



Plant Diversification Through the Devonian in Brazil

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Abstract

Although the plant fossils from the Devonian of Brazil have been known for more than one century, we were able to scratch only a small part of this history. Some international paleobotanical collaborations began in the three main sedimentary basins containing Devonian rocks, but with time, more attention was paid to marine invertebrates and palynomorphs. Nevertheless, recent efforts in the Devonian of the Paraná Basin promoted some contributions in studying fossils from Furnas, Ponta Grossa, and São Domingos Formation. This contribution aims to synthesize and update the existing data on the Devonian plant records from Paraná, Parnaíba, and Amazon basins and to address their biostratigraphic and paleogeographic significance. The Devonian lithostratigraphic units bearing plant fossils were compiled and correlated based on palynological and stratigraphic studies. Some plant material housed in several institutions was briefly described and illustrated. In total, we compiled 25 genera of fossil plants distributed throughout the Lochkovian–Famennian interval. From the range of genera, three stratigraphic intervals and floral stages were identified, named *Cooksonia-Hostinella*, *Haplostigma-Spongiophyton*, and *Protosalvinia*. The early Devonian *Cooksonia-Hostinella* and Late Devonian *Protosalvinia* floral stages show taxa shared between Euramerican and western Gondwanan areas, whereas the late Early to early Late Devonian *Haplostigma-Spongiophyton* floral stage seems more restricted to Gondwanan areas.

Glossary of Terms/List of Abbreviations, Symbols, and Acronyms

Decumbent. A plant laying on the ground with its distal part upright.

Diamictite. A sedimentary rock that consists of poorly sorted terrigenous sediment containing particles that range in size from typical cobbles to boulders, suspended in a matrix of mudstone or sandstone.

Dorsiventral. A structure with two surfaces, upper (dorsal) and lower (ventral).

Euphyllphytina. A subdivision of vascular plants (Tracheophyta), characterized by the differentiation of the main and secondary axes (pseudomonopodial growth) and “true” megaphylls.

Heterosporous. The production of spores of generally two sizes (microspores and megaspores), each developing into a particular type of gametophyte

(macrogametophyte and megagametophyte), and from their fecundation, the sporophytes are born.

Leaf cushions. Leaf structure adpressed to the surface of the outermost cortex of the lycophyte stem, when detached or broken, may or may not leave a true leaf scar.

Malvinokaffric Realm. A Pragian/Emsian–Eifelian low-diversity and high endemic marine fauna mainly comprised of terebratulid, strophomenid, and spiriferid brachiopods as well as calmoniid and some homalonotiid trilobites, which occupied southwestern Gondwana.

Nematophyta. A paraphyletic group of putative land organisms, probably including some algae, land plants, and other enigmatic organisms with unknown affinity from Silurian through Devonian times.

Orthostichy. An imaginary line of a vertical row of appendicular organs along a stem or axis.

Parastichies. Helical arrangement or pattern of appendicular organs along a stem or axis.

Phyllotaxy. Types of an arrangement of leaves on a stem or branch.

Polysporangiomorpha. A Division of plants in which the spore-bearing generation (sporophyte) has branching stems (axes) that terminate in sporangia. The clade includes all land plants (embryophytes) except for the bryophytes (liverworts, mosses, and hornworts). The definition is independent of the presence of vascular tissue.

Progymnosperm. An extinct group of woody, foliated, and spore-bearing plants that lived during the Middle Devonian to Carboniferous. They probably evolved from the trimerophytes and eventually gave rise to the gymnosperms.

Tracheophyta. A Division of plants comprising land plants with a vascular system that contains tracheids or tracheary elements (as vessel elements or fibers) to conduct products of photosynthesis.

Introduction

The Middle–Late Devonian paleobotanical record is known in Brazil since the early geological surveys carried out by the Morgan expedition (1870–1871) and Geological Commission of Brazilian Empire (1875–1878). During these expeditions, Charles Frederick Hartt (1840–1878) and Orville Adalbert Derby (1851–1915) collected some remaining flattened enigmatic plant materials associated with *Spirophyton* (now *Zoophycus* isp.) in three localities from the Amazon Basin of the Pará state (Derby 1877, 1879). These materials were mailed to Sir John William Dawson (1820–1889) and described as *Protosalvinia braziliensis* Dawson 1884 and *P. bilobata* Dawson 1884, and compared with other Devonian plant fossils from the United States and Canada (Dawson 1884, 1886). Over the past 140 years, the search for new plant materials in Brazil, especially in Middle Devonian deposits, stimulated the interest in the dynamic and evolution of vascular plants (Tiffney 1985, Edwards and Berry 1991, Edwards et al. 2000, Gensel and Edwards 2001, Willis and McElwain 2002). Therefore, the understanding of the terrestrial environments and

land colonization processes (Gensel and Edwards 2001) also contributed to the correlation of the Devonian South American deposits and the establishment of phytogeographic units for Western Gondwana (Wnuk 1996, Di Pasquo et al. 2009, 2015, Matsumura et al. 2015a).

The present chapter analyzes floristic data gathered from the Middle Devonian of Brazil and discusses their stratigraphic and paleogeographic significance.

The Devonian Period

The Devonian is the fourth period of the Paleozoic Era; it succeeds the Silurian (ca. 419.2 Ma.) and precedes the Carboniferous (c.a. 358.9 Ma.) and spans about 60 Ma. (Cohen et al. 2013; updated). The Devonian was established by Sedgwick and Murchison (1836, 1839, 1840) based on the study of rock exposures in Devon County (Devonshire) of southwest England. These marine rocks were the equivalent of terrestrial Old Red Sandstone deposits in Wales, north of England, and Scotland (Becker et al. 2012).

The Devonian is divided into the Lower, Middle, and Upper Series. The Lower Devonian contains the Lochkovian, Pragian, and Emsian stages, the Middle into the Eifelian and Givetian stages, and the Upper into the Frasnian and Famennian stages. Global Boundary Stratotype Sections and Points (GSSPs) of the Devonian are located in several areas of the Czech Republic, Uzbekistan, Germany, Morocco, and France (Ogg et al. 2016).

Biostratigraphic zonations and regional to global correlations are mainly based on conodonts (Bultynck 2007), graptolites (Jaeger 1979), and ammonoids (Becker and House 2000). Marine macroinvertebrates such as brachiopods (Brice et al. 2000), trilobites (Chlupac et al. 2000), ostracods (Groos-Uffenorde et al. 2000), and dacroconarids are regionally significant, but they tend to have many endemic characteristics (Boucot et al. 2001). Miospores (Streel et al. 2000) and Chitinozoans (Paris et al. 2000) are essential dating and correlation tools. Macroplants evolved and diversified rapidly, being stratigraphically useful depending on their preservation and the frequency and distribution of plant deposits through time (Edwards et al. 2000).

During Devonian times, two large land masses were forming the paleocontinents Euramerica (including Laurentia, Baltica, and Avalonia cratons) and Gondwana (formed by South American, African, Antarctica, and Indo-Australian plates) separated by the narrow Rheic Ocean. Siberia, Kazakhstan, and China terranes were isolated but also important continental areas (Scotese and McKerrow 1990). Most of these continents, except Siberia and Kazakhstan, occupied the South Hemisphere.

Paleobotanical records documented in these paleocontinents (see Raymond 1987, Edwards 1990, Edwards et al. 2000) demonstrate that fully terrestrial and transitional environments experienced physical changes caused by the origin and diversification of land plants. The evolution of new architectural types with anatomical and

morphological innovations and growth forms of the pteridophyte and progymnosperm groups promoted the establishment from the ground to understory and canopy strata (Meyer-Berthaud et al. 2010). The root and rootlet activities reduced substrate instability and increased the chemical weathering and nutrient availability for terrestrial and continental water bodies and soil formation (Algeo et al. 2001, Driese and Mora 2001). New reproductive strategies, such as heterospory and seed habit, represent one of the most significant evolutionary events in the history of vascular plants. They promoted the advantages in spore-producing, the independence from water for fertilization, and the capacity for embryo dormancy in a changing environment and contributed to the colonization of new, potentially more disturbed habitats (Willis and McElwain 2002). The amelioration of the terrestrial environments and changes in concentration of atmospheric gasses opened new habitats to invertebrate (Shear and Selden 2001) and vertebrate (Blom et al. 2007) invasions in wetlands, besides a wide variety of ecological interactions with fungi (Taylor and Osborn 1996). Therefore, the Devonian Period is characterized by remarkable changes (physical and biological) in terrestrial ecosystems. According to Algeo et al. (2001) and Ströther et al. (2010), plants caused depletion of the carbon dioxide (CO₂) from the atmosphere that may have contributed to a progressive climatic cooling triggering extinction events mainly in the Famennian (Caplan and Bustin 1999, McGhee 2013).

Devonian Paleoclimates of Brazil

According to Scotese et al. (1999) and Torsvik and Cocks (2004), during the Silurian through Middle Devonian times, the Earth experienced a period of global warming (Hot House) with the South Pole located in Gondwana between South America and Africa. It was a time of exceptionally high sea level, forming large epicontinental seas and inferred widespread equable climates. In Torsvik and Cocks (2004) paleogeographic reconstruction, the South Pole was located near the Paraná Basin. Therefore, the Brazilian sedimentary basins are distributed between high (Paraná Basin) to middle (Amazon and Parnaíba basins) latitudes and subjected mainly to cool temperatures. From Early to Middle Devonian times, the high-latitude Malvinokaffric Realm and unweathered mica flakes in muds and sands suggest an extensive cool temperate belt that extended from the pole down to midlatitudes (Scotese et al. 1999, Torsvik and Cocks 2004). Pebble- and cobble-sized particles found in the Ponta Grossa Formation, formerly interpreted as glacial diamictites, are now considered part of a transgressive ravinement surface and reworked by storm actions settled on the top of the new surface (Grahn and Bosetti 2010). During the Latest Devonian through earliest Carboniferous, Ice House conditions occurred, and the South Pole was located near South Africa. Late Devonian glacial records of South America were described and compiled by Caputo (1985) and Caputo et al. (2008), among other authors.

Geological Settings and the Brazilian Devonian Paleontological Records

Paraná Basin

The Paraná Basin is a polycyclic intracratonic and intercontinental basin on the South-American platform, covering ca. 1,600,000 km² in southern Brazil and central Uruguay, eastern Paraguay, and northeastern Argentina (Fig. 1b). Milani et al. (1998, 2007) subdivided the stratigraphic record of this basin into six second-order depositional supersequences, ranging from the Late Ordovician up to the Late Cretaceous. The Devonian rocks of the Paraná Basin are included in the Paraná Supersequence and represented by two sedimentary depositional centers: the Alto Garças Sub-Basin, in the north, and the Apucarana Sub-Basin, in the south (Fig. 1b). Both Sub-Basins were separated by Três Lagoas and Campo Grande highs (Melo 1988, Grahn 1992).

The Apucarana Sub-Basin is deeper than its northern counterpart and includes Devonian sediments averaging much lower sand–shale ratios, which crop out in Paraná State around the Ponta Grossa Arch (Melo 1988, Grahn et al. 2013). Grahn et al. (2013) subdivided the Devonian of the Apucarana Sub-Basin into three formations in ascending order: Furnas, Ponta Grossa, and São Domingos formations, the latter including the Tibagi Member. Revised stratigraphic sequence schemes were proposed by Bergamaschi and Pereira (2001) and Sedorko et al. (2018a). The lithology of the Furnas Formation consists of medium- to coarse-grained sandstones with abundant planar cross-stratification interbedded with conglomeratic and silty layers (Grahn et al. 2013). Paleocurrent patterns show west to southwest directions (Assine 1999). This unit is mostly deposited in marine environments (Assine 1999, 2001, Sedorko et al. 2017) during the early Silurian to early Devonian (Lochkovian). Sedimentologic and trace fossil analyses (Sedorko et al. 2017), marine and terrestrial palynomorphs (Grahn et al. 2013), and land plants (*Cooksonia paranensis* Gerrienne, Bergamaschi, Rodrigues et Steemans 2001 and others plant remains, Mussa et al. 1996, 2002, Gerrienne et al. 2001, 2006, 2022 this volume) gave support to both age and environmental interpretations.

The Ponta Grossa Formation (sensu Grahn et al. 2013) is the most fossiliferous unit characterized by mudstones, siltstones, and black shales with interbedded sandstones (Clarke 1913). A hiatus was established about 4 Myr between the upper Furnas and the lower Ponta Grossa formations (Grahn et al. 2010a). The macrofauna included in the Malvinokaffric Realm is composed of brachiopods (Zabini et al. 2010, 2012, Comniskey and Bosetti 2017), tentaculitoids (Comniskey and Ghilardi 2018), trilobites (Simões et al. 2009, Carbonaro et al. 2016), cnidarians (Van Iten et al. 1992, 2019), and echinoderms (Scheffler et al. 2018). Paleoenvironments include inner to outer shelf stormy marine settings. The latest Pragian to early Emsian age is mainly based on palynomorphs (Grahn 1992, Grahn et al. 2010a, 2013) integrated to macrofossils such as brachiopods, trilobites, and plants (Bosetti et al. 2012). Up to now, the plant remains *Spongiophyton lenticularis* (Barbosa) Krausel emend. Chaloner, Mensah, and Crane 1974, *Octaviona petrii*

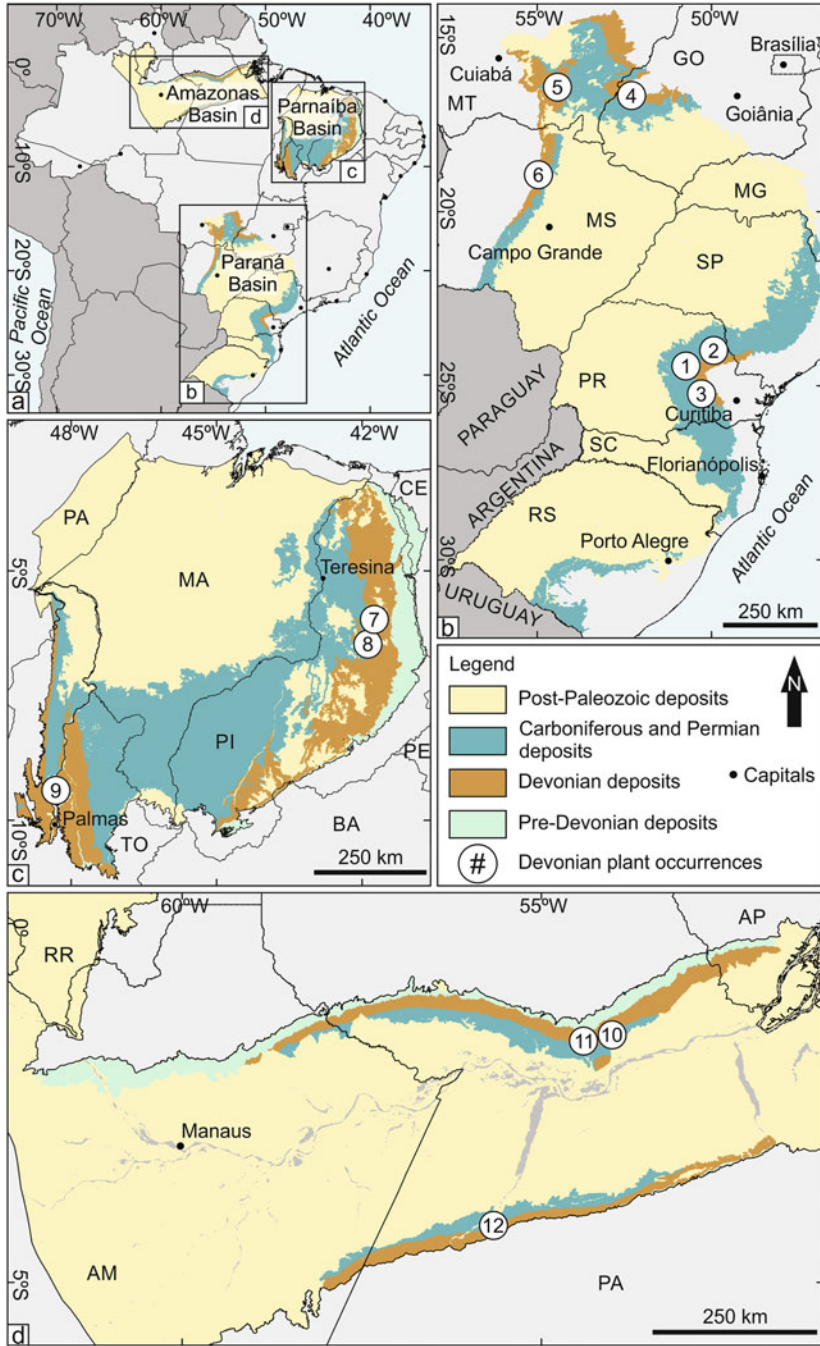


Fig. 1 Location map of the three main Devonian intracratonic basins of Brazil (a), showing the plant-bearing localities in Paraná (b), Parnaíba (c), and Amazon (d) basins. Legend. 1. São Domingos Formation (Matsumura et al. 2015a, 2016); 2. Furnas and Ponta Grossa formations

(Barbosa) Sommer 1954, and *Euzebiola clarkei* (Barbosa) Sommer 1954 were only recovered from the Jaguariaíva municipality (Barbosa 1949, Sommer 1954). *Euzebiola clarkei*, initially considered an algal remain, was redescribed and reinterpreted as cnidarian *Sphenothallus sica* Salter 1856 (Van Iten et al. 1992, 2019).

The lithology of the São Domingos Formation (sensu Grahn et al. 2013) is predominantly composed of sandstones interbedded with argillaceous shale. In the basal, late Emsian part, poorly sorted conglomeratic sandstones occur, followed by shale and micaceous siltstones rich in *Spongiophyton* debris (Kräusel 1954). The macrofauna in this unit is rarer than in the Ponta Grossa Formation and represented by brachiopods (Horodyski et al. 2014, 2019), echinoderms (Scheffler et al. 2018), trilobites (Carbonaro et al. 2016), and fish remains (Richter et al. 2017). A succession of sandstones and sandy mudstones characterized its upper, Eifelian to Givetian part, which is poor in shelly fauna (Bosetti et al. 2011, Horodyski et al. 2014, 2019) but rich in *Haplostigma* Seward 1932 and *Spongiophyton* remains (Matsumura et al. 2013, 2015a, 2016). It culminates in black shale, probably associated with the KAČÁK Event (Grahn et al. 2016, Horodyski et al. 2019). This upper unit is interpreted as a marine continental shelf environment deposited during the early late Emsian to late early Frasnian based on palynological studies (Grahn et al. 2013).

