césari 1987), *Sphenopteridium*-like (sensu Iannuzzi and Pfefferkorn 2002), and *Aneimites*-like (sensu Iannuzzi and Pfefferkorn 2002). Nevertheless, there is no proof to designate them as sterile foliage of *Kegelidium*. Anyway, the occurrence of *Kegelidium* in the Poti Formation Flora improve our knowledge about early seed plants of the Southern Hemisphere, adding to the limited published record of male reproductive structures of **presynangiate** plants from the Mississippian of Gondwana (see Erwin et al. 1994).

Holotype. DGM 1019.

Paratypes. DGM 1012, 1019, 1028.

Collection. Museum of Earth Sciences, ANM (ex- DNPM), Rio de Janeiro.

PTERIDOPHYLLA
Genus *Diplothmema* Stur, 1877
Type-species *D. schuetzei* Stur, 1877
Diplothmema gothanica (Dolianiti) Iannuzzi emend. Iannuzzi et al. 2006
(Figs. 11 and 12; Table 1)

Emended species diagnosis: *"Fronds tri- to quadripinnate?; main rachis bifurcate and geniculate. First-, second- and third-order rachises slightly curved and sinuous, bearing alternately and in different planes pinnae and pinnules inserted at acute angles. Pinnules cuneiform-elongate to lanceolate, decurrent, inserted to rachis by short leaf-stalks, deeply lobed in narrow segments, tapering to rounded entire, slightly incise or unequally bilobulate apex; basal pinnules of pinnae at least five-lobed, intermediate pinnules tree-lobed and apical ones simple and unlobed. Venation dichotomous, arising from one basal vein that divides according to the number of lobes; two veins per lobe run parallel to reach the distal portion of leaf*

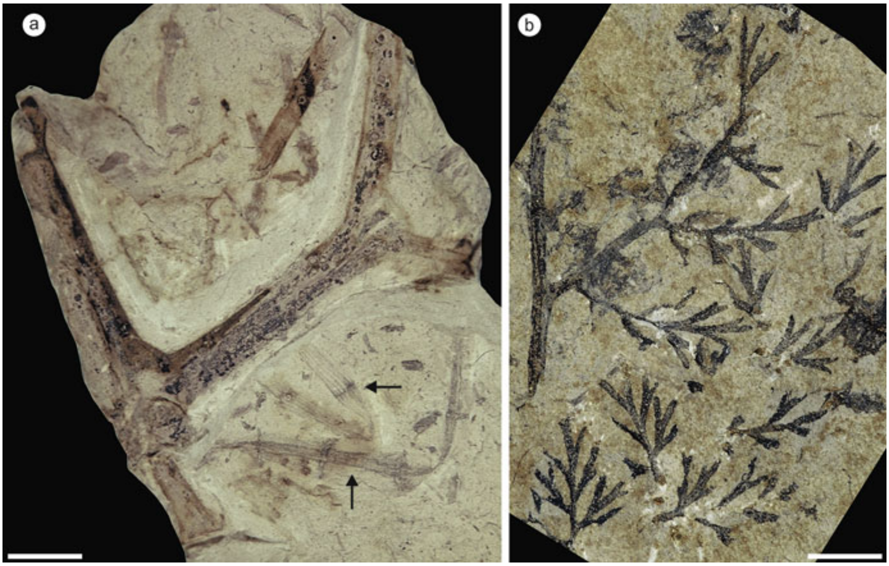

Fig. 11 *Diplothmema gothanica* (Dolianiti) Iannuzzi emend. Iannuzzi et al. 2006. (**a**) GP/3 T 2333. Basal portion of a bifurcate frond, showing the main rachis dividing into primary rachis and this in turn, dividing (on the right side) into secondary rachises (outer and inner). Also, note the presence of narrow *Archaeocalamites*-like stems (black arrows); (**b**) DGM 682. Middle portion of (at least three-pinnated) frond bearing secondary axis(?) and ultimate- and penultimate order pinnae, the latter supporting narrow-laminated pinnules alternately. Scale bars: 1 cm

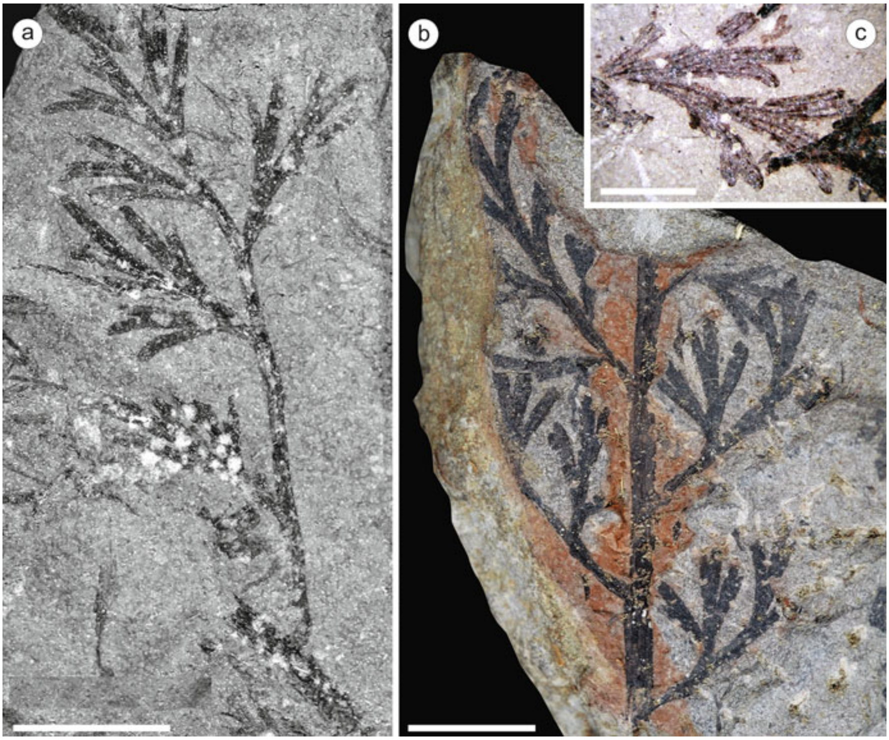

Fig. 12 *Diplothmema gothanica* (Dolianiti) Iannuzzi emend. Iannuzzi et al. 2006. (**a**) DGM 669. Ultimate-order pinna bearing cuneiform-elongate pinnules deeply lobed in narrow segments, tapering to rounded (holotype); (**b**) DGM 673. Ultimate- and penultimate-order pinnae bearing alternately cuneiform pinnules deeply lobed in narrow segments, tapering to rounded, slightly incised or unequally bilobed apex; (**c**) DGM 1027. Pinnules showing details of venation pattern in which at least two veins run parallel per terminal lobe. Scale bars: (**a**–**b**) = 10 mm; (**c**) = 5 mm

margin, many times the veins divides again near to the apex, giving rise to four terminal veins."

Diagnostic features: Frond with basal furcated and geniculate main rachis (Fig. 11a), the insertion in different planes and acute angles of the rachises of penultimate and ultimate orders (Fig. 11b), cuneiform-elongate to lanceolate pinnules deeply lobed in narrow segments, tapering to rounded entire, slightly incised or unequally bilobed apex; two veins per terminal lobe (Fig. 12c).

Comments: This form represents the first specimens described for the Poti Formation (Oliveira 1934, 1935). The species erected by Dolianiti (1954) included in the Euramerican genus *Diplothmema* Stur (1877) promoted by Césari (1987) was accepted by later authors. Indeed, among the Late Paleozoic genera, the specimens assigned to *Diplothmema* have quadripinnate fronds with pinnules deeply divided into very narrow linear segments (lobes). However, the species attributed to *Diplothmema* in Euramerica have only one vein per distal segment of the pinnules

(Boureau and Doubinger 1975), while other South American forms, i.e., *D. gothanica* and *D. bodenbenderi* from Argentina, have at least two veins that distally divide into four shortened terminal veins (Césari 1987, Iannuzzi et al. 2006 – Fig. 12c). This subtle morphological difference can represent different fronds of endemic gymnosperm reproductive structures from South America, such as *Kegelidium lamegoi*, *Occloa cesarean*, *Obandotheca laminesis*, and *Eonotosperma arrondoi* (Dolianiti 1954; Erwin et al. 1994; Césari 1997). They were found associated with *Diplothmema* fronds in Carboniferous strata of the Parnaíba Basin, Brazil, the Paraca Peninsula, Peru, and the province of La Rioja, Argentina, respectively. If the link between some of these reproductive structures and the *Diplothmema* fronds is confirmed, the proposition could justify a new genus for South American fronds in the future. In this case, the whole set of taxa (vegetative and fertile parts) could represent a new family of plants exclusive to Gondwana.

Among the known species of *Diplothmema*, the Argentinean *D. bodenbenderi* is the most similar to *D. gothanica*. Iannuzzi and Pfefferkorn (2002) pointed out that *D. gothanica* is distinguished from *D. bodenbenderi* by having narrower, cuneiform, non-spindled or orbicular pinnules in which the terminal segments are whole or slightly bilobed, never truncated and emarginated. Moreover, those authors also highlighted as diagnostic features of *D. gothanica* the insertion of the third and fourth order rachises and pinnules always at acute angles, never straight, and in slightly different planes, giving the frond a specific three-dimensional branching pattern (see also Iannuzzi et al. 2006).

The revision of Dolianiti's type material and the analysis of new material by Iannuzzi et al. (2006) allowed the synonymization of *A. oliveiranus* and *A. santosi* with *D. gothanica*. Specimens included in these two other species, found in close association with *D. gothanica*, were considered by those authors as different portions (individual variations) of fronds or represented intraspecific variations of *D. gothanica* (Table 1).

Holotype. DGM 669.

Paratypes. DGM 673, 682, 1002, 1009, 1027.

Other specimens. GP/3 T 2333.

Collections. Museum of Earth Sciences, ANM (ex- DNPM), Rio de Janeiro; Depto. Sedimentary and Environmental Geology, IGc, USP, São Paulo.

Genus *Aneimites* Dawson, 1860
Type-species *A. tenuifolia* (Göppert) Dawson, 1860
Aneimites sp. in Iannuzzi and Pfefferkorn, 2014
(Table 1)

Original specific diagnosis: *"Apparently alternate pinnules rounded to spatulate, with 3 to 4 deep lobes. There is not a petiole, proper, but a contracted base of pinnule. The nerves radiate from a basal one divided 5 to 6 times. All nerves are of equal force, and there are not nervils. The nervation is typically fan-shaped."* [English version of the original diagnosis as published by Dolianiti 1954, p. 44].

Diagnostic features: Small rounded-spatulate pinnules, apex sometimes truncate to sublobed-to-lobed, with fan-shaped venation and strongly contracted bases inserted into slender branchlets.