The Alto Garças Sub-Basin occupies much of the states of Mato Grosso do Sul, Mato Grosso, and southwestern Goiás, where extensive outcrops of Devonian rocks occur. It is subdivided into Chapada Group units 1, 2, 3, and 4 (Melo 1988, Mendlowicz Mauller et al. 2009, Grahn et al. 2010b). These units were distinguished by Andrade and Camarço (1980) in southwestern Goiás State and called “Furnas Formation” and “lower, middle and upper members” of the “Ponta Grossa Formation.” The Chapada Group Unit 1 comprises a basal conglomerate to upper whitish sandstones interbedded with laminated micaceous siltstones. The paleocurrent pattern points consistently toward the northwest (Andrade and Camarço 1980). Fossils are generally absent except for the upper part, where a few trace fossils and plant remains were reported (Quadros and Melo 1986, Schubert and Borghi 1991, Rodrigues et al. 1995). The Chapada Group Unit 1 was interpreted as a marginal-marine to shallow marine continental shelf environment probably ranging from late Silurian to Lochkovian age (Grahn et al. 2010b, Sedorco et al. 2017, 2018b) and mostly correlated with Furnas Formation but displays a distinct regional paleocurrent pattern (Melo 1988, Mendlowicz Mauller et al. 2009, Grahn et al. 2010a, b, 2013). Chapada Group Unit 2 consists of a basal conglomerate with



Fig. 1 (continued) (Barbosa 1949, Sommer 1954, Gerrienne et al. 2001, 2006, and in this volume); 3. São Domingos Formation (Kräusel 1954); 4. Chapada Group 4 (Grahn et al. 2016, Carbonaro and Ghilardi (2016), Carbonaro et al. 2018); 5. Chapada Group 1 (Quadros and Melo 1986, Schubert and Borghi 1991, Rodrigues et al. 1995); 6. Chapada Group 2 (Melo 1988, Sedorco et al. 2018b); 7. Itaim and Pimenteira formations (Kräusel and Dolianiti 1957, Suárez-Riglos 1975, Souza et al. 2017); 8. Longá Formation (Duarte 1936, Kegel 1953); 9. Pimenteira Formation (Sommer and Van Boekel 1964); and 10–12. Barreirinha Formation (Dawson 1884, Sommer 1962, Niklas et al. 1976)

sandstones and shales, overlain by reddish sandstones with intercalated siltstones and shales, and toward the top grayish–reddish sandstone layers (Andrade and Camarço 1980, Grahn et al. 2010a, b). Based on the sedimentological and paleontological records, this unit was divided into two sections. The lower part, Chapada Group Unit 2, is well-developed on the northwestern border of the Sub-Basin, ranging from the late Pragian to early Emsian and correlated with the fossiliferous Ponta Grossa Formation (sensu Grahn et al. 2010a, b, 2013). Plant fragments associated with several ichnofabric and marine invertebrates were documented (Melo 1988, Sedorko et al. 2018b). The upper part, Chapada Group Unit 2, is best represented on the northeastern border of the Alto Garças Sub-Basin and dated from the latest Emsian to the earliest Givetian (Mendlowicz Mauller et al. 2009, Grahn et al. 2010b), corresponding to the lower São Domingos Formation (sensu Grahn et al. 2013). Chapada Group Unit 3 is restricted to the northeastern part of the subbasin laterally replaced by the shales and sandstones of the upper part of Chapada Group Unit 2 toward the center of the Alto Garças Sub-Basin. Chapada Group Unit 3 is characterized by reddish medium- to coarse-grained sandstones interbedded with conglomeratic sandstones that were interpreted as a shallow marine to wave-dominated deltaic environment (Andrade and Camarço 1980, Mendlowicz Mauller et al. 2009, Grahn et al. 2010b). The age of Chapada Group Unit 3 is late Emsian and corresponds to the Tibagi Member of the São Domingos Formation in the Apucarana Sub-Basin (Grahn et al. 2013, 2016). The Chapada Group Unit 4 consists of dark-gray shales interbedded with sandstones and siltstones. Grahn et al. (2016), Carbonaro and Ghilardi (2016), and Carbonaro et al. (2018) reported *Haplostigma* sp., *Spongiophyton* sp. and plant debris associated with marine invertebrates. The Chapada Group Unit 4 is correlated with the upper São Domingos Formation of the Apucarana Sub-Basin (sensu Grahn et al. 2010a, 2013). The base of the Chapada Group Unit 4 is related to the maximum flooding surface at the Eifelian–Givetian boundary (Assine 2001, Grahn et al. 2010b), probably associated with the KAČÁK Event (Grahn et al. 2016, Horodyski et al. 2019).

Parnaíba Basin

The intracratonic Parnaíba Basin, formerly named Maranhão Basin, covers an area of ca. 600,000 km² in the states of Ceará, Piauí, Maranhão, Tocantins, and Pará of northeast and north-central Brazil (Fig. 1c). 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 supersequences, ranging from the Early Silurian to the Early Cretaceous. The Devonian sequence developed in an epicontinental sea and was influenced by tectonic events and eustatic sea-level fluctuations. Middle and Late Devonian rock units are, in ascending order, the Itaim, Pimenteira, Cabeças, and lowermost Longá formations in the Canindé Group (Caputo 1985, Melo 1988, Grahn 1992, Grahn et al. 2006, 2008, Breuer and Grahn 2011).

The Itaim Formation consists of micaceous, fine to medium sandstone and silty sandstone beds cropping out on the eastern side of the Parnaíba Basin (Melo 1988, Grahn 1992, Góes and Feijó 1994, Vaz et al. 2007). Sandstone beds interbedded with bioturbated shale and siltstone occur in the subsurface (Grahn 1992, Trindade and Carvalho 2018). The paleoenvironments assigned to Itaim Formation were shallow marine to coastal and deltaic and influenced by tides and storms (Carozzi et al. 1975, Góes and Feijó 1994, Trindade et al. 2015, Trindade and Carvalho 2018). A sparse fauna of molluscs and inarticulate brachiopods are preserved together with trilobite tracks and other traces (Kegel 1953, 1961, Melo 1988). *Spirophyton* (= *Zoophycus* isp.) is locally common, and plant debris is sometimes found associated with putative eurypterid remains (Caster 1948). Recently, *Spongiophyton* remains were recorded in the Itaim Formation (Souza et al. 2017). The age of the Itaim Formation is late Emsian to early Eifelian (Loboziak and Melo 2002, Grahn et al. 2006, 2008).

The Pimenteira Formation records the first widespread Devonian transgression over the Parnaíba Basin, occurring in both the east and west margins of the basin (Melo 1988, Grahn 1992, Breuer and Grahn 2011) and consisting of sandstone with interbeds of siltstone and shale. The sediments were mainly deposited in a shallow marine environment influenced by fluvio-deltaic regimes (Carozzi et al. 1975) and mostly by waves and storms (Melo 1988, Della Fávera 1990). The richest macrofossiliferous horizons are at the base of the Pimenteira Formation. The fauna is a mixture of Malvinokaffric, Old World, and Eastern American elements (Melo 1988), represented by trilobites, brachiopods, molluscs, tentaculitids, crinoids, and fish remains (Kegel 1953, Fonseca and Melo 1987, Maisey and Melo 2005, Ponciano et al. 2012, Scheffler 2015, Figueroa and Machado 2016) besides ichnofossils (Silva et al. 2012). Kräusel and Dolianiti (1957) first described the plant remains (*Archaeosigillaria picosensis* Kräusel et Dolianiti 1957, *Palaeostigma sewardi* Kräusel et Dolianiti 1957, *Protolepidodendron kegeli* Kräusel et Dolianiti 1957, and *Spongiophyton* sp.). The herbaceous lycopsid *Haplostigma* sp. has also been poorly reported (Suárez-Riglos 1975 and P. V. Oliveira pers. comm. 2018). At the western margin, only *Spongiophyton* has been constantly reported in Tocantins State (Andrade Ramos 1957, 1967, Sommer and Van Boekel 1964, Andrade Ramos and Barbosa 1967). At the eastern margin, the age of the Pimenteira Formation is Eifelian, and at the western margin, this unit reaches up to the late Frasnian to early Famennian (Grahn et al. 2006). A gap corresponding to late Givetian and early Frasnian is present, in both boreholes and outcrops, all over the basin (Melo 1988, Grahn 1992, Grahn et al. 2006). In the subsurface, the late Frasnian transgression is recorded in the form of finely laminated, radioactive dark shales in the upper Pimenteira Formation.

The Cabeças Formation was originally defined by Plummer (1948) for a sequence of coarse sandstones, locally conglomeratic and rarely by thin interbedded shales and siltstones cropping out in the eastern margin of the basin (Melo 1988, Grahn 1992, Vaz et al. 2007). The paleoenvironmental interpretations indicate a marine-deltaic environment with the influence of tides and storms (Góes and Feijó 1994) and by floods in a fluvio-deltaic system (Ponciano and Della Fávera 2009). The unit culminates with a diamictite interpreted as deltaic progradation related to the Famennian glaciation (Caputo 1985, Caputo et al. 2008, Barbosa et al. 2015). The

fossil assemblage is apparently restricted to its lower section, the Passagem Member, and differs from the underlying Pimenteira Formation by calmoniid trilobites, rhynchonellid brachiopods (Melo 1988), and crinoids (Scheffler et al. 2010). The age of the Cabeças Formation is probably the latest Eifelian–early Givetian at the base, not younger than late Frasnian–early or possibly late Famennian at the top (Grahn 1992, Loboziak and Melo 2002).

The Longá Formation (Albuquerque and Dequech 1946) is characterized by laminated sandstone and greenish–gray shales with interbedded bioturbated siltstone cropping out along the upper Longá River, State of Piauí. Its lowermost exposition yields a shelly fauna (brachiopods, molluscs, and trilobites) in at least one locality (Kegel 1953), suggesting a latest Famennian age. In the subsurface, Duarte (1936) reported brachiopods, possible asterozoans, plant remains, and fish scales. The paleoenvironment is generally interpreted as a transgressive, storm-dominated, shallow sea (Caputo 1985, Góes and Feijó 1994, Vaz et al. 2007). The uppermost Longá Formation yields greenish–gray, dark, bituminous, sideritic, pyritic, and micaceous silty shale and siltstone beds with subordinate dropstones of early Carboniferous, probably Tournaisian, age (Grahn et al. 2006, Playford et al. 2012).

Amazon Basin

The intracratonic Amazon Basin covers an area of ca. 500,000 km² in the states of Amazonas, Pará, and Amapá in North Brazil (Fig. 1d). The basin is delimited by the Purus Highs in the west, and by the Gurupá arch in the east (Cunha et al. 2007). The Paleozoic sedimentary record of the Amazon Basin was influenced by tectonic events and eustatic sea-level fluctuations. Cunha et al. (2007) divided the basin into four supersequences from the late Ordovician to late Permian. The Devonian–Tournaisian sequence includes the Urupadi Groups of Emsian–Givetian and Curuá Group of Late Frasnian–Late Famennian and represents a marine depositional stage with glacial influence in the latter. The Urupadi Group contains, in ascending order, the Maecuru and Ererê formations. The Maecuru Formation is characterized by white to gray, cross-stratified sandstones with interbedded conglomerate and few siltstones, interpreted as shallow marine environments influenced by waves and storms, ranging from the late Emsian to early Eifelian (Melo and Loboziak 2003). On the northern flank of the Amazon Basin, these beds have yielded the highest diversity of any Brazilian Devonian (Eifelian) shelly fauna first recorded by pioneer workers from outcrops of the Maecuru and Curuá rivers (Rathbun 1874, 1879, Katzer 1897, Clarke 1899, 1913). The brachiopods are common to the Eastern American Realm and/or the Old World Realm, and only a few genera show Malvinokaffric Realm affinities (Carvalho 1975). However, the trilobites (Melo 1988, Carvalho and Ponciano 2015) and crinoids (Scheffler et al. 2015) show Malvinokaffric affinity.

The Ererê Formation is constituted by sandstones, siltstones, and shales, interpreted as shallow marine environments and deposited during the late Eifelian to Early Givetian (Melo and Loboziak 2003). The lower and upper part of the Ererê Formation reflects a transgression and a regression, respectively. The invertebrate

fauna is impoverished and less diverse than that of the Maecuru Formation (Scheffler 2015, Carvalho and Ponciano 2015). The shelly fauna includes brachiopods, trilobites, tentaculitids, bivalves, gastropods, and ostracodes described by early workers Rathbun (1874, 1879), Clarke (1899, 1913), Katzer (1897), and Hartt and Rathbun (1875).

The Curuá Group sensu Cunha et al. (2007) contains, in ascending order, Barreirinha, Curiri, and Oriximiná formations. The Barreirinha Formation consists of well-laminated dark-gray to black shales with subordinate sandstones and siltstones cropping out along the Tapajós River, State of Pará. Macrofossils are rare and include plant remains, brachiopods, trilobites, pelecypods, and gastropods (Rathbun 1874, Clarke 1913). Conodonts, fish remains, and an unidentified nautiloid were also documented (Melo 1988). Cunha et al. (2007) considered the “lower Curiri Formation” sensu Melo and Loboziak (2003) as the topmost Barreirinha Formation, Urariá Member, Late Famennian. The “lower Curiri Formation” is characterized by siltstones and shales with *Spirophyton* (= *Zoophycus* isp.) and *Protosalvinia* remains (= *Protosalvinia/Spirophyton* Zone) (Niklas et al. 1976, Loboziak et al. 1997, Melo and Loboziak 2003).

The Curiri Formation consists mainly of diamictites and, secondarily, sandstones, siltstones, and shales deposited in glacial to peri-glacial environments during the latest Famennian (“Strunian”) (Melo and Loboziak 2003, Cunha et al. 2007).

The Oriximiná Formation consists of sandstones with interbedded siltstones deposited in marginal marine settings during the early Tournasian (Playford and Melo 2012). Up to now, no macrofossils are known in this unit except for the finding in the subsurface of the herbaceous lycophyte *Lycopodites amazonica* Dolianiti 1967, in 2.041–2.044 meters in well 1-RX-4-AM (Melo and Loboziak 2003).

Additional Middle Devonian Plant Remains

Some plant remains have been reported from several poorly studied localities in Brazil. In the Upper Tapajós Basin (Amazonas, Pará, and Mato Grosso states), Santiago et al. (1980) reported possible graptolite remains associated with plant cuticles and spores from the Borrachudo Formation and plant cuticles and spores from the São Benedito Formation at the border of the states of Amazonas, Pará, and Mato Grosso. Also, Costa (1978) recovered *Spongiophyton* and sporomorphs from the Borrachudo Formation in the westernmost region of Mato Grosso State. In the Jatobá Basin of Pernambuco State, Mussa et al. (1994) reported plant remains associated with marine invertebrates in the Inajá Formation.

Materials and Methods

The paleobotanical material illustrated herein (Figs. 3 and 4) comes from different Devonian localities of the Paraná, Parnaíba, and Amazon basins. Materials are housed at the following institutions: (i) Paleobotany Collection of the Stratigraphy

and Paleontology Laboratory of the Geoscience Department of the State University of Ponta Grossa (UEPG), under the acronym DEGEO/MP; (ii) Collection of the Paleozoic Fossils of the Biosciences Institute of the Federal University of State of Rio de Janeiro (UNIRIO), under the acronym UNIRIO-P; (iii) Paleobotany Collection of the Geology and Paleontology Department of the National Museum of the Federal University of Rio de Janeiro (MN/UFRJ), under the acronym MN-Pb; (iv) Paleobotany Collection of the Paleontology and Stratigraphy Department of the Geoscience Institute of Federal University of Rio Grande do Sul (UFRGS), under the acronym MP-Pb; and (v) Paleobotany collection of the Paleontology Laboratory of Federal University of Piauí (UFPI), under the acronym LPP.

The paleontological materials are mostly preserved as impressions and compressions, with some bearing parts and counterparts and cuticles preserved (Schopf 1975). Some specimens three-dimensionally preserved from the Parnaíba Basin are described herein. Detachment technique (Leclercq 1960) using steel needles and stereomicroscope used to clean and improve the fossils. Some specimens preserved as fossil compressions bearing cuticles were disaggregated from the matrix using concentrated hydrofluoric acid (40%) per 24 h. The residues bearing cuticles mounted with cellosize-entellan products and slides were studied and photographed with Canon T6i digital camera and 60 mm macro lens at the UFRGS.

Palynologic studies were carried out in four samples obtained from the plant interval bearing *Haplostigma-Spongiophyton* of two outcrops of the São Domingos Formation in Paraná State and two more from the interval level with *Protosalvinia* of the Barreirinha Formation, Amazon Basin, Pará State (Fig. 1). Standard palynologic maceration was followed by applying hydrochloric acid (25%), and hydrofluoric acid (40%) and several washes with distilled water allowed the neutralization of residues, which were sieved using 10 and 25 μm meshes and slides mounted with jelly glycerine. The microscopic analysis was performed using light microscopes Nikon E200 and Leica DM500, bearing a fluorescence device, and pictures were taken with video cameras Labomed 5.0 and Amuscope 14 Mp, respectively. Cuticles of *Protosalvinia* present in the sample treated for palynology were picked directly from the rock with a nail and cleaned with hydrofluoric acid into an Eppendorf, whereas others were obtained from a supervised maceration with hydrofluoric acid in a Petry dish. After the careful neutralization of those remains, microscopic analyses were performed using a stereoscope Leica EC3 bearing a video camera 3 Mp, the light microscopes mentioned, and also some complete specimens of *Protosalvinia* and cuticles mounted in stubs were analyzed in a SEM Phenom Pro unmetallized in low vacuum (di Pasquo and Vilá 2019). All these procedures were carried out (MDP) at the *Centro de Investigaciones Científicas y Tecnológicas de Transferencia a la Producción* (CICYTTP-CONICET-ER-UADER), Diamante, Entre Ríos Province, Argentina, and materials housed under the acronym CICYTTP (di Pasquo and Silvestri 2014). The main results obtained are presented in this contribution.