Comments: This form represents one of the first specimens assigned by Oliveira (1935) as *Sphenopteris obtusiloba*. Later, Dolianiti (1954) classified this set of small terminal pinnules as one more species of *Adiantites*, that is *Adiantites alvaro-albertoi*. He recognized that this form was different from others described in the same contribution, namely *A. gothanica*, *A. oliveiranus,* and *A. santosi,* recently transferred to the genus *Diplothmema* (see above). Recognizing the difference that the pinnules of this form show compared to the others described by Dolianiti for the Poti Formation Flora, Rigby (1969) recombined it in the genus *Triphyllopteris* (Table 1). Later, Césari (1986) included these specimens in *Eusphenopteris sanjuanina*. Recently, Iannuzzi and Pfefferkorn (2014) included these specimens in the genus *Aneimites* without assigning a species.

The fragmented state of the specimens precludes a more precise classification at a specific level of this material. Although terminal pinnules are relatively well preserved, the lack of information about the frond branching system as a whole makes it difficult to assign this material to any genus. Similar pinnules are known from various genera of the Carboniferous, among them *Adiantites*, *Aneimites,* and *Eusphenopteris*. Hence, this material is provisionally included in *Aneimites* because it has small pinnules, tightly contracted at the base and inserted through thin branchlets into the rachis until more complete material can be recovered in the future.

Study material. DGM 669, 1010, 1020, 1021, 1022, 1023, 1910, 1911, 1913, 1914.

Collection. Museum of Earth Sciences, ANM (ex- DNPM), Rio de Janeiro.

Poti Formation Microflora

As mentioned under section "Age," palynological associations of the Poti Formation are essentially known from subsurface siltstones and mudstones of several boreholes drilled in the central part of Parnaíba Basin (Melo and Loboziak 2000) and from subsurface diamictites and siltstones of several boreholes drilled in the Tocantins River (Streel et al. 2012). Until now, only the Roncador Creek outcrop has provided palynologically fertile samples that have been studied and described by Di Pasquo and Iannuzzi (2014). The floral deposits recorded at the lower part of the same outcrop at Roncador creek are composed of *Fedekurtzia* cf. *F. argentina* and *Notorhacopteris* cf. *N. kellaybelenensis* (see Iannuzzi et al. 2006; Di Pasquo and Iannuzzi 2014). This confirms the appearance of the genus *Fedekurtzia* in the Mississippian of northern South America and represents the first record of macro- and microfossils in association in this unit.

The palynological study of six samples of carbonaceous shales and siltstones of the Poti Formation revealed diverse assemblages composed of 58 spore species and five species of chlorophycean algae. One of the samples yielded 32 reworked species, 9 spores and 23 microplankton species, from the Mid–Late Devonian and Tournaisian and corroborated the unconformable contact between the Poti and its underlying Longá Formation (Fig. 3, Melo and Loboziak 2003, Di Pasquo and Iannuzzi 2014). Stratigraphically significant are *Anapiculatisporites amplus* Playford et Powis, *Anapiculatisporites concinnus* Playford, *Apiculiretusispora microseta* Ravn, *Foveosporites pellucidus* Playford et Helby, *Grandispora maculosa* Playford et Helby, *Verrucosisporites morulatus* (Knox) Potonié et Kremp emend. Smith et Butterworth, and *Waltispora polita* (Hoffmeister, Staplin et Malloy) Smith et Butterworth, pointing to Visean age. *Densosporites spinosus* Dybová et Jachowicz, *Knoxisporites ruhlandi* Doubinger et Rauscher, *Punctatisporites subvaricosus* Playford, *Reticulatisporites* (*Cordylosporites*) *magnidictyus* Playford et Helby, *Retusotriletes mirabilis* (Neville) Playford, *Tricidarisporites phippsae* Playford et Satterthwait are age-diagnostic taxa of the middle to late Visean (Figs. 13 and 14). They confirm the assignment of the assemblages to the late Visean R. *magnidictyus* (= Mag) Zone (Fig. 15, Di Pasquo and Iannuzzi 2014).

The Mag Zone Melo and Loboziak 2003 was defined in the Oriximaná and Faro formations of the Amazonas Basin of Brazil. *Reticulatisporites magnidictyus* and other cosmopolitan species found in the palynoflora at Roncador creek confirm its correlation (e.g., Iannuzzi and Rösler 2000; Azcuy et al. 2007; Di Pasquo and Iannuzzi 2014) with the Mag Zone in Peru (Azcuy and Di Pasquo 2005; Di Pasquo et al. 2018, 2019b) and Bolivia (Fasolo et al. 2006; Azcuy et al. 2007; Di Pasquo et al. 2018, 2019a), the MQ Zone of Argentina (Milana and Di Pasquo 2019; Valdez Buso et al. 2020), and the *Grandispora maculosa* zonal assemblage of Australia (Playford 1991, 2017; Jones and Truswell 1992) and northern Africa (Coquel et al. 1995).

From the botanical affinities of spore species of the Poti Formation, major plant groups have been recognized: Pteridophyta (*Punctatisporites, Convolutispora, Verrucosisporites*) and subordinated, Lycophyta (*Cristatisporites, Densosporites, Vallatisporites*), Sphenophyta (*Calamospora*), and Pteridospermophyta (*Cyclogranisporites*) (Di Pasquo and Iannuzzi 2014). A few typical plant fossils from the Poti Formation, such as dwarf lycopsids and the genera *Archaeocalamites*, *Paulophyton*, *Aneimites*, *Fryopsis*, *Sphenopteridium*, *Fedekurtzia*, *Nothorhacopteris*, *Diplothmema*, *Kegelidium,* and *Lagenospermum* (see Iannuzzi and Pfefferkorn 2002, Iannuzzi et al. 2006, Di Pasquo and Iannuzzi 2014, and Table 1), are mostly in agreement with those major groups.