Descriptions of the Plant Megafossils

Superdivision Polysporangiomorpha Kenrick et Crane 1997

Division Tracheophyta Sinnott 1935

Genus *Cooksonia* Lang 1937 emend. Gonez et Gerrienne 2010

Cooksonia paranensis Gerrienne, Bergamaschi, Pereira, and Rodrigues et Steemans 2001 (Fig. 3)

Diagnosis: Erect plant with naked isotomously branching axes, 1.0–1.5 mm wide and up to c. 31 mm high. The branching angle ranges from 30 to 70°; sporangia appear at the end of each axis, having a plate shape or bowl shape at its top, 0.9–3.3 mm in diameter and approximately 1.0–3.0 mm in height; the axis widens often considerably beneath the sporangium; axis/sporangium transition gradual; and sporangium more or less sunken within the axis and not projecting beyond it. Spores and other anatomic features unknown.

Figured material: MN 2154-Pb.

Stratigraphic and geographic range: topmost of the Furnas Formation, Paraná Basin, Jaguariáiva Municipality, Paraná State, Southern Brazil.

Age: Lower Devonian (Fig. 2).

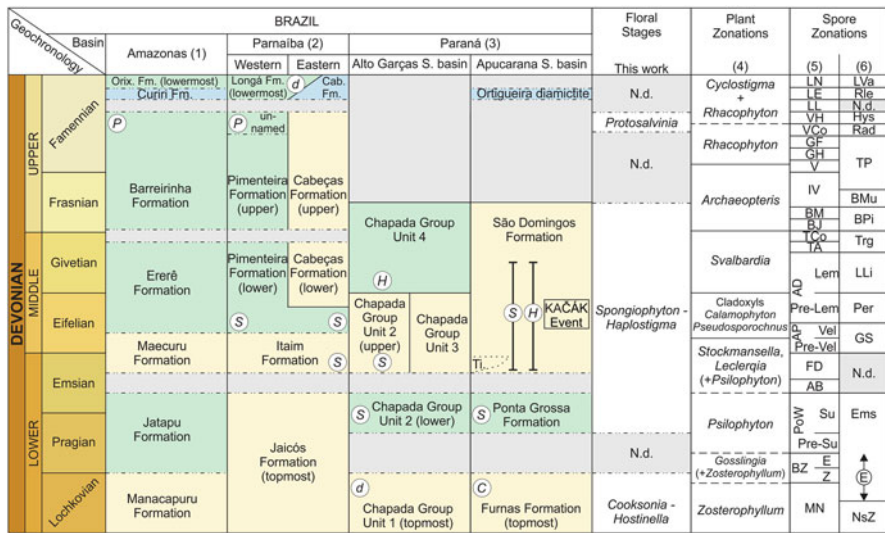
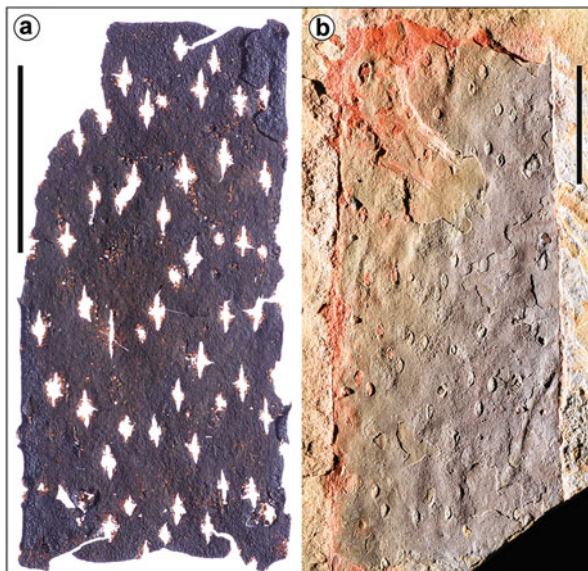


Fig. 2 Correlation chart of the Devonian lithostratigraphic units of Brazil, plant levels are indicated by the letters: C = *Cooksonia*, S = *Spongiophyton*, H = *Haplostigma*, P = *Protosalvinia*, and D = plant debris. 1. Amazon Basin (Caputo 1985, Cunha et al. 2007, Melo and Loboziak 2003); 2. Parnaíba Basin (Niklas et al. 1976, Loboziak and Melo 2002, Grahn et al. 2005, 2006, 2008, Vaz et al. 2007); 3. Paraná Basin (Grahn et al. 2000, 2010a, b, 2013, 2016); 4. Devonian Plant Zonation after Edwards et al. (2000); 5. Western European miospore zonation after Streeel et al. (1987) and Steemans (1989); and 6. Western Gondwanan (North Brazil) miospore zonation after Melo and Loboziak (2003). Orix. Fm. = Oriximiná Formation. Cab. Fm. = Cabeças Formation. Ti = Tibagi Member of the São Domingos Formation. N. d. = no data. Green and yellow colors represent siltstones and/or shales and sandstones, respectively. Blue color represents diamicites

Fig. 3 *Cooksonia paranensis*, MN 2154-Pb, and scale bar = 10 mm



Fig. 4 (a) *Spongiophyton lenticulare*, DEGEO/MP-7961; (b) *Spongiophyton lenticulare*, DEGEO/MP-3632, scale bars = 5 mm



Description: The figured specimen is a naked stem preserved as a coaly impression with 50 mm length and 1 mm width. An isotomous branching is presumed (~20 mm), and each terminal axis (0.5 mm width) is slightly curved, bearing a sporangium, bowl- to trumpet-shaped (3 mm height and 2 mm width) at its end.

Remarks: The specimen resembles *Cooksonia paranensis*, first described by Gerrienne et al. (2001) from Jaguariaíva municipality. This species shows erect naked axes that bear up to three levels of isotomous branching. The transition between the terminal axis and sporangium is gradual. At the eastern border of the Paraná Basin, *Cooksonia*-like and other plant remains were also reported in Carambeí (Machado et al. 2007), Tibagi (Bigarella et al. 1966), and Ponta Grossa (Rodrigues et al. 1989, Milagres et al. 2007, 2018) municipalities. At the western border and in coeval Chapada Group unit 1, rhyniophyte-like and psilophyte-like remains were reported in Mato Grosso (Schubert and Borghi 1991) and Goiás states (Quadros and Melo 1986, Rodrigues et al. 1995). These records require more detailed studies.

Similar coeval plant fossil assemblages were described from the Villavicencio and Talacasto formations in Argentina (Edwards et al. 2001, 2009), Santa Rosa Formation in Bolivia (Di Pasquo and Noetinger 2008), and Cerrezuelo Formation in Uruguay (Sprechmann et al. 1993). *Cooksonia* is considered a cosmopolitan genus frequently reported from late Silurian deposits in Euramerica (Edwards and Richardson 2004) and North (Libya) and Western Gondwana (Morel et al. 1995). The occurrence of *Cooksonia* in the Lower Devonian of Brazil suggests a dispersion from Bolivia and supports the hypothesis of an ice-free south pole during the earliest Devonian, as discussed by Gerrienne et al. (2001, 2006) and Milagres et al. (2007,

2018). Finally, Raymond et al. (2006) established a paleophytogeographic unit called the South Laurussian–Northwest Gondwanan that includes the Brazilian and Bolivian records and is extended by the late Silurian–Early Devonian interval.

Order Spongiophytales Sommer 1959

Family Spongiophytaceae Kräusel 1954

Genus *Spongiophyton* (Kräusel) Chaloner, Mensah, and Crane 1974

Spongiophyton lenticulare (Barbosa) Kräusel emend. Chaloner, Mensah, and Crane 1974 (Fig. 4a, b)

Diagnosis: *Thallus cylindrical in shape up to 12 mm in diameter. The cuticular tissue has lenticular pores of various sizes, up to 0.8 mm in the longest dimension, elongated parallel to the length of the thallus, and greater concentration of pores on one surface. The inner surface of the cuticle with a cellular reticulum, cells typically 50 µm wide and 100 µm long, with a pronounced arrangement in longitudinal series.*

Figured material: DEGEO/MP-7961 and 3632.

Stratigraphic and geographic range: São Domingos Formation (Paraná Basin), Tibagi Municipality, Paraná State, Southern Brazil.

Age: Middle Devonian (Fig. 2).

Description: The specimens are compressions of vegetative thalli, up to 10 mm wide, rarely branching dichotomously and bearing lenticular (1.0 × 0.6 mm) to oval (0.6 × 0.3 mm) pores in shape and randomly distributed on both surfaces of the thallus. Cuticles preserved. Base and apex broken, reproductive structures unknown (Fig. 4a, b).

Remarks: These specimens most closely resemble *Spongiophyton lenticulare*, as described by Kräusel (1954) and Chaloner et al. (1974). They differ from *S. nanum* (Kräusel) emend. Chaloner, Mensah, et Crane 1974 and *S. minutissimum* (Kräusel) emend. Gensel, Chaloner, et Forbes 1991 by presenting larger thalli, up to 5 mm wide, and bearing bigger lenticular pores, 1 × 0.6 mm, equally distributed over the whole surface of the thallus. In the Paraná Basin, the first report of *S. lenticulare* was in the Early Devonian of Jaguariaíva (Barbosa 1949) and in the late Early Devonian Ponta Grossa municipalities, Paraná State (Kräusel 1954). Although *Spongiophyton* is the most typical element of the Middle Devonian flora in Brazil, the specimens being poorly preserved in most of the deposits, its assignment attained at the generic level. After Kräusel (1954), *Spongiophyton* was widely recorded in Paraná (Mato Grosso and Goiás states, Melo 1988, Carbonaro et al. 2018) and Parnaíba basins (Piauí and Tocantins states, Kräusel and Dolianiti 1957, Andrade Ramos 1957, 1967, Sommer and Van Boekel 1964, Souza et al. 2017). *Spongiophyton lenticulare* was also reported from the Los Monos Formation in Bolivia (Boureau and Pons 1973) and Takoradi Sandstone in Ghana (Chaloner et al. 1974). Similar specimens illustrated as *Paleostigma* sp. by di Pasquo et al. (2015, Fig. 5.2, 5, and 7) from the Los Monos Formation in Bolivia are assignable to *Spongiophyton lenticulare* (MDP).

Spongiophyton nanum (Kräusel) Chaloner, Mensah, and Crane 1974 (Fig. 5a, b)

Diagnosis: *Thallus cylindrical, originally circular or elliptical in cross-section, dichotomizing several times, with rounded apices. Branches typically 2–5 mm wide and up to 25 mm long (incomplete). Cuticle penetrated by numerous circular to elliptical pores 200–300 µm in diameter, with edges beveled on the outer face. Pores*

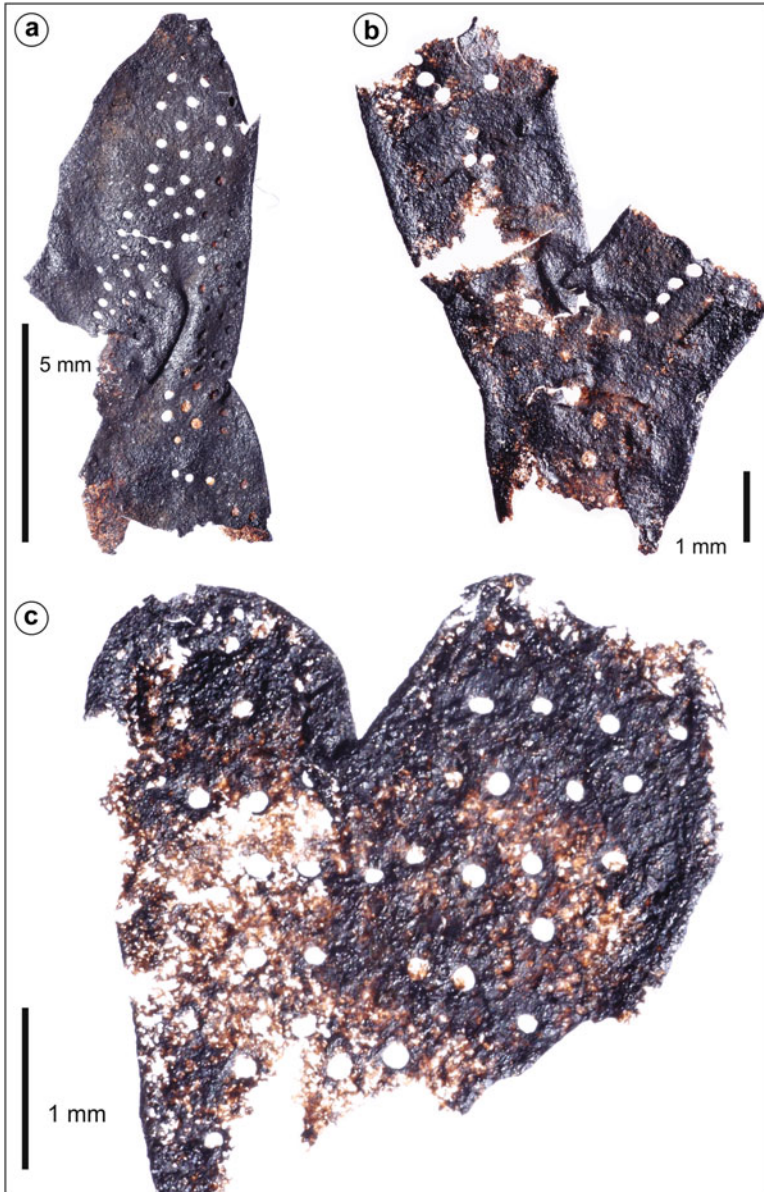


Fig. 5 (a) *Spongiophyton nanum*, DEGEO/MP-7963, scale bar = 5 mm; (b) *Spongiophyton nanum*, DEGEO/MP-7965, scale bar = 1 mm; and (c) *Spongiophyton minutissimum*, DEGEO/MP-7980, and scale bar = 1 mm

principally confined to one face, this porous surface having the thicker cuticle with ridges forming a cellular reticulum, cells typically 40 μm long, 20–30 μm wide, oriented with the longer axis parallel to the length of the thallus.

Figured material: DEGEO/MP-7963 and 7965.

Stratigraphic and geographic range: São Domingos Formation (Paraná Basin), Tibagi Municipality, Paraná State, Southern Brazil.

Age: Middle Devonian (Fig. 2).

Description: The specimens are preserved as compressions with cuticles of vegetative thalli, up to 3–5 mm wide, usually branching dichotomously with rounded apices and bearing rounded (0.1 mm in diameter) to oval (0.2 × 0.1 mm) pores randomly distributed only on the thicker surface of the thallus (= porous surface). The aporous surface is barely preserved because of its thinness. In some specimens, the pores are loosely aligned along the thallus. Base broken and reproductive structures unknown (Fig. 5a, b).

Remarks: These specimens most closely resemble *Spongiophyton nanum*, as characterized by Kräusel (1954) and Chaloner et al. (1974). They differ from *S. lenticulare* and *S. minutissimum* by presenting slender thalli (up to 5 mm wide), branching dichotomously and circular pores aligned longitudinally and principally confined to one surface of the thallus (porous surface). At the western border of the Paraná Basin, *Spongiophyton nanum* was only recorded at Mato Grosso State (?Chapada Group 2, Matsumura et al. 2017). In addition, *Spongiophyton nanum* was reported in Ghana (Takoradi Sandstone, Chaloner et al. 1974).

Spongiophyton minutissimum (Kräusel) Gensel, Chaloner, and Forbes 1991 (Fig. 5c)

Diagnosis: *Thallus cylindrical, originally circular or elliptical in cross-section, and at least 2 cm long and 0.2–5.5 mm in width. Thalli may exhibit constrictions along their length, and branch dichotomously several times, with most lobes 3–10 mm long and with rounded apices. Short erect branches (1–2 mm long) occur on porous surface of some thalli. Pores mostly distributed on one surface, two to four times thicker than the aporous surface (75–250 μm vs 30–60 μm), the thicker cuticle extending beyond the margins onto the edge of the aporous surface. Porous and aporous surfaces smooth, aporous surface often longitudinally folded. Inner surfaces of the cuticle may retain rectangular cell outlines, 20–43 μm long and 9–12 μm wide, although often degraded and vermiform in appearance. Pores circular to oval, randomly spaced, 22.5 × 9 μm to 99 × 90 μm in diameter, with vertical, fissured, or occasionally beveled edges.*

Figured material: DEGEO/MP-7980.

Stratigraphic and geographic range: São Domingos Formation (Paraná Basin), Tibagi Municipality, Paraná State, Southern Brazil.

Age: Middle Devonian (Fig. 2).

Description: Specimens consist of very thick compressions of dorsiventral thalli, up to 3 mm wide, rarely branching dichotomously and bearing small circular (0.5 mm in diameter) to oval-shaped (0.9 × 0.5 mm) pores randomly distributed only on the thicker surface of the thallus (= porous surface). The branched thallus has lobed apices, and the pores are aligned in an arc shape. Base broken and reproductive structures unknown (Fig. 5c).

Remarks: The specimens most closely resemble those of *Spongiophyton minutissimum*, as proposed by Kräusel (1954) and Gensel et al. (1991). They differ

from *S. lenticulare* and *S. nanum* by presenting a small, lobed thallus (up to 3 mm wide), being rarely branched, bearing small and circular pores confined to one surface of the thallus (porous surface) and sometimes aligned in an arc. Up to now, *S. minutissimum* occurred at the eastern border of the Paraná Basin and has been documented in the USA (Wisconsin, Kuglitsch et al. 1998) and Canada (La Garde and Battery Point formations, Gensel et al. 1991).

Subdivision Lycophytina Kenrick et Crane 1997

Class Lycopsidea Scott 1909

Genus *Haplostigma* Seward 1932

Type species: *Haplostigma irregulare* (Schwartz) Seward 1932

General remarks: Taxonomic revision is out of the scope of this work. Therefore, we follow Carrizo and Azcuy (2015)'s amendment of the genus, and also their description of *Haplostigma furquei* and the other species of this genus established by Matsumura et al. (2015a) based on the comparison of stem and leaf cushions in detail with other Devonian lycopsids from the literature. Therefore, this genus includes herbaceous lycopsid stems frequently up to 20 mm wide and rarely branched dichotomously. Other diagnostic characters are the following: enlarged spine-like leaf cushions forming rounded to subhexagonal patterns, arranged in pseudo-sigillarioid to sigillarioid phyllotaxis; leaf cushions forming well-defined vertical ridges (orthostichies); leaves not persistent, but when present, they are slender and unbranched; and reproductive structures unknown. Currently, *Haplostigma* includes five morphospecies that are further described below, except for *H. lineare* (Walkom) McLoughlin et Long 1994. Of them, the presence of leaves as an important taxonomic character was indicated for *H. furquei*, unbranched leaf-type appendages, slender, up to 7 mm long (Gutiérrez 1996, Carrizo and Azcuy 2015), *H. baldisii*, robust, falcate, and slightly flattened along the ad-abaxial axes and with acute apices (Gutiérrez and Archangelsky 1997), *H. irregulare*, slender, up to 2 mm long, and apparently little persistent leaf-type appendages (Matsumura et al. 2015a, present study).

Haplostigma irregulare Seward 1932 (Fig. 6a)

Diagnosis: *Stems possibly succulent, reaching a diameter of at least 5 cm, probably occasionally forked; surface smooth, some branches having a few or no scars and without appendages (decorticated), and the stouter branches characterized by spirally disposed scars transversely oval or circular-shaped. The appendages were stiff and spinous without foliage-leaves. The cortical tissue near the base of each microphyll was composed of relatively strong cells.*

Figured material: DEGEO/MP-4621.

Stratigraphic and geographic range: São Domingos Formation (Paraná Basin), Tibagi Municipality, Paraná State, Southern Brazil (Matsumura et al. 2015a).

Age: Middle Devonian (Fig. 2).

Description: Stem fragments of herbaceous lycopsids, preserved as compression, up to 20 mm long. Leaf cushions are rounded to longitudinally oval in vertically aligned ridges. In lateral view, when the leaf bases are preserved, the leaf cushions show a spine-like projection of 1 mm on their upper parts (arrows in Fig. 6a). They are equidistantly separated from adjacent leaf cushions and arranged in a

pseudosigillarioid phyllotaxis in which orthostichies and uniform parastichies are well-defined. Ridges are laterally separated by straight longitudinal to slightly sinuous grooves. The leaf is slender, nonpersistent, distally undivided, and up to 2 mm long. Reproductive structures are not recognized (Fig. 6a).

Remarks and comparisons: This species is distinguished from *H. furquei* described below, having pseudosigillarioid phyllotaxis and a vertical distance between leaf cushions on the same ridge greater than the horizontal distance between alternating ridges. They also differ from *H. baldisii*, which is characterized by sigillarioid phyllotaxis; parastichies are not defined, a vertical distance between leaf cushions on the same ridge less than the horizontal distance between alternating ridges. Enations are falcate and slightly flattened along the adaxial axis. They also differ from *H. kowiensis* characterized by smaller and longitudinally elongated hexagonal leaf cushions, and from *H. lineare*, by elliptical to fusiform leaf cushions with sigillaroid phyllotaxis (Matsumura et al. 2015a). In the Paraná Basin, *Haplostigma irregulare* was first reported in Jaguariaíva (Barbosa 1949), and later Ponta Grossa (Kräusel 1954) municipalities. Recently, specimens that resemble *H. irregulare* were illustrated by Carbonaro et al. (2018) and Grahn et al. (2016) from the Chapada Group unit 4 in Goiás State. In the Parnaíba Basin, Suárez-Riglos (1975) reported but did not illustrate, *Haplostigma* sp. *H. irregulare* was documented in the Upper Bokkeveld Group of South Africa (Anderson and Anderson 1985) and in Tarija Basin in Argentina and southern Bolivia (di Pasquo et al. 2013, 2015). From the latter region, several specimens illustrated as *Haplostigma* sp., showing different grades of decortication and one of them bearing spine-like undivided projections (di Pasquo et al. 2015, Fig. 6.3–4), are herein assigned to *H. irregulare* and only one (Fig. 4.4) to *H. lineare* based on their morphologic similarities. Racheboeuf et al. (2012) described one specimen of a lycophyte *Protolepidodendron* sp.? aff. *Protolepidodendron scharianum* (Krejčí) Potonié and Bernard 1904, partially dichotomic stem lacking leaves from possibly Eifelian deposits at Pisacaviña in Bolivia. The genus *Protolepidodendron* (Krejčí) Gothan ex Potonié 1921, and its type species *Protolepidodendron scharianum* defined from the Lower Devonian of China, is characterized by having a wider stem with a smooth surface, with nonpersistent and unbranched leaves with slender spine-like, somewhat forked (Jurina 2009). Matsumura et al. (2015a) compared this genus with *Haplostigma* and maintained them separated in agreement with Jurina (2009). The single Bolivian specimen exhibits morphologic features of *Haplostigma irregulare*, particularly having a similar arrangement and size of ovoid leaf cushions with a circular vascular scar (central position) and probably belonging to this taxon.

Haplostigma furquei (Frenguelli) Gutiérrez 1996 emend. Carrizo et Azcuy 2015 (Figs. 6b, 7a)

Diagnosis: *Lycophyte axes with herbaceous aspect, simple and? branched stems, medium to robust size, and up to 13 cm long and 1.5 cm wide. Helicoidal to pseudosigillarioid phyllotaxis with up to 18 leaves by gyre. The separation distance between gyres is 1 to 1 and ½ times the width of the leaf bases. In lateral view, (vascularized?) leaves are up to 9 mm long, with a strongly asymmetric conical base, markedly decurrent on the abaxial side and steep decline on the adaxial one,*

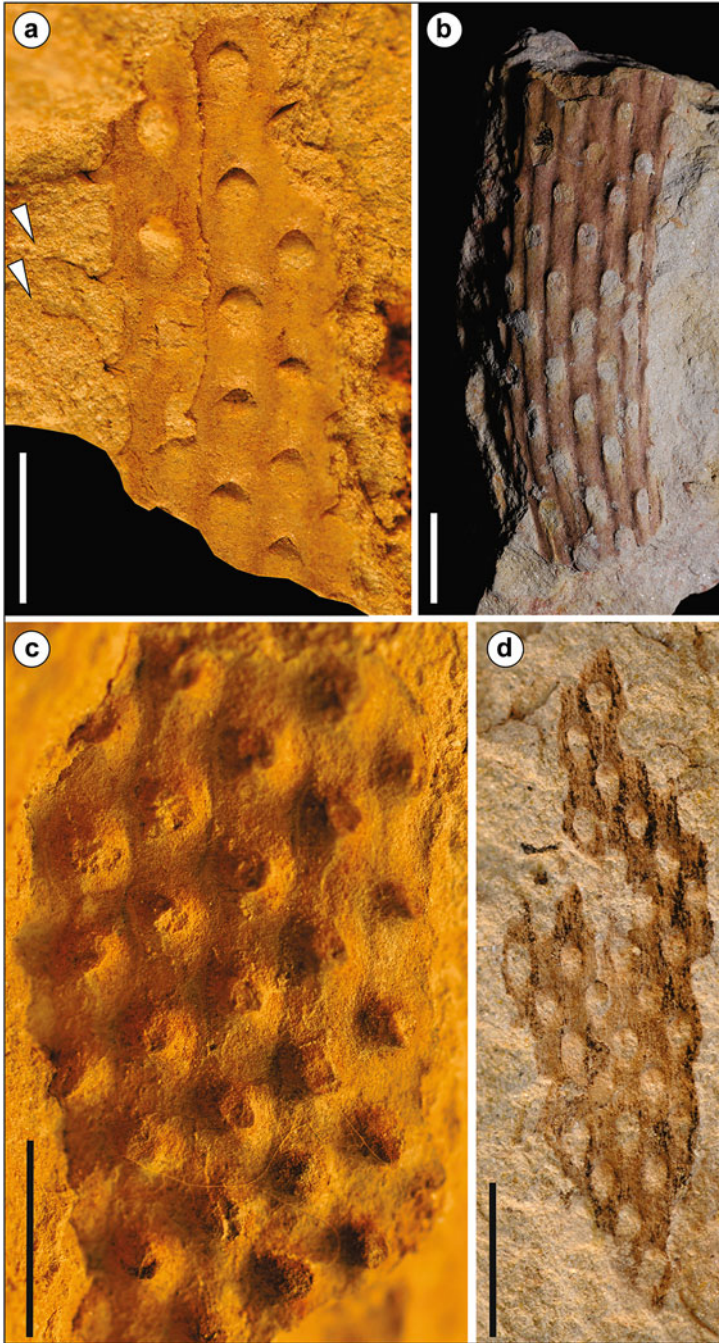


Fig. 6 (a) *Haplostigma irregularis*, DEGEO/MP-4621, and scale bar = 5 mm; (b) *Haplostigma furquei*, DEGEO/MP-7457a, and scale bar = 10 mm; (c) *Haplostigma baldisii*, DEGEO/MP-2886, and scale bar = 5 mm; and (d) *Haplostigma* cf. *kowiensis*, DEGEO/MP-4972a, and scale bar = 5 mm

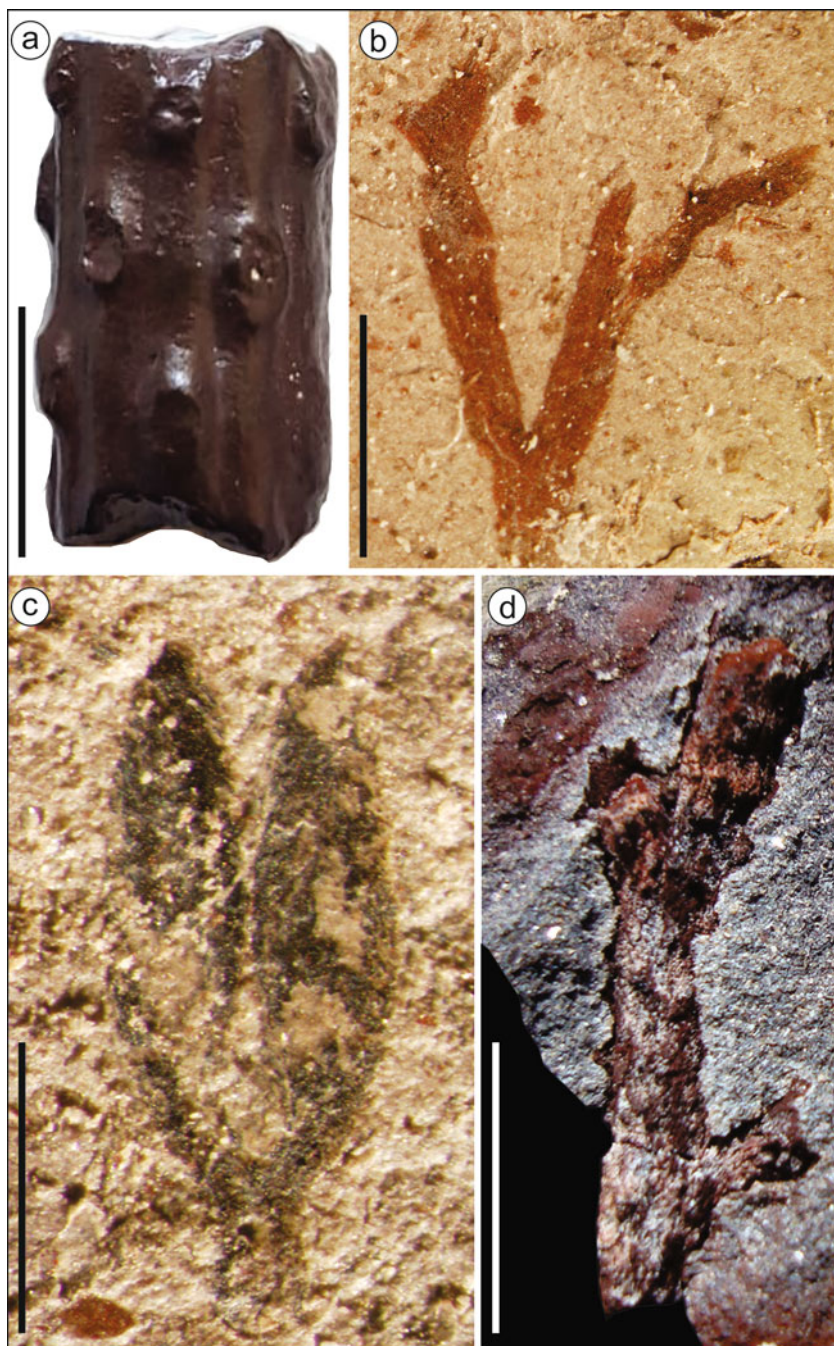


Fig. 7 (a) *Haplostigma firquei*, LPP V-153, and scale bar = 10 mm; (b) *Tracheophyta incertae sedis*, UNIRIO 0014P, and scale bar = 5 mm; (c) *Euphylllophytina incertae sedis A*, UNIRIO 0012 P, and scale bar = 5 mm; and (d) *Euphylllophytina incertae sedis B*, UNIRIO 049-P, scale bar = 5 mm

showing lengthwise faded contours with the neighboring leaves. The width at the base rapidly decreases, gaining in its middle part a laminar aspect, characterized of subparallel entire margins and with a pronounced tendency to bend adaxially. The leaf is divided into three segments with acuminate ends at its distal portion. The middle segment, adaxially recurved, is the larger (1.5 mm long), flanked at the base by two shorter lateral segments (0.8 mm long) inserted into the larger segment at acute to straight angles. On the stem, the leaf bases are conserved. They have irregular surfaces of rupture, with spine form aspect, vertically aligned forming narrow ribs, with convex margins to pass through the base, and separated by narrow grooves of undulating contours. If the fracture surface coincides with the surface of the stem, false leaf scars of oval design are observed. Tissue brands are usually preserved in leaf bases.

Figured materials: DEGEO/MP-7457a and LPP V-153.

Stratigraphic and geographic range: São Domingos Formation (Paraná Basin), Tibagi Municipality, Paraná State, Southern Brazil (Fig. 6b). Pimenteira Formation (Parnaíba Basin), São João da Canabrava Municipality, Piauí State, Northeastern Brazil (Fig. 7a).

Age: Middle Devonian (Fig. 2).

Description: The analyzed material consists of stem fragments preserved as compression (Fig. 6b) and cast (Fig. 7a), up to 100 mm long and 20 mm wide. Leaf cushions are round to longitudinally oval, in vertically aligned ridges with pseudosigillarioid phyllotaxis, six to seven leaf cushions along each half-turn of the stem. Orthostichies and uniform parastichies are well-defined. Sometimes, in better-preserved specimens, ridges are separated by slightly sinuous longitudinal grooves. The vertical distance between leaf cushions on the same ridge is greater (up to three times the length of the leaf cushion) than the horizontal distance between alternating ridges. Reproductive structures, leaves, and leaf traces are not recognized (Figs. 6b and 7a).

Remarks: *H. furquei* recorded in Paraná (Matsumura et al. 2015a) and Parnaíba (this work) basins of Brazil morphologically agree with specimens illustrated from Chiguá, Punta Negra, and Los Monos formations of Argentina (Gutiérrez 1996, Di Pasquo et al. 2009), in the Iquiri and Los Monos formations of Bolivia (Di Pasquo et al. 2013, 2015) and the El Toco Formation of Chile (Moisan et al. 2011).

Haplostigma baldisi Gutiérrez et Archangelsky 1997 (Fig. 6c)

Diagnosis: Unbranched, subherbaceous lycophyte, bearing simple, short, robust enations with a sigillarioid phyllotaxis, leaf cushions arranged in regular longitudinal rows and alternated. Wide, somewhat constricted ribs separated by zigzag furrows along the axis. Falcate enations (microphyll), with variably truncate (broken) to acute apices, slightly flattened along the ad–abaxial axis of transverse-oval section.

Studied material: DEGEO/MP-2886.

Stratigraphic and geographic range: São Domingos Formation (Paraná Basin), Tibagi Municipality, Paraná State, Southern Brazil.

Age: Middle Devonian (Fig. 2).

Description: Fragmented stems of herbaceous lycopsids bearing broken appendages, preserved as compression, up to 20 mm long and 10 mm wide. Transverse oval to subhexagonal leaf cushions present on the surface; 6–8 leaf cushions on each half-turn of the stem form vertically aligned ridges in sigillarioid phyllotaxy. Orthostichies and scalariform parastichies are well defined. The ridges are separated by zigzag grooves. The vertical distance between leaf cushions on each ridge is smaller (up to three times the length of the leaf cushion) than the horizontal distance between alternating ridges. Reproductive structures, leaves, and leaf traces not recognized (Fig. 6c).

Remarks: Documented in the São Domingos Formation, Paraná Basin of Brazil (Matsumura et al. 2015a) and in the Chiguá Formation of Argentina (Gutiérrez and Archangelsky 1997).

Haplostigma sp. cf. *H. kowiensis* Anderson et Anderson 1985 (Fig. 6d)

Diagnosis: Stem consistently narrow (± 10 mm diam.), fleshy; leaf scars small (± 0.5 mm diam.), circular, spaced more closely across diameter than along axis of stem resulting in conspicuous low angle ($\pm 5^\circ$ from horizontal) rows; and leaves diverge at 50° from the axis.

Figured material: DEGEO/MP-4972a.

Stratigraphic and geographic range: São Domingos Formation (Paraná Basin), Tibagi Municipality, Paraná State, Southern Brazil.

Age: Middle Devonian (Fig. 2).

Description: Stem fragments with broken appendages, preserved as compressions, up to 25 mm long and 5 mm wide. Round to longitudinally oval leaf cushions are present on the stem surface. The leaf cushions are vertically aligned, forming ridges with pseudosigillarioid phyllotaxy. Orthostichies and uniform parastichies are well defined. Occasionally, the ridges are laterally separated by straight longitudinal to slightly sinuous grooves. The leaf cushions are equidistant, and usually six to seven leaf cushions are present on each half-turn of the stem. Reproductive structures and leaves are not recognized (Fig. 6d).

Remarks: *H. kowiensis* recorded in Upper Bokkeveld and Witteberg groups of South Africa (Anderson and Anderson 1985) morphologically agrees with those from the Paraná Basin, Brazil (Matsumura et al. 2015a).

Tracheophyta *incertae sedis*

Figured material: UNIRIO 0014P.

Stratigraphic and geographic range: Pimenteira Formation (Parnaíba Basin), Picos Municipality, Piauí State, Northeast Brazil.