Importance of the Poti Flora in the Mississippian

The Poti Formation Flora was considered as part of the warm-temperate *Paraca Floral Realm*, distinguished from the **Amerosinian** (**Euramerican**) **Realm** to the north and the **Gondwanan Realm** to the south (Iannuzzi and Pfefferkorn 2002). The *Paraca Floral Realm* was established based on the presence of similar macrofloras and microfloras in South America (Peru, Bolivia, Argentina, and Brazil), Africa (Niger), India, and Australia, dated as late Mississippian (late Visean–earliest

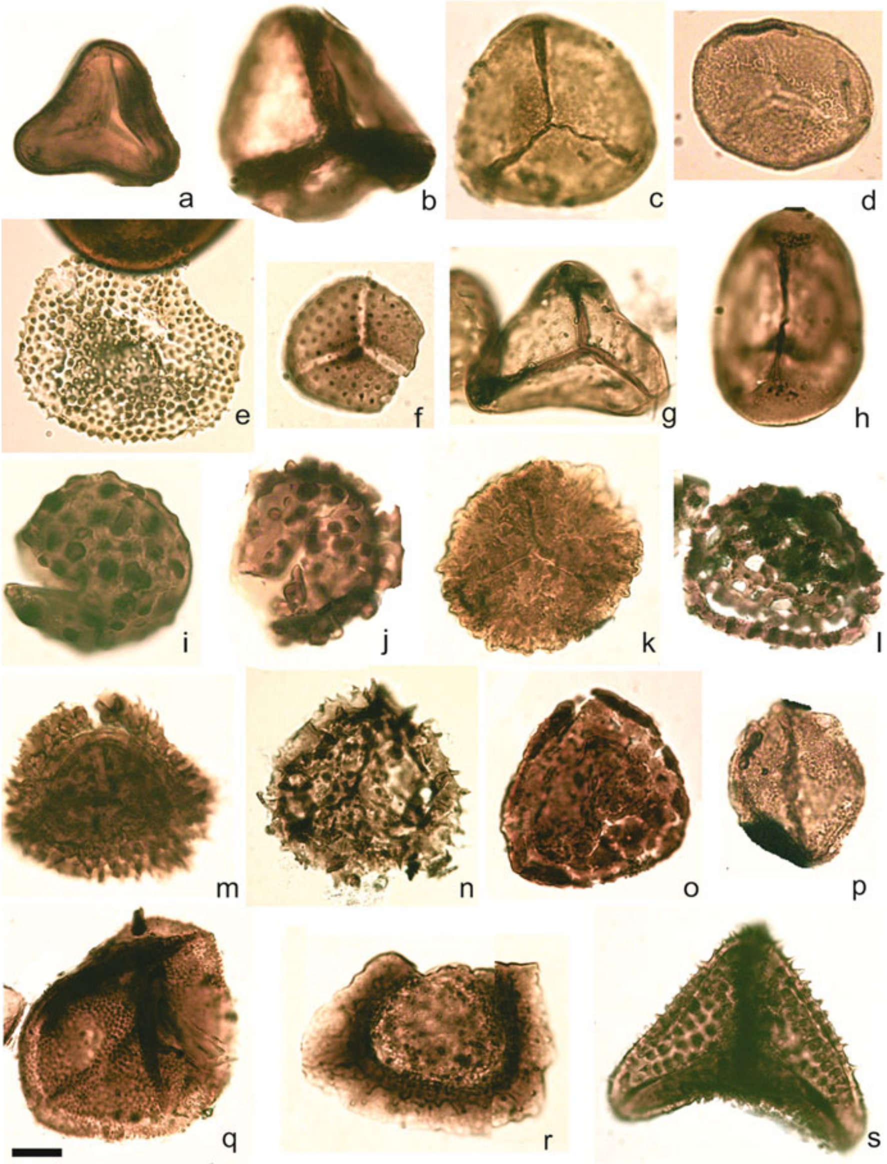

Fig. 13 Palynomorphs 1. Autochthonous species in the assemblage of the Poti Formation at Roncador creek.(**a**) *Waltzispora polita* (Hoffmeister, Staplin et Malloy) Smith et Butterworth, MP-P 9742 B26/0; (**b**) *Gulisporites torpidus* Playford, MP-P 9743 J32/1; (**c**) *Leiotriletes tortilis* Playford, MP-P 9743 S25/3; (**d**) *Punctatisporites subvaricosus* Playford, MP-P 9743 T9/1; (**e**) *Dibolisporites microspicatus* Playford, MP-P 9743 D8/1; (**f**) *Anapiculatisporites concinnus* Playford, CICYTTP-Pl 582(1) X57/3; (**g**) *Anapiculatisporites amplus* Playford et Powis, MP-P 9742-A T33/1; (**h**) *Retusotriletes mirabilis* (Neville) Playford/P. digressus Playford, MP-P

Serpukhovian) from several localities and radioisotopic data from Australia and South America (Iannuzzi and Pfefferkorn 2002; Césari et al. 2011; Valdez Buso et al. 2020). It represents a widespread frost-free climate (zone-biome) in a wide belt on Gondwana that reached from 30° to as far as 60° South and existed directly before the onset of the major episode of the Carboniferous–Permian glaciations (Fig. 16). These floras are dominated by pteridosperm foliage (*Diplothmema Notorhacopteris*, *Triphyllopteris*, *Sphenopteridium*) and the occurrence of tree-lycopsids (*Tomiodendron*) and shrubby sphenopsids (*Archaeocalamites*). According to Iannuzzi and Pfefferkorn (2002), the origin of this particular zonobiome Paraca was due to the interplay of (1) climate oscillations, (2) several kinds of long-distance plant dispersal within, between or through zonobiomes, and (3) plate motion.