Age: Middle Devonian (Fig. 2).

Description: Impression of a naked stem, 1 mm wide, bearing at least two times isotomous branching. Base and apices are not preserved.

Remarks: Due to high fragmentary state, it is assigned to Tracheophyta group. Euphyllophytina *incertae sedis* A.

Figured material: UNIRIO 0012P.

Stratigraphic and geographic range: Pimenteira Formation (Parnaíba Basin), Picos Municipality, Piauí State, Northeast Brazil.

Age: Middle Devonian (Fig. 2).

Description: The specimen preserved as compression consists of paired sporangia. Each sporangium shows a fusiform shape of 7 mm in length and 2 mm in width.

Remarks: Due to the high fragmentary state, we assigned it to Euphyllrophytina group, probably related to *Psilophyton*, which includes naked and spiny stems, branched pseudomonopodially and dichotomously and paired sporangia.

Euphyllrophytina *incertae sedis* B.

Figured material: UNIRIO 0049P.

Stratigraphic and geographic range: Pimenteira Formation (Parnaíba Basin), Picos Municipality, Piauí State, Northeast Brazil.

Age: Middle Devonian (Fig. 2).

Description: A cast of a fragmented stem, 11 mm in length, and with two lateral and alternate branching. The whole stem surface presents some rounded to spine-like emergences (Fig. 7d).

Remarks: Despite the material does not allow more accurate and reliable identification, we suggest a probable relationship with *Psilophyton*.

Nonvascular or vascular plant.

Family Protosalviniaceae Sommer 1962

Genus *Protosalvinia* (Dawson) Sommer et Van Boekel 1966

Remarks: *Protosalvinia* is an enigmatic plant-like organism of possible terrestrial origin (Niklas and Phillips 1976, Niklas et al. 1976, Gray and Boucot 1979, Romankiw et al. 1988). The genus includes the species: *P. braziliensis* Dawson 1884, *P. bilobata* (Dawson) Sommer 1962, *P. ravenna* (White) Arnold 1954, *P. furcata* (Dawson) Arnold 1954, and *P. arnoldii* Bharadwaj and Venkatachala 1960. According to Niklas and Phillips (1976), *P. ravenna* and *P. furcata* forms could be ontogenetically derived from a *P. arnoldii* stage, whereas Niklas et al. (1976) considered all forms of *Protosalvinia* as ontogenetic stages and ecotypes of one single natural species (*P. braziliensis*). The genus is used as an essential guide fossil (*Protosalvinia-Spirophyton* Zone, Niklas et al. 1976, Loboziak et al. 1997), mainly associated with spore (*Vallatisporites hystricosus* Interval Zone, Melo and Loboziak 2003) and conodont zonations (*Trachytera* Zone, Over et al. 2009). Recently, Rooney et al. (2013) considered *Retusotriletes loboziakii* the dispersed miospore of *Protosalvinia* spp. and assigned it to the Famennian VCo Miospore Zone (Fig. 2). Quijada et al. (2016) analyzed biomarkers in *Protosalvinia* and revealed land plant affinity.

Protosalvinia braziliensis Dawson 1884 (Fig. 8a)

Diagnosis: *Sporocarps* thin, carbonaceous, circular, oval, or reniform, 3–6 mm in diameter, enclosing macrospores, which vary in number from 3 or 4 to as many as 25. Thick cuticle with an internal structure of dense hexagonal cells (Niklas et al. 1976).

Figured material: MP-Pb 5131.

Stratigraphic and geographic range: Barreirinha Formation (Amazon Basin), Pará State, North Brazil (Cunha et al. 2007).

Age: Late Devonian (Late Famennian, Cunha et al. 2007).

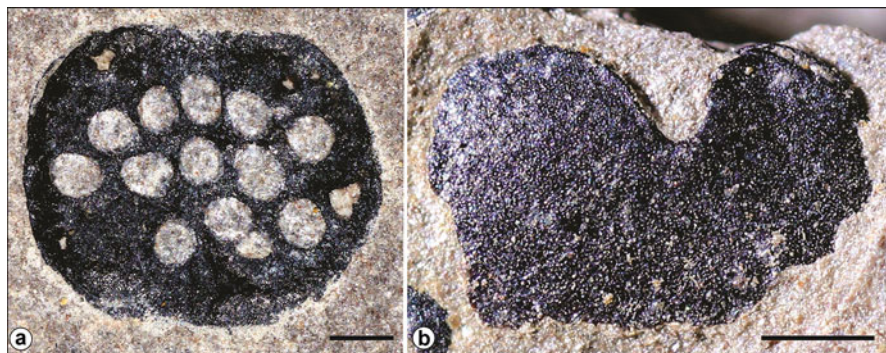


Fig. 8 (a) *Protosalvinia braziliensis*, MP-Pb 5131, and scale bar = 1 mm; (b) *Protosalvinia bilobata*, MP-Pb 5133, and scale bar = 1 mm

Description: Specimens are compressions consisting of an oval thallus, with 5 mm in length and 4 mm in width, having 13 rounded shallow small depressions, and apparently arranged in three arched rows.

Remarks: Tetrads of spores not observed in situ (Fig. 8a) but recovered from palynologic residues addressed below (*Retusotriletes loboziaki*).

Comparisons: The specimen closely resembles *Protosalvinia braziliensis* Dawson 1884 and differs from *P. bilobata* by presenting a circular to oval shape, unlobed, and bearing a higher number of rounded shallow depressions. In the Parnaíba Basin, Niklas et al. (1976) recorded *Protosalvinia arnoldii* in well 2-SL-I-MA. *Protosalvinia* was recorded in Famennian black shales of the Appalachian, Michigan, and Illinois basins of the United States (Schopf and Schwietering 1970, Matthews 1983, Over et al. 2009) and the Michigan Basin of Canada (Russell 1985).

Protosalvinia bilobata (Dawson) Sommer 1962 (Fig. 8b)

Diagnosis: Thalli oval or reniform, 2–6 mm in length, very rarely more “each showing two rounded prominences at the ends,” seldom more than two, “with a depression in the middle and sometimes a raised neck or isthmus at one side connecting the prominences.” Structure of thallus pseudocellular. Spore tetrads situated in circular openings, which seem to be cut out of the wall of the thallus, in the depression, numbering from one to many, but mostly two or three. In this opening, the tetrads appear to be supported by a membrane (Niklas et al. 1976).

Figured material: MP-Pb 5133.

Stratigraphic and geographic range: Barreirinha Formation (Amazon Basin), Pará State, North Brazil.

Age: Late Devonian (Fig. 2).

Description: The specimen is a flattened compression with preserved cuticle and consists of the bilobed thallus, with 2 mm length and 2.5 mm width. Each lobe is 1–1.5 mm wide and oval-shaped.

Remarks: Tetrads of spores not observed in situ (Fig. 8b), but recovered from palynologic residues addressed below (*Retusotriletes loboziaki*).

Comparisons: The specimen resembles *Protosalvinia bilobata* (Dawson) Sommer 1962 and differs from *P. braziliensis* by presenting a bilobed thallus. It also differs from *P. furcata* by having two lobes, rounded to reniform in shape. According to Niklas et al. (1976), *P. bilobata* may represent an ontogenetic stage of *P. furcata*. *Protosalvinia bilobata* was originally described as *Sporangites (Protosalvinia) biloba* (Dawson 1884) and later as *Protosalvinia (Sporangites) bilobata* (Dawson 1886). Sommer (1951, 1962) provided a historical review and redescribed this species based on new materials from Amazon Basin.

Palynology (Plant Microfossils)

Four palynoassemblages were obtained from two outcrops of the São Domingos Formation associated with the plant interval bearing *Haplostigma-Spongiophyton* in Paraná State (Fig. 1) and two more from the interval level with *Protosalvinia* in the Barreirinha Formation, Amazon Basin, Pará State, further described herein. The vertical distribution of palynomorph taxa is depicted in Table 1a, 1b, 1c, 1d and 1e.

São Domingos Formation

Several contributions documented the paleontologic content from the early late Emsian to late early Frasnian of the São Domingos Formation of the Apucarana Sub-Basin (sensu Grahn et al. 2010a, 2013), Southern Brazil. From the Early Givetian localities, black shales bearing land plants (*Haplostigma* sp.), and underlying Lilliput fauna and/or Extra-Malvinokafric (invasors) marine invertebrates represent the Eifelian-Givetian Kačák event. Despite many Middle Devonian rocks at different localities resulting palynologically barren or yielding a poor recovery due to coarse sandy nature and intense oxidation, several works were published, including palynology and results obtained from other fossil groups (e.g., Bosetti et al. 2011, Grahn et al. 2013, Matsumura et al. 2013, 2015a, b, c, 2016, Horodyski et al. 2014, 2019, Sedorko et al. 2018a, b).

We present new palynologic information obtained from this unit at two localities of Tibagi Municipality (Fig. 1).

Itáytyba Section (24°23'55"S, 50°20'16"W)

The São Domingos Formation crops out along the upper section of the Tibagi–Ventania succession (Fig. 1) located at the right margin of the BR-153 highway at Km 184 in Tibagi Municipality (e.g., Matsumura et al. 2013, 2015a, 2016). This section (16 m) is rich in Middle Devonian well-preserved plant fossils in the Paraná Basin. The lower part of the outcrop is composed of poorly sorted conglomeratic sandstones, followed upward by shale and micaceous siltstone layers with plant debris and several ichnofossils (vertical and horizontal structures) and a few marine invertebrates (brachiopods and trilobites). Its upper part records at its base a flooding surface correlated to the Kačák global anoxic event (Horodyski et al. 2014, 2019),

Table 1a Vertical distribution of palynomorph taxa of six studied samples from Mid–Late Devonian of Brazil. The references concerning the authority of taxa are not included in the list unless they are mentioned in the text

TAXA/sample collection number		CICYTTP-PI820	CICYTTP-PI1146	CICYTTP-PI1147	CICYTTP-PI1148	MP-Pb 5132	MP-Pb 5133
CHLOROPHYCEAE							
<i>Botryococcus</i>				X	X	X	X
SPORES	Total species	31	11	22	13	28	39
<i>Acinosporites lindlarensis</i> Riegel 1968		X	X	X			
<i>Acinosporites apiculatus</i> (Streel) Streel 1967		X					
<i>Dibolisporites farraginis</i> McGregor et Canfield 1982		X	X	X			
<i>Emphanisporites rotatus</i> McGregor 1964 emend. McGregor 1973		X	X	X	X		
<i>Grandispora permulta</i> (Daemon) Loboziak, Streel et Melo 1999		X	X	X			
<i>Leiotriletes balapucensis</i> di Pasquo 2007		X	X	X	X		CF
<i>Acinosporites acanthomamillatus</i> Richardson 1965		X		X	X		
<i>Acinosporites eumamillatus</i> Loboziak, Streel et Burjack 1988		X		X		X	X
<i>Craspedispora paranensis</i> Loboziak, Streel et Burjack 1989		X		X	X		X
<i>Cyclogranisporites plicatus</i> Allen 1965		X		X	X		
<i>Endoculeospora altobellii</i> di Pasquo 2007		X		X			
<i>Geminispora lemurata</i> Balme 1962 emend. Playford 1983		X		X	X		
<i>Grandispora gabesensis</i> Loboziak et Streel 1989		X		X			
<i>Leiotriletes pagius</i> Allen 1965		X		X			
<i>Acinosporites ledundae</i> Ottone 1996		X				X	X

(continued)

Table 1a (continued)

TAXA/sample collection number		CICYTTP-PI820	CICYTTP-PI1146	CICYTTP-PI1147	CICYTTP-PI1148	MP-Pb 5132	MP-Pb 5133
CHLOROPHYCEAE							
<i>Botryococcus</i>				X	X	X	X
SPORES	Total species	31	11	22	13	28	39
<i>Apiculatasporites adavalensis</i> Balme 1988		X					
<i>Apiculatisporis</i> sp.		X					
<i>Apiculiretusispora</i> sp.		X					
<i>Camarozonotriletes parvus</i> Owens 1971		X					
<i>Dibolisporites echinaceus</i> (Eisenack) Richardson 1965		X					
<i>Dibolisporites gaspiensis</i> (McGregor) Breuer et Steemans 2012		X					
<i>Dibolisporites turriculatus</i> Balme 1988		X					
<i>Dibolisporites</i> spp.		X					
<i>Endosporites longiradiatus</i> Menéndez et Pöthe de Baldis 1967		X					
<i>Grandispora daemontii</i> Loboziak, Strel et Burjack 1988		X					
<i>Punctatisporites</i> sp.		X					
<i>Samarisporites</i> sp. Breuer et Grahn 2011		X					
<i>Verrucosisporites premnus</i> Richardson 1965		X					
<i>Verrucosisporites tumulentus</i> Clayton et Graham 1974		X					
<i>Archaeozonotriletes variabilis</i> Naumova emend. Allen 1965		X					X
<i>Calamospora</i> spp.		X				X	X

(continued)

Table 1a (continued)

TAXA/sample collection number		CICYTTP-PI820	CICYTTP-PI1146	CICYTTP-PI1147	CICYTTP-PI1148	MP-Pb 5132	MP-Pb 5133
CHLOROPHYCEAE							
<i>Botryococcus</i>				X	X	X	X
SPORES	Total species	31	11	22	13	28	39
Undetermined spore			X				
<i>Acinosporites</i> spp.			X				
<i>Grandispora cassidea</i> (Owens) Massa et Moreau-Benoit			X				
<i>Grandispora fibrilabrata</i> Balme 1988			X				
<i>Grandispora pseudoreticulata</i> (Menéndez et Pöthe de Baldis) Ottone 1996			X	X	X		
<i>Grandispora</i> spp.			X	X	X		
<i>Samarisporites eximius</i> (Allen) Loboziak et Streele 1989			X	X	X		
<i>Cristatisporites streelii</i> Breuer et Steemans 2013				X			
<i>Grandispora macrotuberculata</i> (Archangelskaya) McGregor 1973				X	X		
<i>Grandispora velata</i> (Richardson) McGregor				X			
<i>Retusotriletes paraguayensis</i> Menéndez et Pöthe de Baldis 1967				X			
<i>Samarisporites praetervisus</i> Allen 1965				X			
<i>Verruciretusispora ornata</i> (Menéndez et Pöthe de Baldis) di Pasquo 2005				X	X		
<i>Grandispora mammillata</i> Owens 1971					X		
<i>Grandispora protea</i> (Naumova) Moreau-Benoit 1980					X		

Table 1b

SPORES	CICYTTP- PI820	CICYTTP- PI1146	CICYTTP- PI1147	CICYTTP- PI1148	MP-Pb 5132	MP-Pb 5133
<i>Anapiculatisporites</i> sp.					X	X
<i>Apiculiretusisporta nitida</i> Owens 1971					X	X
<i>Apiculiretusispora verrucosa</i> (Caro-Moniez) Streeel in Becker et al. 1974					X	X
<i>Auroraspora macra</i> Sullivan 1968					X	X
<i>Cyclogranisporites</i> sp.					X	X
<i>Cymbosporites catillus</i> Allen 1965					X	X
<i>Cymbosporites cyathus</i> Allen 1965					X	X
<i>Leiotriletes struniensis</i> Moreau-Benoit 1979					X	X
<i>Lophozonotriletes media</i> Taugourdeau-Lantz 1967					X	X
<i>Lophozonotriletes</i> spp.					X	X
<i>Retusotriletes crassus</i> Clayton et al. 1980					X	X
<i>Rugospora flexuosa</i> (Juschko) Bivsheva 1985					X	X
<i>Rugospora radiata</i> (Juschko) Bivsheva 1985					X	X
<i>Stenozonotriletes forticulus</i> Balme et Hassell 1962					X	X
<i>Tumulispora rarituberculata</i> (Luber) Potonié 1966					X	X
<i>Velamisporites perinatus</i> (Hughes et Playford) Playford 1971					X	X
<i>Verrucosisorites scurrus</i> (Naumova) McGregor et Camfield 1982					X	X
<i>Chelinospora timanica</i> (Naumova) Loboziak et Streeel 1989					X	
<i>Endoculeospora setaceae</i> (Kedo) Avkhimovitch et al. 1988					X	
<i>Geminospora punctata</i> Owens 1971					X	
<i>Granulatisporites</i> sp.					X	
<i>Microreticulatisporites</i> <i>araneum</i> Higgs et al. 1988					X	
<i>Samarisporites triangulatus</i> Allen 1965					X	

(continued)

Table 1b (continued)

SPORES	CICYTTP- PI820	CICYTTP- PI1146	CICYTTP- PI1147	CICYTTP- PI1148	MP-Pb 5132	MP-Pb 5133
<i>Teichertospora torquata</i> (Higgs) Foster et Balme 1994					X	
<i>Verrucosporites</i> spp.					X	
<i>Ancyrospora langi</i> (Taugourdeau-Lantz) Allen 1965						X
<i>Apiculatisporis morbosus</i> Balme et Hassell 1962						X
<i>Archaeozonotriletes columnus</i> Allen 1965						X
<i>Bascaudaspora cf. collicula</i> (Playford) Higgs et al. 1988						X
<i>Chelinospora ligurata</i> Allen 1965						X
<i>Convolutispora ampla</i> Hoffmeister, Staplin et Malloy 1955						X
<i>Convolutispora tegula</i> Allen 1965						X
<i>Cordylosporites glumaceus</i> (Byvsheva) Playford et Melo 2012						X
<i>Cristatisporites imperpetuus</i> (Sennova) Obukhovskaya 1986						X
<i>Cymbosporites magnificus</i> (McGregor) McGregor et Camfield 1982						X
<i>Cyrtospora cristifera</i> (Luber et Waltz) emend. Van der Zwan 1979						X
<i>Geminospora piliformis</i> Loboziak et al. 1988						X
<i>Grandispora echinata</i> Hacquebard 1957						X
<i>Leiotriletes</i> sp. cf. <i>L. balapucensis</i> di Pasquo 2007						X
<i>Punctatisporites debilis</i> Hacquebard						X
<i>Retusotriletes loboziaki</i> Rooney et al. 2013						X
<i>Verrucosporites depressus</i> Winslow 1962						X