1. Climate oscillations occur at different scales in the Earth history (Montañez et al. 2016). The alternation of warm and cold intervals on the scale of several million years (Montañez et al. 2007; Fielding et al. 2008) are known by researchers as long-term ***Greenhouse*** and ***Icehouse*** phases. A shorter time scale is represented by the **Milankovitch cycles** triggered by astronomical forces with 400, 100, 41, and 26 thousand years. Plant dispersal, even over long distances, is so rapid that they can respond to all these types of oscillations, including the shortest Milankovitch cycles. The major problem is that stratigraphic resolution in **deep time** is not high enough yet to detect the faster processes. In most cases, it can only be deduced that these short cycles existed, and synthesis of a set of small changes preserved in the rocks is recorded that occurred over a longer period, usually on the million-year scale. Regarding long-term climate cycles, the late Visean–earliest Serpukhovian interval lies within the longest period of the Phanerozoic Icehouse phase known as the Late Paleozoic Ice Age (LPIA), which began in the latest Devonian and extended up to the middle Permian (Montañez et al. 2007). More specifically, the analysis of sedimentary sequences that were dated by radioisotopic methods shows glacial beds at 338 Ma (mid-Visean) and at 325 Ma (later Serpukhovian), leaving a 13 Ma long interval (see Césari et al. 2011; Valdez Buso et al. 2020 and references therein) when the Paraca floras occurred. Therefore, a relatively short (in a million-year scale) greenhouse time

◄

Fig. 13 (continued) 9743 J33/4; (**i**) *Verrucosisporites gobbettii* Playford, MP-P 9743 G11/2; (**j**) *Raistrickia baculosa* Hacquebard, MP-P 9742 R32/0; (**k**) *Cristatisporites colliculus* Playford, MP-P 9743 V33/0; (**l**) *Cristatisporites peruvianus* Azcuy et Di Pasquo, MP-P 9742-A U31/1; (**m**) *Cristatisporites echinatus* Playford, MP-P 9742 H27/1; (**n**) *Densosporites spinosus* Dybová et Jachowicz, CICYTTP-Pl 582(1) H52/1; (**o**) *Cristatisporites menendezii* (Menéndez et Azcuy) Playford, MP-P 9742 S20/1; (**p**) *Aratrisporites saharensis* Loboziak, Clayton et Owens, MP-P 9742 R30/4; (**q**) *Spelaeotriletes balteatus* (Playford) Higgs, MP-P 9742–1 M34/4; (**r**) *Densosporites regalis* (Bharadwaj et Venkatachala) Smith et Butterworth, CICYTTP-Pl 582(1) F36/2; (**s**) *Tricidarisporites phippsae* Playford et Satterthwait, MP-P 9743 T12/1. Scale bar: 10 μm; except for (**l**), (**o**), and (r) = 13.5 μm

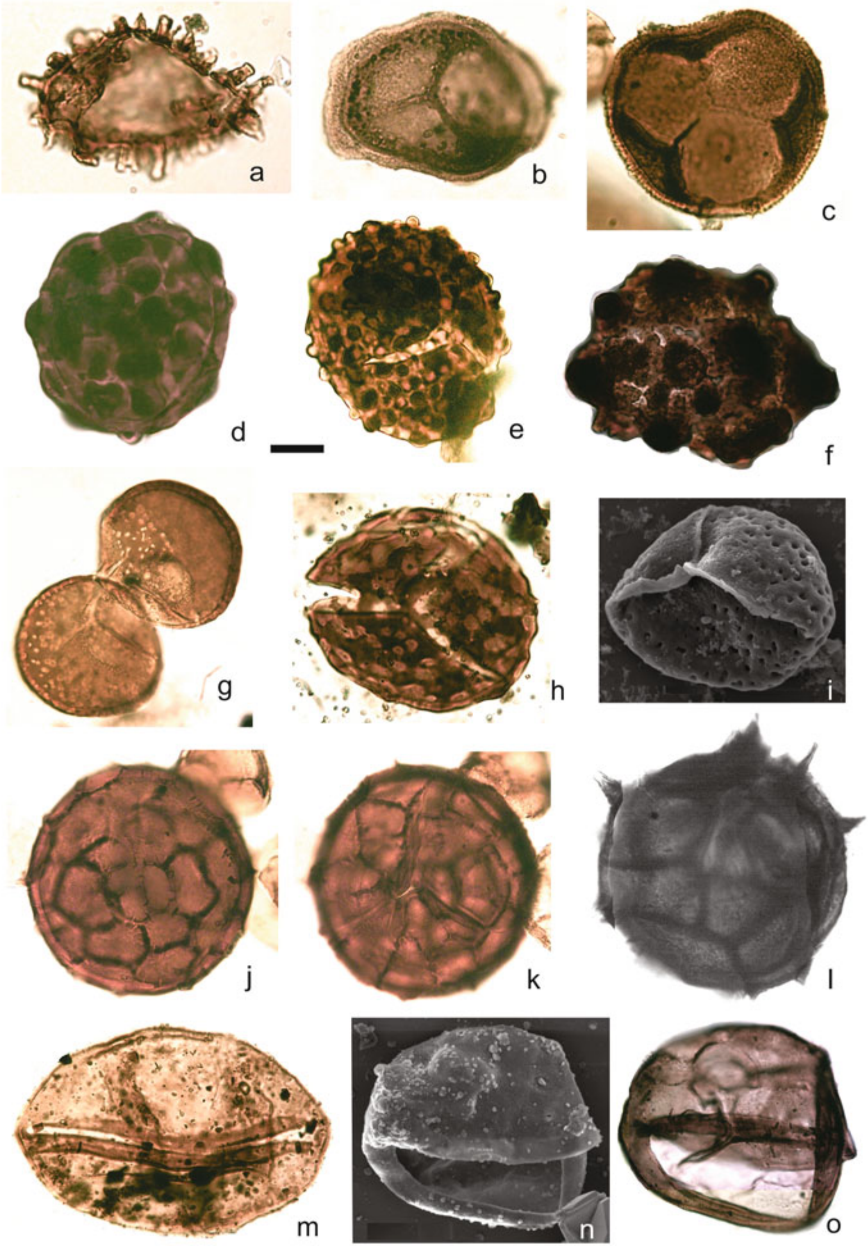

Fig. 14 Palynomorphs 2. Autochthonous species in the assemblage of the Poti Formation at the Roncador creek. (**a**) *Raistrickia clavata* Hacquebard, MP-P 9743 Y12/2; (**b**) *Grandispora maculosa* Playford et Helby, MP-P 9742-A W31/4; (**c**) *Apiculiretusispora microseta* Ravn, MP-P 9742 N18/1; (**d**) *Verrucosisporites congestus* Playford, MP-P 9743 K13/3; (**e**) *Verrucosisporites morulatus*

existed in the late Visean to early Serpukhovian (Pfefferkorn et al. 2014). The warming in the late Visean is also supported by data from marine invertebrate faunas that reach significant diversification on global sea-rises and expanded from tropical seas to mid- and high-latitude oceans (Raymond et al. 1990; Powell et al. 2009). The common presence of tree-lycopsids and pteridosperms with a tree habit in Paraca floras is an indication that these vegetational communities lived under conditions of frost-free climate (Iannuzzi and Pfefferkorn 2002). Nevertheless, there is a record of punctual glacial deposits in the Visean strata of South America (e.g., Pfefferkorn et al. 2014, Di Pasquo et al. 2018, Milana and Di Pasquo 2019, Valdez Buso et al. 2020) indicating that minor warming and cooling oscillations – probably related to Milankovitch cycles – happened during this time as expected from Holocene climate patterns.

2. Long-distance plant dispersal: The plants lived during an interval of greenhouse conditions as indicated by the occurrence of tree-lycopsids and width and extent of the floral belt, circumstances that facilitated the long-distance dispersal of the plants inside this belt and into it from other parts of the globe (Pfefferkorn et al. 2014). Pfefferkorn et al. (2014) recognized six types (I–IV) of long-distance dispersal of plants, and the origin of some elements from Paraca floral realm are part of this analysis. At least two types were relevant to the establishment of the Paraca floras. Type I is within **zonobiome** dispersal. During the late Mississippian **greenhouse**, some plants such as *Notorhacopteris kellaybelenesis, Triphyllopteris boliviana, Fryopsis frondosa*, *Tomiodendron* sp., and ?*Sphenopteridium intermedium* spread longitudinally throughout the Paraca (temperate zonobiome) belt across Gondwana between Peru and Australia (Fig. 16; Iannuzzi and Pfefferkorn 2002), illustrating a good example of Type I. Type VI represents the migration of plants from one zonobiome to another. The main challenge for each species is to survive different paleogeographic and paleoclimatic conditions. An example is the dispersal of the tree-lycopsid *Tomiodendron* from the northern temperate zonobiome (**Angaran Floral Realm**) through the tropics (Euramerican floral realm) to the southern warm-temperate zonobiome, the Paraca floral belt (Alleman and Pfefferkorn 1988; Iannuzzi and Pfefferkorn 2002).
3. Plate motion: During the late Devonian–Pennsylvanian interval, the continent of Gondwana experienced a large clockwise rotation (Scotese et al. 1979; Scotese

Fig. 14 (continued) (Knox) Potonié et Kremp emend. Smith et Butterworth, CICYTTP-Pl 582(3) C50/1; (**f**) *Pustulatisporites gibberosus* (Hacquebard) Playford, MP-P 9742 S11/0; (**g**) *Foveosporites pellucidus* Playford et Helby, MP-P 9743 R27/2; (**h**) *Foveosporites pellucidus* Playford et Helby, MP-P 9739 V56/1; (**i**) *Foveosporites pellucidus* Playford et Helby, CICYTTP-Pl 584(SEM); (**j**–**k**) *Reticulatisporites magnidictyus* Playford et Helby emend. Playford, MP-P 9743 N31/2; (**l**) *Reticulatisporites magnidictyus* Playford et Helby emend. Playford, MP-P 9743 U15/3; (**m**) *Calamospora* sp., MP-P 9742–1 Y58/0; (**n**) *Calamospora* sp., CICYTTP-Pl 584(SEM); (**o**) *Calamospora* sp., MP-P 9742–1 K40/2. Scale bar: (**a**–**c**), (**e**), (**h**–**i**) = 10 μm; (**d**), (**f**–**g**) = 13.5 μm; (**m**) = 15 μm; and (**j**–**l**), (**n**–**o**) = 20 μm