Table 1c

TAXA/sample collection number		CICYTTP-PI820	CICYTTP-PI1146	CICYTTP-PI1147	CICYTTP-PI1148	MP-Pb 5132	MP-Pb 5133
PHYTOPLANKTON	Total species	13	13	25	21	30	30
<i>Gorgonisphaeridium</i> spp.		X	X	X	X	X	X
<i>Leiosphaeridia</i> spp.		X	X	X	X		
<i>Navifusa bacilla</i> (Deunff) Playford 1977		X	X	X	X	X	X
<i>Verhynchium polyaster</i> Staplin 1961		X		X	X	X	X
<i>Quadrisorites granulatus</i> (Cramer) Ströther 1991		X			X		
<i>Quadrisorites variabilis</i> (Cramer) Ottone et Rossello 1996		X			X		
<i>Verhynchium trispinosum</i> (Eisenack) Deunff 1954		X			X	X	X
<i>Cymatiosphaera subtrita</i> Playford et Dring 1981		X					
<i>Cymatiosphaera apiaria</i> Ottone 1996		X					
<i>Diexalophasis remota</i> (Deunff) emend. Playford 1977		X					
<i>Multiplicisphaeridium ampliatus</i> Playford 1977		X					
<i>Muraticavea munificus</i> Wicander et Wood 1981		X					
<i>Leiosphaeridia</i> spp.		X	X	X	X	X	X
<i>Pterospermella</i> spp.			X	X	X	X	X
<i>Duvernaysphaera</i> spp.			X	X	X		
<i>Evittia sommeri</i> Brito 1967			X	X	X		
<i>Exochoderma arca</i> Wicander et Wood 1981			X	X			
<i>Exochoderma irregularis</i> Wicander 1974			X	X			
<i>Exochoderma</i> spp.			X	X	X	X	X
<i>Pterospermella</i> spp.			X	X	X		
<i>Verhynchium</i> spp.			X	X	X	X	X
<i>Winwaloesia distracta</i> (Deunff) Deunff 1977			X				
<i>Arkonites bilixus</i> Legault 1973				X	X		
<i>Cymatiosphaera</i> spp.				X	X	X	X
<i>Dactylofusa fastidiosa</i> (Cramer) Eisenack et al. 1976				X			
<i>Estiastra spinireticulata</i> Oliveira et Burjack 1997				X			
<i>Exochoderma triangulata</i> Wicander et Wood 1981				X			
<i>Hapsidopalla exornata</i> (Deunff) Playford 1977				X			

(continued)

Table 1c (continued)

TAXA/sample collection number		CICYTTP-PI820	CICYTTP-PI1146	CICYTTP-PI1147	CICYTTP-PI1148	MP-Pb 5132	MP-Pb 5133
PHYTOPLANKTON	Total species	13	13	25	21	30	30
<i>Maranhites</i> spp.				X	X	X	X
<i>Michrystidium</i> spp.				X			
<i>Polyedryxium embudum</i> Cramer 1964				X			
<i>Polyedryxium</i> spp.				X	X	X	X
<i>Pterospermella pernambucensis</i> (Brito) Eisenack et al. 1973				X			
<i>Triangulina alargada</i> Cramer 1964				X	X		
<i>Tunisphaeridium caudatum</i> Deunff et Evitt 1968				X			
<i>Michrystidium</i> spp.				X		X	X
<i>Duvernaysphaera angelae</i> Deunff 1964					X		
<i>Hemiruptia legaultii</i> Ottone 1996					X	X	X
<i>Unellium piriforme</i> Rauscher 1969					X		
<i>Multiplicisphaeridium escobaides</i> (Cramer) Eisenack et Cramer 1973						X	X
<i>Baltisphaeridium</i> sp. cf. <i>B. distentum</i> Playford 1977						X	X
<i>Mediocorpe conspicuo</i> Oliveira ex Loboziak et al. 1997						X	X
<i>Dictyotidium</i> spp.						X	X
<i>Horologinella quadrispina</i> Jardiné et al. 1972						X	X
<i>Horologinella horologia</i> (Staplin) Jardiné et al. 1972						X	X
<i>Maranhites britoi</i> Stockmans et Williére 1969						X	X
<i>Maranhites moesii</i> (Sommer) Brito 1967 emend. Burjack et Oliveira 1989						X	X
<i>Orygmahapsis pachyderma</i> Colbath 1990						X	X
<i>Papulogabata annulata</i> Playford et Dring 1981						X	X
<i>Pterospermella capitana</i> Wicander 1974						X	X
<i>Stellinium comptum</i> Wicander et Loeblich 1977						X	X

(continued)

Table 1c (continued)

TAXA/sample collection number		CICYTTP-PI820	CICYTTP-PI1146	CICYTTP-PI1147	CICYTTP-PI1148	MP-Pb 5132	MP-Pb 5133
PHYTOPLANKTON	Total species	13	13	25	21	30	30
<i>Stellinium octoaster</i> (Staplin) Jardiné et al. 1972						X	X
<i>Tornacia stela</i> Wicander 1974						X	X
<i>Umbellasphaeridium deflandrei</i> (Moreau-Benoit) Jardiné et al. 1972						X	X
<i>Umbellasphaeridium saharicum</i> Jardiné et al. 1972						X	X
<i>Tasmanites</i>						X	X

Table 1d

TAXA/sample collection number			CICYTTP-PI1146	CICYTTP-PI1147	CICYTTP-PI1148		
CHITINOZOA	Total species	CICYTTP-PI820	6	4	3	MP-Pb 5132	MP-Pb 5133
<i>Angochitina daemoni</i> Grahn et al. 2000			X				
<i>Fungochitina pilosa</i> (Collinson et Scott) Grahn et Melo, 2002			X				
<i>Fungochitina</i> sp. cf. <i>F. pilosa</i> (Collinson et Scott)			X				
<i>Ramochitina stiphrospinata</i> Grahn et Melo 2005			X				
<i>Ramochitina</i> sp. 2 Grahn et al. 2003			X				
cf. <i>Spinachitina aciculata</i> Muller et al. 2009			X				
<i>Angochitina</i> sp. Noetinger et di Pasquo 2011				X			
<i>Fungochitina</i> sp. Ottone 1996				X			
<i>Hoegisphaera</i> sp.				X			
<i>Lagenochitina praeavelinoi</i> Grahn et Melo 2004				X	X		
<i>Ramochitina ramosi</i> Sommer et Boekel 1964					X		
<i>Ramochitina</i> sp. C Gaugris et Grahn 2006					X		

Table 1e

MEGASPORES	Total species	2	2	1	1
<i>Verrucisporites</i> sp. cf. <i>V. yabrinensis</i> Marshall et al. 2007		X			
<i>Biharisporites</i> sp.		X			
<i>Biharisporites parviornatus</i> Richardson 1965			X		
<i>Jhariatriletes emsiensis</i> (Moreau-Benoit) Breuer et Steemans 2012			X		
Undetermined				X	X

characterized by the predominance of shaly–silty sandstone layers poor in invertebrates and other macrofossils except for the abundance of plant stems of *Spongiophyton* and *Haplostigma* mainly into friable shale–siltstones.

One palynologically productive shale sample (CICYTTP-PI 820) was obtained from this plant interval that yielded a diverse assemblage of well-preserved palynomorphs (30%), amorphous organic matter (40%), and phytoclasts (30%), especially cuticles. A silicified imprint of a large megaspore with a smooth wall, 1 mm in diameter, assigned herein to *Trileites langi* Eisenack (Fig. 9), found in the same rock sample associated to this palynoflora.

The palynoassemblage comprises trilete spores (55%), phytoplankton (45%), and scarce megaspores and scolecodonts. Numerous species of spores of the genera *Apiculatisporis*, *Calamospora*, *Chelinospora*, *Dibolisporites*, *Grandispora*, and *Punctatisporites*, together with megaspores, are documented. The main species of spores are *Acinosporites acanthomammillatus* Richardson, *Acinosporites apiculatus* (Streel) Streel, *Acinosporites eumammillatus* Loboziak, Streel et Burjack, *Acinosporites lindlarensis* Riegel, *Apiculatasporites adavalensis* Balme, *Apiculiretusispora nitida* Owens, *Archaeozonotriletes variabilis* Naumova emend. Allen, *Chelinospora ligurata* Allen, *Camarozonotriletes parvus* Owens, *Craspedispora paranaensis* Loboziak et al., *Cyclogranisporites plicatus* Allen, *Cymbosporites catillus* Allen, *Dibolisporites echinaceus* (Eisenack) Richardson, *Dibolisporites farraginis* McGregor et Camfield, *Dibolisporites gaspiensis* (McGregor) Breuer et Steemans, *Dibolisporites turriculatus* Balme, *Emphanisporites rotatus* McGregor emend. McGregor, *Endoculeospora altobellii* di Pasquo, *Endosporites longiradiatus* Menéndez et Pöthe de Baldis, *Geminospora lemurata* Balme emend. Playford, *Grandispora daemonii* Loboziak, Streel et Burjack, *Grandispora gabesensis* Loboziak et Streel, *Grandispora permulta* (Daemon) Loboziak, Streel et Melo, *Leiotriletes balapucensis* di Pasquo, *Leiotriletes pagius* Allen, *Samarisporites praetervisus* Allen, *Samarisporites* sp. Breuer et Grahn, *Verrucosisporites premnus* Richardson, *Verrucosisporites tumultus* Clayton et Grahn, and megaspores *Verrucisporites* sp. cf. *V. yabrinensis* Marshall et al. and *Biharisporites* sp. The acritarchs and prasinophytes are variably represented by *Arkonites bilixus* Legault, *Cymatiosphaera subtrita* Playford et Dring, *Cymatiosphaera apiaria* Ottone, *Diexalophasis remota* (Deunff) emend. Playford, *Muraticavea munifica* Wicander et Wood, *Navifusa bacilla* (Deunff) Playford, *Quadrissporites granulatus* (Cramer) Ströther, *Quadrissporites variabilis* (Cramer) Ottone in Ottone et Rossello, and species of *Gorgonisphaeridium* and *Leiosphaeridia* (Fig. 10).

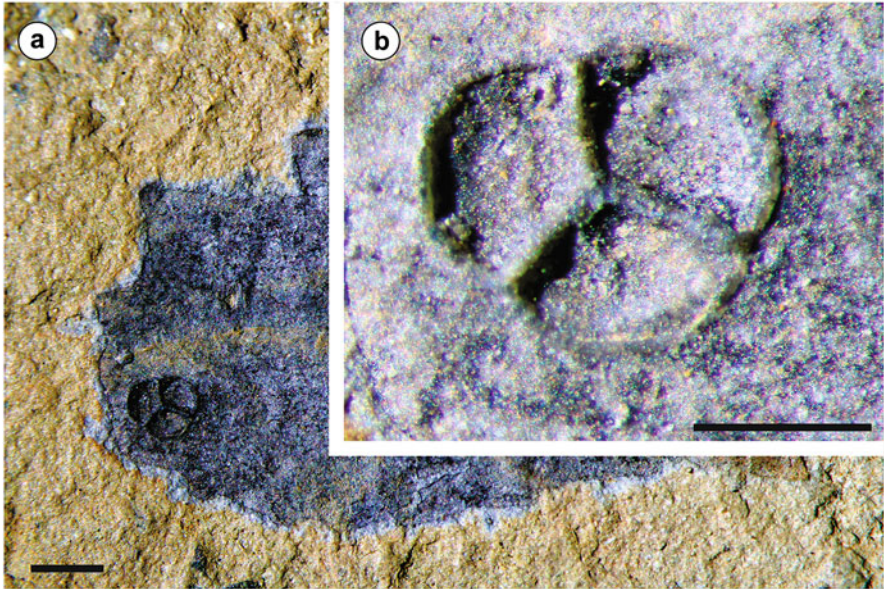


Fig. 9 *Trileites langi* Eisenack, silicified specimen from Itaytiba (CICYTTP-PI 820)

Most of these spores and phytoplankton species are shared with the early Givetian palynofloras of the upper *São Domingos* Formation documented by Bosetti et al. (2011) and Grahn et al. (2013) from the same region. An early mid Givetian age is supported based on co-occurrence of diagnostic species such as *Acinosporites eumammillatus*, *Apiculatasporites adavalensis*, *Archaeozonotriletes variabilis*, *Arkonites bilixus*, *Camarozonotriletes parvus*, *Chelinospora ligurata*, *Craspedispora paranaensis*, *Cymatiosphaera apiaria*, *Endosporites longiradiatus*, *Geminospora lemurata*, *Grandispora daemonii*, and *Muraticavea munifica*, which allowed the correlation with the *G. lemurata*–*C. ligurata* Zone Melo and Loboziak 2003 (Fig. 2). Two megaspores documented herein for the first time in Brazil are *Trileites langi*, which is known from the mid Givetian–early Frasnian (McGregor and Playford 1992) and *Verrucisporites* sp. cf. *V. yabrinensis*, from the Givetian of Saudi Arabia (Marshall et al. 2007).

This age agrees with previous information on the stratigraphic position of the plant assemblage associated (Matsumura et al. 2015a, 2016) overlying the Kačák Event (Bosetti et al. 2011, Grahn et al. 2016, Horodyski et al. 2019). Grahn et al. (2016), Carbonaro and Ghilardi (2016), and Carbonaro et al. (2018) reported *Haplostigma* sp., *Spongiophyton* sp., and plant debris associated with marine invertebrates at the base of the Chapada Group Group Unit 4 in the Alto Garças Sub-Basin (Fig. 1). Common species with our palynoassemblage of the *São Domingos Formation* (e.g., *Chelinospora ligurata*, *Geminospora lemurata*, and *Verrucosporites premnus*) support their correlation and reinforce the age of the maximum flooding surface at the Eifelian–Givetian boundary (Assine 2001, Grahn et al. 2010b).

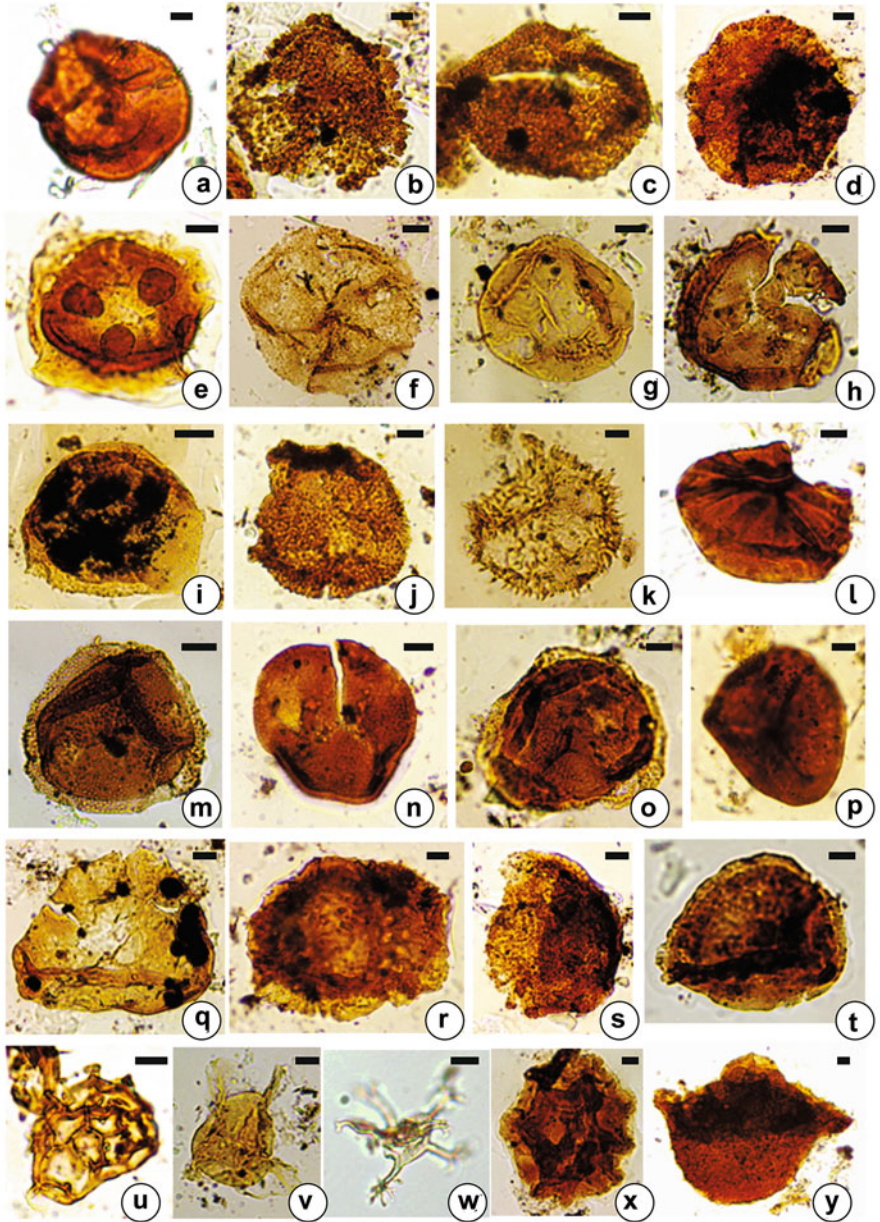


Fig. 10 Palynomorphs of the São Domingos Formation at Itáyitiba section: (a) *Archaeozonotriletes variabilis* Naumova emend. Allen. CICYTTP-PI 820-1 O37-2; (b) *Acinosporites eumammillatus* Loboziak, Strel et Burjack. CICYTTP-PI 820-8 E47-3; (c) *Acinosporites ledundae* Ottone. CICYTTP-PI 820-7 N50; (d) *Acinosporites apiculatus* (Strel) Strel. CICYTTP-PI 820-3 E43-1; (e) Undetermined spore. CICYTTP-PI 820-8 L48 (similar to *Discernisporites* sp. A Higgs et al. from the LL-LE zones); (f) *Apiculatasporites adavalsensis* Balme. CICYTTP-PI 820-3 M50-3; (g) *Calamospora*

Vila Rici Section (25° 6'37"S, 50° 12'19"W)

Three samples were collected from the São Domingos Formation in the Vila Rici section, located in the Contorno district in Ponta Grossa county (Fig. 1). The co-occurrence of palynomorphs and land plants in the sampled interval was favored thanks to the fact that the weathering process had not started (Matsumura et al. 2015b). The basal portion of a 5.5 m thick section (c. 20 m length) is composed of dark to light gray shales with parallel lamination and bearing *Spongiophyton* spp. and *Haplostigma* sp., whereas siltstones and fine to medium-grained sandstones with bioturbation (several ichnofossil types) and trilobites calmoniids and crinoids (*Ctenocrinus* sp.) were recognized in the upper portion. The three palynoassemblages recovered from the two first meters of this section yielded well-preserved and diverse palynomorphs (50%), phytoclasts (20%) dominated by cuticles, and amorphous organic matter (30%).