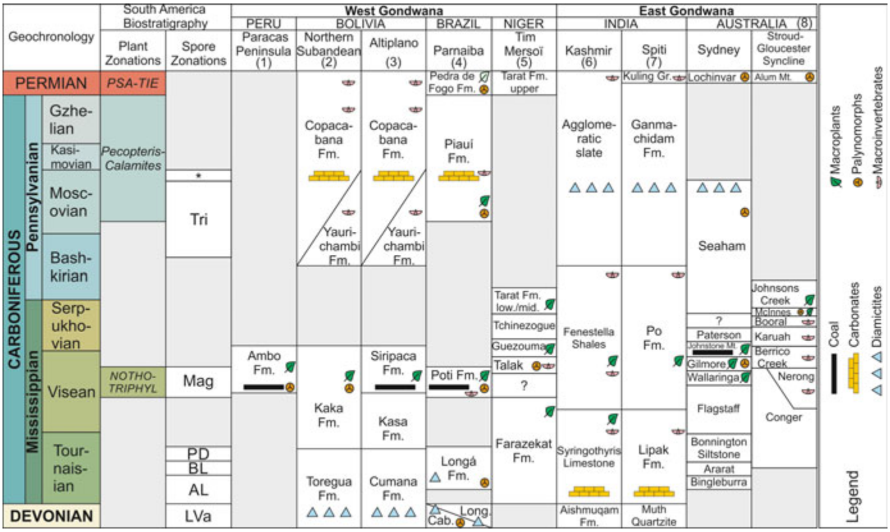

Fig. 15 Biostratigraphic correlation of the Poti macro- and microfloral assemblages, included in *Notorhacopteris-Triphyllopteris* (NOTHO-TRIPHYL) and *Reticulatisporites magnidictyus* (Mag) zones, with other Mississippian assemblages of Western (Peru, Bolivia, Brazil, Niger) and Eastern Gondwana (India, Australia). Note that all floras similar to Poti are associated to coal deposits and positioned in the Visean-Serpukhovian interval throughout Gondwana. Data based on: (1) Di Pasquo and Azcuy (2005) and Di Pasquo et al. (2018, 2019b), for Peru; (2–3) Fasolo et al. (2006), Di Pasquo (2008), Di Pasquo et al. (2018, 2019a), for Bolivia; (4) Playford and Dino (2000), Melo and Loboziak (2003), and Di Pasquo and Iannuzzi (2014), for Brazil; (5) Coquel et al. (1988, 1995), for northern Africa; (6–7) Tripathi and Singh (1985), for India; (8) Playford (1991), Jones and Truswell (1992), and Playford (2017), for Australia. General correlation based on Iannuzzi and Pfefferkorn (2002). Legend: PSA-TIE = *Psaronius-Tietea*; LVa = *Retispora lepidophyta-Vallatisporites vallatus* Interval Zone; AL = *Radiizonates arcuatus-Waltzispora lanzonii* Interval Zone; BL = *Spelaeotriletes balteatus-Neoraistrickia loganii* Interval Zone; PD = *Spelaeotriletes pretiosus-Colatisporites decorus* Interval Zone; Tri = *Spelaeotriletes triangulus* Assemblage Zone; * = *Striomonosaccites incrassatus* Zone, *Illinites unicus* Zone, *Striatosporites heyleri* Zone, and *Raistrickia cephalata* Zone

and McKerrow 1990; Eldridge et al. 2000). Due to this movement, western Gondwana (South America and Africa) shifted from higher to lower latitudes while simultaneously eastern Gondwana (Australia, India, Antarctica) displaced in reverse, from lower to higher latitudes. In addition to data provided by paleomagnetic studies (polar drift curve), sedimentary sequences found in western and eastern Gondwana confirm these plate motions based on the preservation of paleoclimatically sensitive lithologies (Fig. 16). Marine carbonates, as indicators of relatively warm waters, are essentially restricted to the Mississippian deposits in Australia, while in South America, they were found in the Pennsylvanian of central-northern basins. An opposite situation occurs concerning deposits of glacial-origin diamictites, indicators of colder climates, which are found in late Devonian-Mississipian deposits in South America and Pennsylvanian ones in India and Australia, see Fig. 16 (Veevers and Powell 1987; Scotese

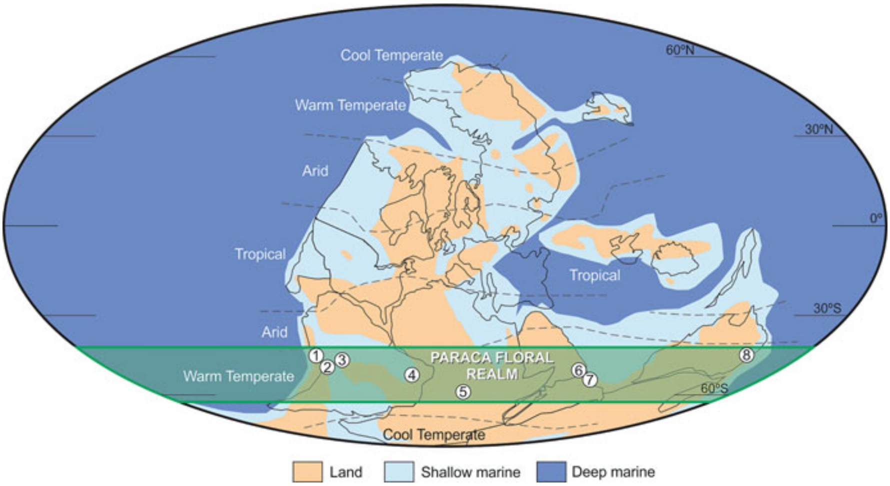

Fig. 16 World map of the late Visean showing the position of the circum-*Gondwana Paraca Floral Realm* of late Visean–earliest Serpukhovian time, based on macro- and microfloras found in South America [Peru (1), Bolivia (2 and 3), and Brazil (4)], Africa [Niger (5)], India (6 and 7), and Australia (8) (modified after Iannuzzi and Pfefferkorn 2002). Continental positions after the computer program "Plate Tracker" (Eldridge et al. 2000) for the latest Visean (330 m.y.)

> and Barret 1990; Díaz-Martínez et al. 1993; Di Pasquo et al. 2017, 2018). Therefore, the Paraca Realm supports that Gondwana occupied an intermediate position characterized by a wide, warm temperate climatic belt between 30° and 60° South during the late Visean and early Serpukhovian interval, in which coal beds are also commonly present (Scotese 2000, Figs. 15 and 16). The paleogeographic configuration allowed the dispersal of plants adapted to this climate between east and west of Gondwana, assuming that there were no other significant barriers across this continent.

Given the characteristic genera of the Paraca floral realm, unfortunately, the tree-lycopsid *Tomiodendron*, which is typical from the Angaran floral realm, is not present in the Poti Formation Flora. The shrubby sphenopsid *Archaeocalamites* is not confirmed because of the absence of leaves and/or fertile structures associated with the small sphenopsid stems recovered (Fig. 11, Table 1). Among pteridosperm foliage, *Triphyllopteris* is not present, although this genus has been attributed to different elements of Brazilian flora in the past (see section "Historical Overview of the Poti Formation Flora"). Other foliage like *Fryopsis* and *Sphenopteridium* are assigned with doubts due to the fragmentary state of the specimens. Those taxa are widespread recorded in Mississippian strata of the tropical Euramerican region (Iannuzzi and Pfefferkorn 2002, Pfefferkorn et al. 2014). Among the typical pteridosperm genera of the Paraca floral realm, only *Notorhacopteris* and *Diplothmema* are present (Table 1). Therefore, the Poti flora shares some elements with other floras of the Paraca floral realm in South America, for instance, *Notorhacopteris* cf. *N. kellaybelenensis*, ?*Sphenopteridium* sp., ?*Fryopsis* sp., *Paulophyton sommeri*, *Aneimites* sp., *Diplothmema* cf. *D. bodenbenderi*, along with the presence of *Fedekurtzia.* On the other hand, there are some typical **endemic** elements of the Parnaíba Basin, such as *Kegelidium lamegoi* and *Diplothmema gothanica* together with some palynomorph species documented for the first time in Brazil and/or South America (*Densosporites spinosus*, *Knoxisporites ruhlandi, Tricidarisporites phippsae,* and *Retusotriletes mirabilis*). This mixture of species, some endemic and others not, are probably due to unique semiarid climatic conditions prevailed in this region of Brazil, whereas Peru, Bolivia, and Australia were located in more humid regions (Iannuzzi and Rösler 2000; Di Pasquo and Iannuzzi 2014).

The evolution of plants was likely triggered by dispersal due to recognized morphologically related taxa between the northern and southern hemispheres. The ancestor of the monopinnate frond *Notorhacopteris* that closely resembles European monopinnate fronds classified as *Rhacopteris* and *Anisopteris* give rise to the Family Austrocalixcaeae characterized by *Fedekurtzia* (Coturel and Césari 2017) and *Notorhacopteris* fronds (Azcuy et al. 2011; Carrizo and Azcuy 2015), most sterile and some fertile with cupule-like organs exclusive of the Southern Hemisphere (Vega and Archangelsky 2001). This group of plants that probably evolved from immigrant Euramerican pteridosperms with triphyllopterid fronds is documented for the first time in the Parnaíba Basin, interpreted as their center of origin in Gondwana during the Mississippian (Di Pasquo and Iannuzzi 2014). Other putative pteridosperms such as *Diplothmema* fronds show discrete morphological discrepancies with corresponding fronds from Euramerica (Iannuzzi et al. 2006), and they are found in close association with endemic fructifications (i.e., *Kegelidium lamegoi*, *Occloa cesariana*, *Obandotheca laminesis,* and *Eonotosperma arrondoi* – in Dolianiti 1954, Erwin et al. 1994, Césari 1997) suggesting they are only forms from western Gondwana. Lastly, only the *Paulophyton*, a whisk-like plant, seems to correspond to an evolutionary lineage of putative ferns that originated in Gondwana. They would have evolved entirely in Gondwana from ancestral forms that lived in Argentina during the early Mississippian or even late Devonian times (see Carrizo and Azcuy 2015). Perhaps, it is because of this that these forms are so unusual and different from other contemporary spore-producing plants occurring in the Mississippian.

Conclusion

The Poti Flora (macro- and microelements) represents a mixture of forms of Euramerican and Gondwanan origin, which dispersed over long distances over a time of mild climates, evolving into exclusive endemic taxa in this region. This unique floral composition, but similar to that of other plant fossil localities of similar age (late Mississippian) distributed throughout Peru, Bolivia, Niger, India, and Australia, allowed to establish the Paraca Floral Realm. This realm represents a wide (30° to 60° South) translongitudinal temperate belt on Gondwana that existed before the onset of the major late Carboniferous–early Permian episode of the Late Paleozoic Ice Age (LPIA).

The evolutionary stage of this flora is compatible with other Mississippian floras around the world, contrasting the absence of tree lycopsids and the occurrence of ferns with psilophytic habits and non-synangiate microsporangiate fructifications. The endemism recorded in the Poti Flora may be explained by macroclimatic constraints since the Parnaíba Basin would have been situated inside the Gondwana continent in a semiarid climatic zone during the mid-to-late Mississippian, differently of other floras located in continental rims and wetter zones.

Cross-References

▶ Earliest Evidence of Land Plants in Brazil
▶ Ice-Hothouse Transition and Palynological Evidence in Brazil
▶ Late Paleozoic Ice Age Flora from the Paraná Basin
▶ Plant diversification through the Middle Devonian in Brazil

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