The lower sample CICYTTP-PI 1146 yielded abundant spores (*Acinosporites lindlarensis* Riegel, *Dibolisporites farraginis* McGregor et Camfield, *Emphanisporites rotatus* McGregor emend. McGregor, *Grandispora cassidea* (Owens) Massa et Moreau-Benoit, *Grandispora fibrilabrata* Balme, *Grandispora permulta* (Daemon) Loboziak, Streel et Melo, *Grandispora pseudoreticulata* (Menéndez et Pöthe de Baldis) Ottone, *Leiotriletes balapucensis* di Pasquo, and *Samarisporites eximius* (Allen) Loboziak et Streel), and phytoplankton (acritarchs/prasinophytes, *Evittia sommeri* Brito, *Exochoderma arca* Wicander et Wood, *Exochoderma irregularis* Wicander, *Navifusa bacilla* (Deunff) Playford, and *Winwaloesia distracta* (Deunff) Deunff). Several chitinozoan species (*Angochitina daemoni* Grahn et al., *Fungochitina pilosa* (Collinson et Scott), *Fungochitina* sp. cf. *F. pilosa* (Collinson et Scott), *Ramochitina stiphrospinata* Grahn et Melo, *Ramochitina* sp. 2 Grahn et al., and cf. *Spinachitina aciculata* Mauller et al.), and



Fig. 10 (continued) sp. CICYTTP-PI 820-7 F43-1; **(h)** *Camarozonotriletes parvus* Owens. CICYTTP-PI 820-8 E40; **(i)** *Craspedispora paranaensis* Loboziak et al. CICYTTP-PI 820-7 N51-4; **(j)** *Dibolisporites gaspiensis* (McGregor) Breuer et Steemans. CICYTTP-PI 820-7 E41; **(k)** *Dibolisporites turriculatus* Balme. CICYTTP-PI 820-7 E41; **(l)** *Emphanisporites rotatus* McGregor emend. McGregor. CICYTTP-PI 820-8 E40; **(m)** *Endoculeospora altobellii* di Pasquo. CICYTTP-PI 820-7 W57-3; **(n)** *Geminospora lemurata* Balme emend. Playford. CICYTTP-PI 820-3 E45-1; **(o)** *Grandispora daemonii* Loboziak, Streel et Burjack. CICYTTP-PI 820-8 N30-4; **(p)** *Leiotriletes pagius* Allen. CICYTTP-PI 820-7 H30-4; **(q)** *Leiotriletes balapucensis* di Pasquo. CICYTTP-PI 820-8 H30-4; **(r)** *Samarisporites* sp. Breuer et Grahn. CICYTTP-PI 820-3 V49-4; **(s)** *Verrucosisporites tumultus* Clayton et Graham. CICYTTP-PI 820-3 G41-4; **(t)** *Endosporites longiradiatus* Menéndez et Pöthe de Baldis. CICYTTP-PI 820-7 W31-3; **(u)** *Cymatiosphaera apiaria* Ottone. CICYTTP-PI 820-8 W31-1; **(v)** *Cymatiosphaera subtrita* Playford et Dring. CICYTTP-PI 820-8 D38-2; **(w)** *Multiplicisphaeridium ampliutum* Playford. CICYTTP-PI 820-1 R37; **(x)** *Muraticavea munificus* Wicander et Wood. CICYTTP-PI 820-8 Q55-1; and **(y)** *Verrucisporites* sp. cf. *V. yabrinensis* Marshall et al. CICYTTP-PI 820-8 K54-4. Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 µm unless specified.

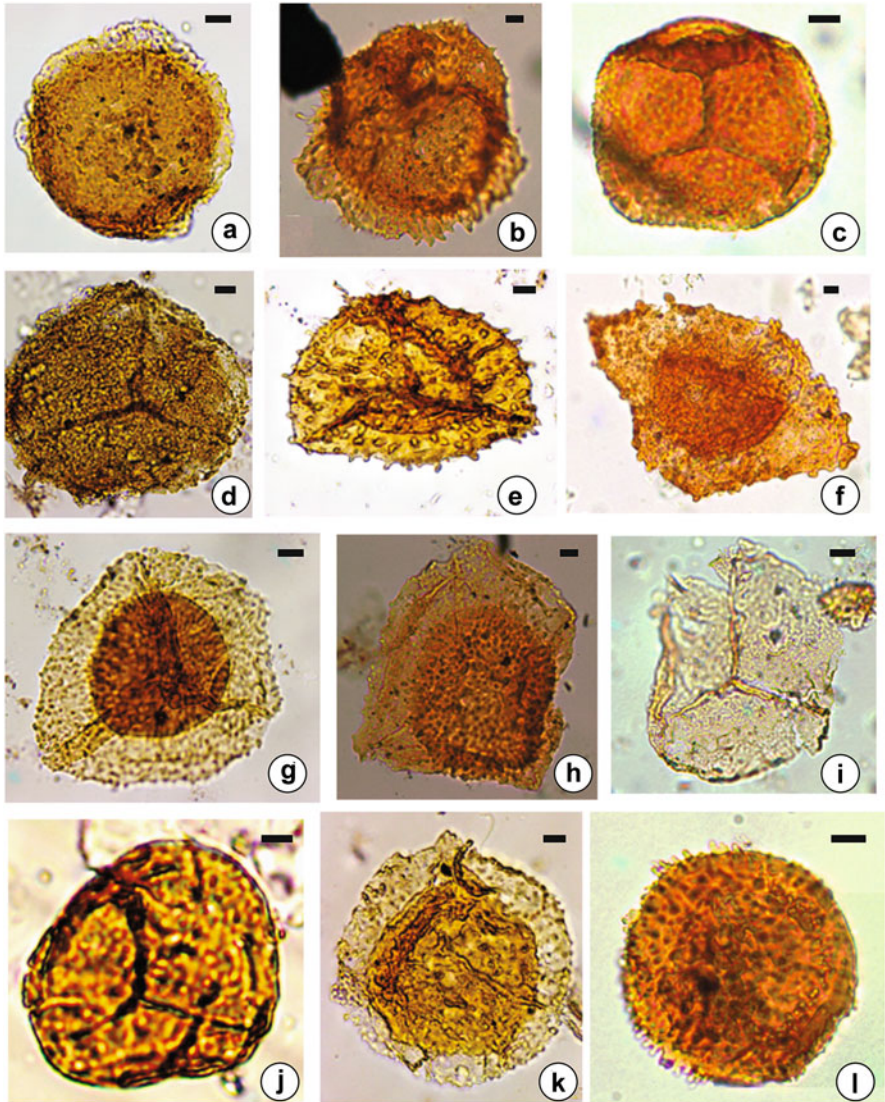


Fig. 11 Palynomorphs of the São Domingos Formation at Vila Ricci: (a) *Craspedispora paransensis* Loboziak, Streeel et Burjack. CICYTTP-PI 1148-1 E20; (b) *Cristatisporites streeelii* Breuer et Steemans. CICYTTP-PI 1147-1 B54; (c) *Geminospora lemurata* Balme emend. Playford. CICYTTP-PI 1148-1 R31; (d) *Grandispora fibrilabrata* Balme. CICYTTP-PI 1146-1 O49; (e) *Grandispora cassidea* (Owens) Massa et Moreau-Benoit. CICYTTP-PI 1146-1 Q49; (f) *Grandispora macrotuberculata* (Archangelskaya) McGregor. CICYTTP-PI 1148-1 M57; (g) *Grandispora permulta* (Daemon) Loboziak, Streeel et Melo. CICYTTP-PI 1147-1 E32-1; (h) *Grandispora pseudoreticulata* (Menéndez et Pöthe de Baldis) Ottone. CICYTTP-PI 1147-1 F60; (i) *Leiotriletes balapucensis* di Pasquo. CICYTTP-PI 1146-1 Q37; (j) *Retusotriletes paraguayensis* Menéndez et Pöthe de Baldis. CICYTTP-PI 1147-1 Q39; (k) *Samarisporites eximius* (Allen) Loboziak et Streeel. CICYTTP-PI 1148-1 W39; and (l) *Verruciretusispora ornata* (Menéndez et

megaspores (*Biharisporites parviornatus* Richardson, *Jhariatriletes emsiensis* (Moreau-Benoit) Breuer et Steemans) are also present (Figs. 11, 12, and 13).

Other species are added in the sample CICYTTP-PI 1147, like the spores *Acinosporites acanthomamillatus* Richardson, *Acinosporites eumamillatus* Loboziak, Strel et Burjack, *Craspedispora paranensis* Loboziak, Strel et Burjack, *Cristatisporites streelii* Breuer et Steemans, *Cyclogranisporites plicatus* Allen, *Endoculeospora altobellii* di Pasquo, and *Geminospora lemurata* Balme emend. Playford, *Grandispora gabesensis* Loboziak et Strel, *Grandispora macro-tuberculata* (Archangelskaya) McGregor, *Grandispora velata* (Richardson) McGregor, *Leiotriletes pagius* Allen, *Retusotriletes paraguayensis* Menéndez et Pöthe de Baldis, *Samarisporites praetervisus* Allen, *Verruciretusispora ornata* (Menéndez et Pöthe de Baldis) di Pasquo, the phytoplanktonic species *Arkonites bilixus* Legault, *Dactylofusa fastidiona* (Cramer) Eisenack et al., *Estiastra spinireticulata* Oliveira et Burjack, *Exochoderma triangulata* Wicander et Wood, *Hapsidopalla exornata* (Deunff) Playford, *Polyedryxium embudum* Cramer, *Pterospermella pernambucensis* (Brito) Eisenack et al., *Triangulina alargada* Cramer, *Tunisphaeridium caudatum* Deunff et Evitt, *Verhyachium polyaster* Staplin, and chitinozoans *Angochitina* sp. Noetinger et di Pasquo, *Fungochitina* sp. Ottone, *Hoegisphaera* sp., and *Lagenochitina praeavelinoi* Grahn et Melo are also documented.

Few more taxa have appeared in the upper sample CICYTTP-PI 1148 spores *Grandispora mammillata* Owens, *Grandispora protea* (Naumova) Moreau-Benoit, phytoplankton *Duvernaysphaera angelae* Deunff, *Hemiruptia legaultii* Ottone, *Quadrisporites granulatus* (Cramer) Ströther, *Quadrisporites variabilis* (Cramer) Ottone et Rossello, *Unellium piriforme* Rauscher, *Verhyachium trispinosum* (Eisenack) Deunff, and together with *Lagenochitina praeavelinoi*, *Ramochitina ramosi* Sommer et Boekel, and *Ramochitina* sp. C Gaugris and Grahn.

Several species of prasinophycean (*Duvernaysphaera*, *Cymatiosphaera*, *Leiosphaeridia*, *Polyedryxium*, and *Pterospermella*) and acritarchs (*Exochoderma*, *Gorgonisphaeridium*, *Michrystridium*, and *Verhyachium*) are documented in the three samples, and *Maranhites* and the chlorophycean *Botryococcus brauni* are in low frequency in the upper two samples.

Some of the cuticles associated to the palynomorphs in both localities above show an arrangement and shape of cells and stomata (Figs. 12k and 14a) that are similar to cuticles obtained from stem compressions of *Haplostigma* found in the Givetian–Frasnian Los Monos and Iquiri formations (di Pasquo et al. 2015). A few unpublished cuticle specimens are illustrated herein in Fig. 14 for comparison. More detailed morphologic and geochemical studies are ongoing (see di Pasquo et al. 2015, Matsumura et al. 2016).



Fig. 11 (continued) Pöthe de Baldis) di Pasquo. CICYTTP-PI 1148–1 W41. Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 μm unless specified.

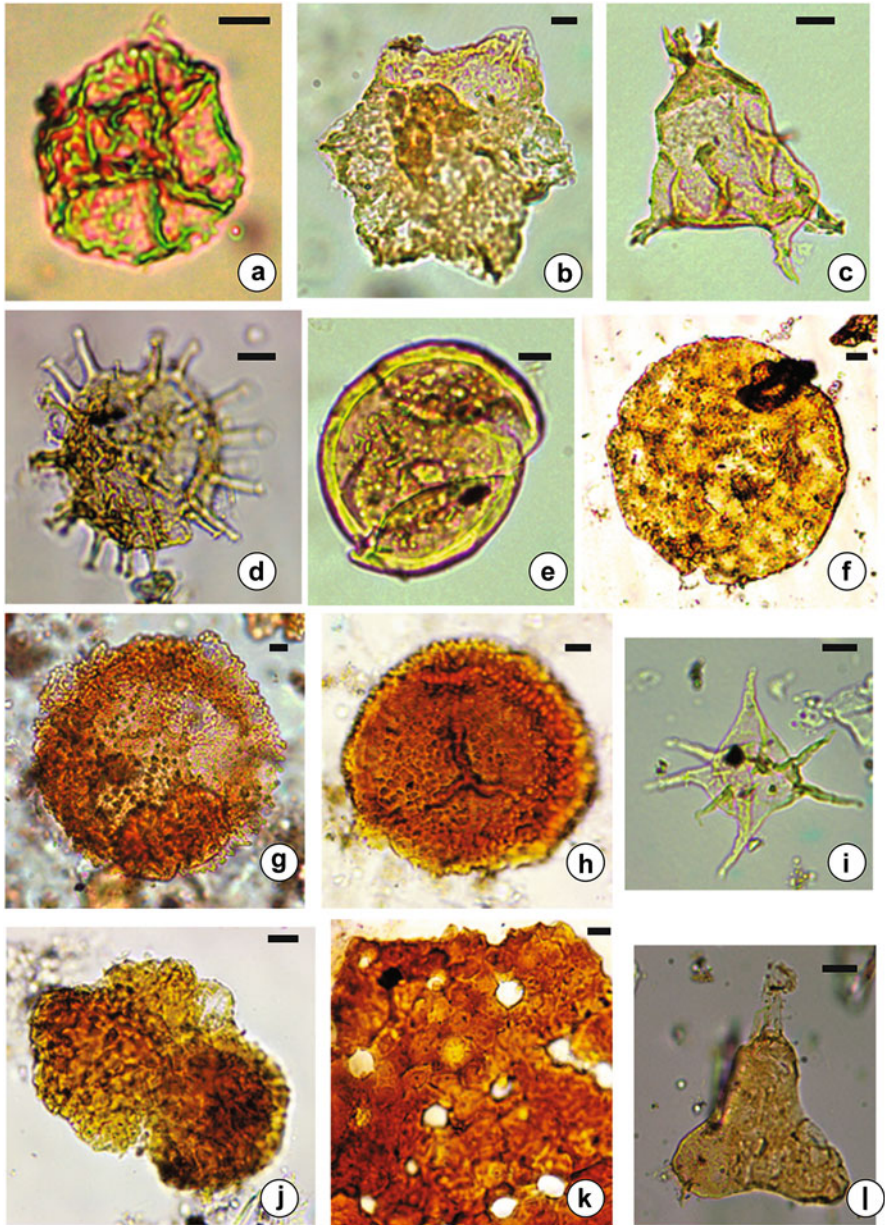


Fig. 12 Palynomorphs of the São Domingos Formation at Vila Ricci section: (a) *Arkonites bilixus* Legault. CICYTTP-PI 1148-1 Y43-4; (b) *Estiastra spinureticulata* Oliveira et Burjack. CICYTTP-PI 1147-1 H32; (c) *Evittia sommeri* Brito. CICYTTP-PI 1148-1 B23-3; (d) *Hapsidopalla exornata* (Deunff) Playford. CICYTTP-PI 1147-1 O53-4; (e) *Hemiruptia legaultii* Ottone. CICYTTP-PI 1148-1 N22; (f) *Maranhites mosesii* (Sommer) Brito emend. Burjack et Oliveira. CICYTTP-PI G49-4; (g) *Jhariatriteles emsiensis* (Moreau-Benoit) Breuer et Steemans. CICYTTP-PI 1146-1 S50; (h) *Biharisporites parviornatus* Richardson. CICYTTP-PI 1146-1 M58-4;

An Early Givetian age is supported based on co-occurrence of diagnostic species *Acinosporites eumammillatus*, *Arkonites bilixus*, *Biharisporites parviornatus*, *Craspedispora paranensis*, *Cristatisporites streelii*, *Dactylofusa fastidiona*, *Estiastra spinireticulata*, *Exochoderma triangulata*, *Hapsidopalla exornata*, *Fungochitina pilosa*, *Fungochitina* sp. cf. *F. pilosa*, *Grandispora cassidea*, *Grandispora fibrilabrata*, *Grandispora permulta*, *Lagenochitina praeavelinoi*, *Ramochitina stiphrospinata*, *Ramochitina* sp. 2 Grahn et al., cf. *Spinachitina aciculata*, *Ramochitina ramosi*, *Ramochitina* sp. C Gaugris and Grahn, and *Unellium piriforme*. These taxa mainly support the correlation with the *G. lemurata*–*C. ligurata* Zone Melo and Loboziak 2003 and *Ramochitina stiphrospinata* Grahn 2005 of Brazil. These palynofloras are included in the Floral Stage *Spongiophyton*–*Haplostigma* proposed in this work (Figs. 2 and 15). Correlatable early Givetian palynofloras of the upper São Domingos Formation documented by Bosetti et al. (2011) and Grahn et al. (2013) from the same region shared spore and phytoplankton species with our assemblages. Other similar plant assemblages with *Spongiophyton*, *Haplostigma*, and Eifelian–Frasnian palynoassemblages were also recognized in the Los Monos Formation at Angosto del Pescado, northern Argentina, Balapuca, Yesera, and Mataral areas from southern Bolivia (di Pasquo 2007, di Pasquo et al. 2009, 2015, Noetinger 2015, Noetinger et al. 2018), and other Givetian formations from the Falkland Islands (Marshall 2016) and Brazil yet mentioned (Fig. 16a).

The mixture of marine and terrestrial components of the palynofacies of the three samples studied agrees with the interpretation of a shallow marine to littoral environment of deposition for the studied section (Matsumura et al. 2015b, c). Pieces of evidence are the presence of different types of amorphous organic matter, mostly of fine granular type (yellow fluorescence), likely derived from marine algal remains, and less frequent fibrous and lumpy types (orange fluorescence) of more varied sources together with similar frequencies of terrestrial (spores, megaspores, cuticles, and *Botryococcus*) and marine components (acritarchs and prasinophycean) with subordinated chitinozoans in the three samples. This interpretation coincides with other studies of the São Domingos Formation in Ponta Grossa (e.g., Bosetti et al. 2011, Grahn et al. 2013, Matsumura et al. 2013, 2015a, 2016, Horodyski et al. 2014, 2019, Sedorko et al. 2018a).

Barreirinha Formation

Euxinic conditions in the lower shale section of the Barreirinha Formation decrease to its upper part (Urariá Member, Late Famennian), characterized by interbedded and



Fig. 12 (continued) (i) *Unellium piriforme* Rauscher. CICYTTP-PI 1148–1 B33; (j) *Botryococcus*. CICYTTP-PI 1147–1 C45; (k) Cuticules. CICYTTP-PI 1146–1 J50–2; and (l) *Triangulina alargada* Cramer. CICYTTP-PI 1148–1 Y43–4

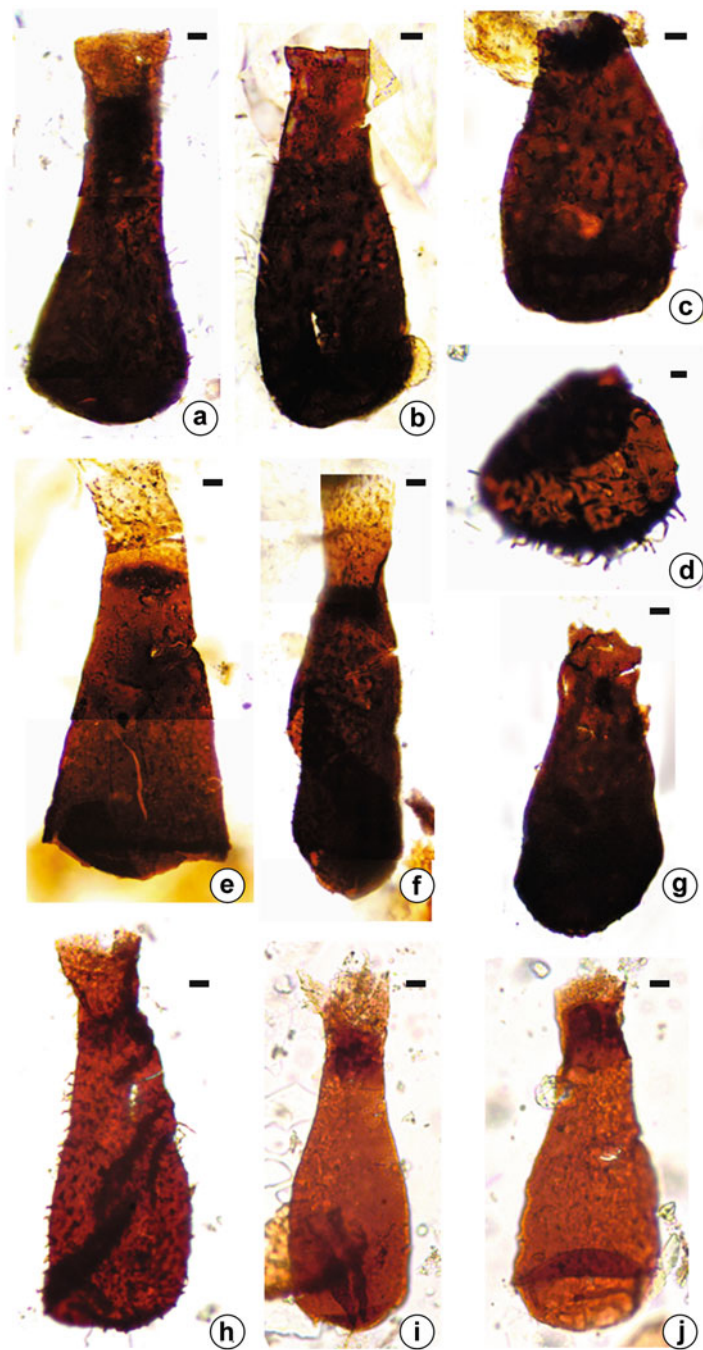


Fig. 13 Palynomorphs of the São Domingos Formation at Vila Ricci section: (a) *Angochitina daemoni* Grahn et al. CICYTTP-PI 1146-1 E41; (b and c) *Fungochitina pilosa* (Collinson et Scott) in Grahn; (b) CICYTTP-PI 1146-1 D30-2; (c) CICYTTP-PI 1146-1 Y33-1;

interlaminated siltstones and shales with *Protosalvinia* (= *Protosalvinia/Spirophyton* Zone). This interval is well developed throughout the basin due to increasing freshwater influx, and the environment tends to become brackish. Their lower content of organic matter and trace minerals and the presence of bioturbations *Spirophyton* (= *Zoophycus* isp.) also indicate less reducing conditions (Niklas et al. 1976, Loboziak et al. 1997, Melo and Loboziak 2003, Cunha et al. 2007). The *Protosalvinia*-bearing fine clastics correspond to the initial phase of the Upper Devonian glaciation extended from marginal conditions directly in front of the ice lobes or between them to offshore conditions in the center of the basin. Extensive glaciation was probably the major factor in destroying the brackish littoral habitats of *Protosalvinia* and the disappearance of this widespread “alga” from the Amazon Basin (see Niklas et al. 1976).

Composition of Palynoassemblages

Two palynoassemblages described in this work were obtained from two gray laminated shales (MP-Pb 5132 and 5133) below and above fine sandstone beds with current structures (Fig. 17a–b).

In the latter sample, there are numerous compressions of *Protosalvinia* parallel to the plane of stratification as described above, and from some of those specimens, cuticles are illustrated using a microscope with white and fluorescent lights (Fig. 17). The general morphology of our specimens agrees with detailed studies carried out by Phillips et al. (1972) from the Famennian of Kentucky (USA) and Amazon basin by Niklas et al. (1976). These cuticles exhibit a surface pattern of dense, variably rounded to polygonal cells and internal structure preserved.

The quali–quantitative palynofacies features of MP-Pb 5132 show abundant AOM (60%, fine and other types) and less frequent cuticles of *Protosalvinia* among few other types of phytoclasts (20%), and palynomorphs represented by phytoplankton (65%) and spores (35%).

The palynofacies of MP-Pb 5133 presents a higher proportion of phytoclasts derived from *Protosalvinia* (50% most cuticles) and less AOM (30%, fine) and palynomorphs (20%), represented by phytoplankton (60%) and spores (40%), almost all well-preserved with variable sizes from 20 μm to over 200 μm . Pyrite is present in the exine of palynomorphs.

In both samples, acritarchs and prasinophyceae of the genera *Cymatiosphaera*, *Dictyotidium*, *Exochoderma*, *Gorgonisphaeridium*, *Leiosphaeridia* (variable sizes),



Fig. 13 (continued) (d) *Ramochitina stiphrospinata* Grahn et Melo. CICYTTP-PI 1146–1 Q49; (e) cf. *Spinachitina aciculata* Mauller et al. CICYTTP-PI 1146–1 O18; (f) *Ramochitina* sp. 2 Grahn et al. CICYTTP-PI 1146–1 O18; (g) *Angochitina* sp. Noetinger et di Pasquo. CICYTTP-PI 1147–1 J36–1; (h) *Ramochitina ramosi* Sommer et Boekel. CICYTTP-PI 1148–1 M58–1; (i) *Lagenochitina praeavelinoi* Grahn et Melo. CICYTTP-PI 1148–1 M55–4; and (j) *Ramochitina* sp. C Gaugris et Grahn. CICYTTP-PI 1148–1 V55–2. Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 μm unless specified.

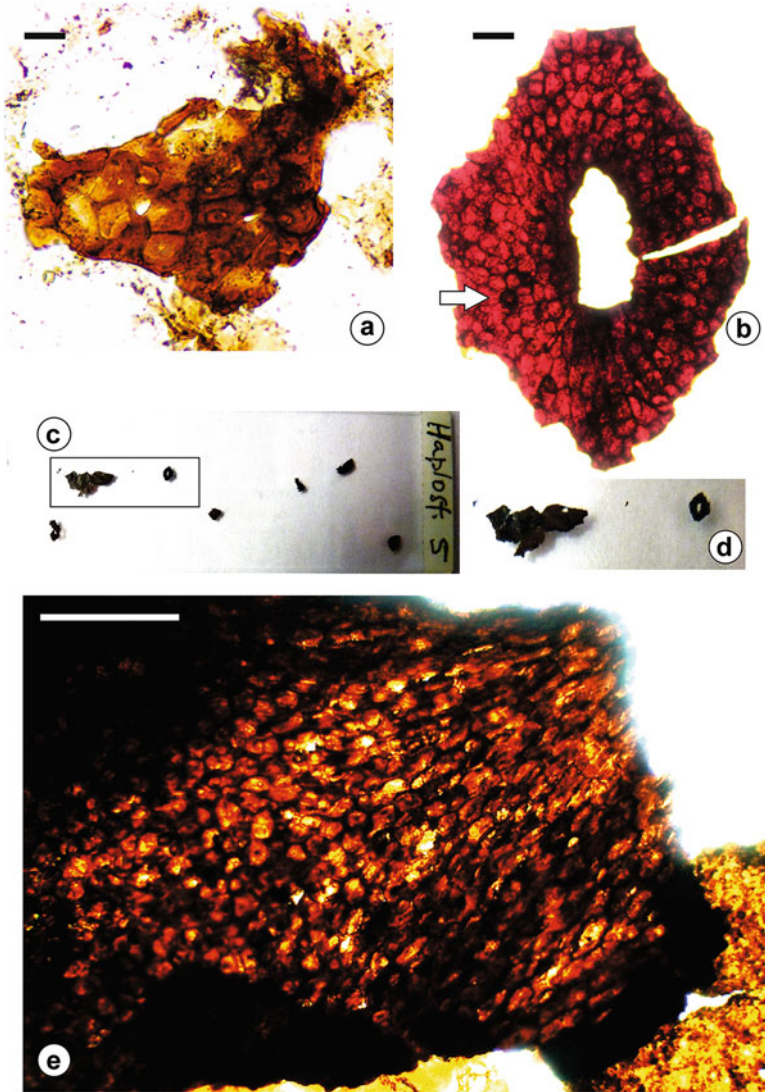


Fig. 14 (a) Cuticle assignable to *Haplostigma* present in slide 820–4 Q31 from the São Domingos Formation at Itaytiba section (b–e). Cuticles picked from compressions of *Haplostigma* and mounted in water pictured with a light microscope, present in the Los Monos Formation at Yesera Centro in Bolivia (di Pasquo et al. 2015, unpublished pictures); (b) morphology of stomata and cells (encircled). Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 μm unless specified.

Maranhites, *Michrystridium*, *Pterospermella*, *Polyedryxium*, and *Veryhachium* are fairly well represented whereas the chlorophycean *Botryococcus* is in low frequency. The species documented are *Baltisphaeridium* sp. cf. *B. distentum* Playford (see

Geochronology Genera	DEVONIAN						
	Lower			Middle		Late	
	Lochk.	Prag.	Ems.	Eif.	Giv.	Fras.	Fam.
<i>Aberlemnia</i>							
<i>Brasilophyton</i>							
<i>Ciguelia</i>							
<i>Conchulophyton</i>							
<i>Cooksonia</i>							
<i>Edwardsnella</i>							
<i>Hostinella</i>							
<i>Jaguariaivía</i>							
? <i>Lyonophyton</i>							
<i>Pertonella</i>							
<i>Petriaia</i>							
<i>Psilophytites</i>							
<i>Salopella</i>							
<i>Sphaerulophyton</i>							
<i>Sporogonites</i>							
<i>Steganotheca</i>							
<i>Sulculiphyton</i>							
<i>Tarrantia</i>							
<i>Octaviona</i>			—				
<i>Spongiophyton</i>			—	—	—	—	—
<i>Haplostigma</i>				—	—	—	—
<i>Palaeostigma</i>				—	—	—	—
<i>Protolepidodendron</i>				—	—	—	—
<i>Archaeosigillaria</i>				—	—	—	—
<i>Protosalvinia</i>							—
Stratigraphic Intervals	Earliest Devonian	late Early–early Late Devonian					Latest Devonian
Floral Stages	<i>Cooksonia–Hostinella</i>	<i>Spongiophyton–Haplostigma</i>					<i>Protosalvinia</i>

DEVONIAN PLANT OCCURRENCES IN BRAZIL

Fig. 15 Informal floral stages proposed to Devonian deposits from Brazil. Legend: Lochk., Lochkovian; Prag., Pragian; Ems., Emsian; Eif., Eifelian; Giv., Givetian; Fras., Frasnian; Fam., Famennian; SI., Stratigraphic Intervals; and FS., Floral Stages; line = taxa occurrences, dashed line = doubted record or occurrence of the taxa

Wicander and Playford 2013), *Hemiruptia legaultii* Ottone, *Horologinella quadrispina* Jardiné et al., *Horologinella horologia* (Staplin) Jardiné et al., *Maranhites britoi* Stockmans et Williére, *Maranhites mosesii* (Sommer) Brito emend. Burjack et Oliveira, *Mediocorpe conspicuo* Oliveira ex Loboziak et al., *Multipliscisphaeridium escobaides* (Cramer) Eisenack et Cramer, *Navifusa bacilla* (Deunff) Playford, *Orygmahapsis pachyderma* Colbath, *Papulogabata annulata* Playford et Dring, *Pterospermella capitana* Wicander, *Stellinium comptum* Wicander et Loeblich, *Stellinium octoaster* (Staplin) Jardiné et al., *Tornacia stela* Wicander, *Umbellasphaeridium deflandrei* (Moreau-Benoit) Jardiné et al., *Umbellasphaeridium saharicum* Jardiné et al., *Verhyachium trispinosum* (Eisenack) Stockmans et Williére, *Verhyachium polyaster* Staplin, and *Tasmanites* (Fig. 18).

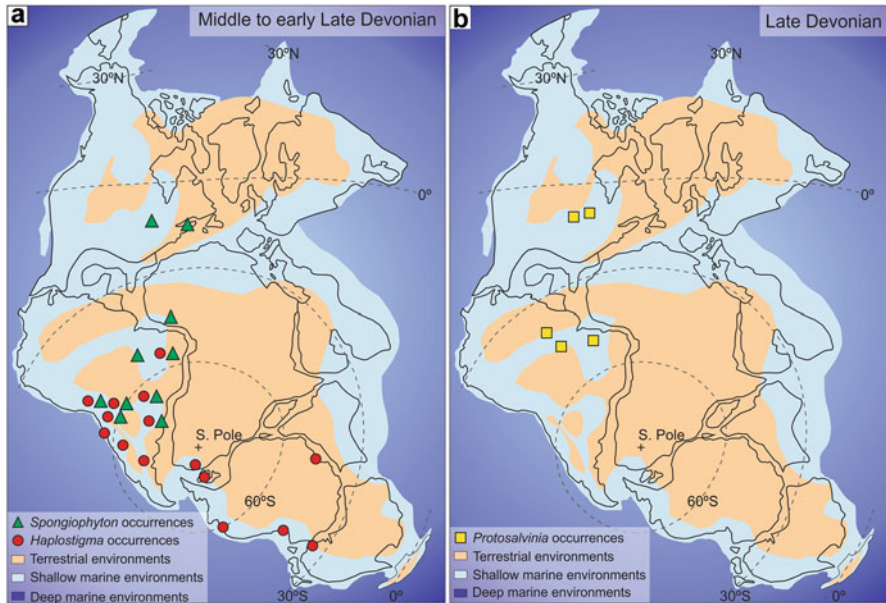


Fig. 16 Middle to early Late Devonian (a) and Late Devonian (b) paleogeographic reconstructions of Young (1990), showing the occurrences of the *Spongiophyton*, *Haplostigma*, and *Protosalvinia*

Species present in the two samples are the following: *Acinosporites eumammillatus* Loboziak et al., *Acinosporites ledundae* Ottone, *Apiculiretusispora nitida* Owens, *Apiculiretusispora verrucosa (fructicosa)* (Caro-Moniez) Strel in Becker et al., *Auroraspora macra* Sullivan, *Cymbosporites catillus* Allen, *Cymbosporites cyathus* Allen, *Leiotriletes struniensis* Moreau-Benoit, *Lophozonotriletes media* Taugourdeau-Lantz, *Retusotriletes crassus* Clayton et al., *Rugospora flexuosa* (Juschko) Bivsheva, *Rugospora radiata* (Juschko) Bivsheva, *Stenozonotriletes forticulus* Balme et Hassell, *Tumulispora rarituberculata* (Luber) Potonié, *Velamispurites perinatus* (Hughes et Playford) Playford, *Verrucosisporites scurrus* (Naumova) McGregor et Camfield, and species of the genera *Anapiculatisporites*, *Calamospora*, *Cyclogranisporites*, and *Lophozonotriletes*.

In the sample MP-Pb 5132, *Chelinospora timanica* (Naumova) Loboziak and Strel, *Endoculeospora setaceae* (Kedo) Avkhimovitch and Higgs in Avkhimovitch et al., *Geminospora punctata* Owens, *Microreticulatisporites araneum* Higgs et al., *Samarisporites triangulatus* Allen, *Teichertospora torquata* (Higgs) Foster and Balme, and species of the genera *Granulatisporites* and *Verrucosisporites* appeared.

In the sample MP-Pb 5133, *Ancyrospora langi* (Taugourdeau-Lantz) Allen, *Apiculatisporis morbosus* Balme et Hassell, *Archaeozonotriletes variabilis* Naumova emend. Allen, *Archaeozonotriletes columnus* Allen, *Bascaudaspora cf. collicula* (Playford) Higgs et al., *Chelinospora ligurata* Allen, *Convolutispora ampla* Hoffmeister et al., *Convolutispora tegula* Allen, *Cordylosporites glumaceus* (Byvsheva) Playford et Melo, *Craspedispora paranensis* Loboziak et al.,

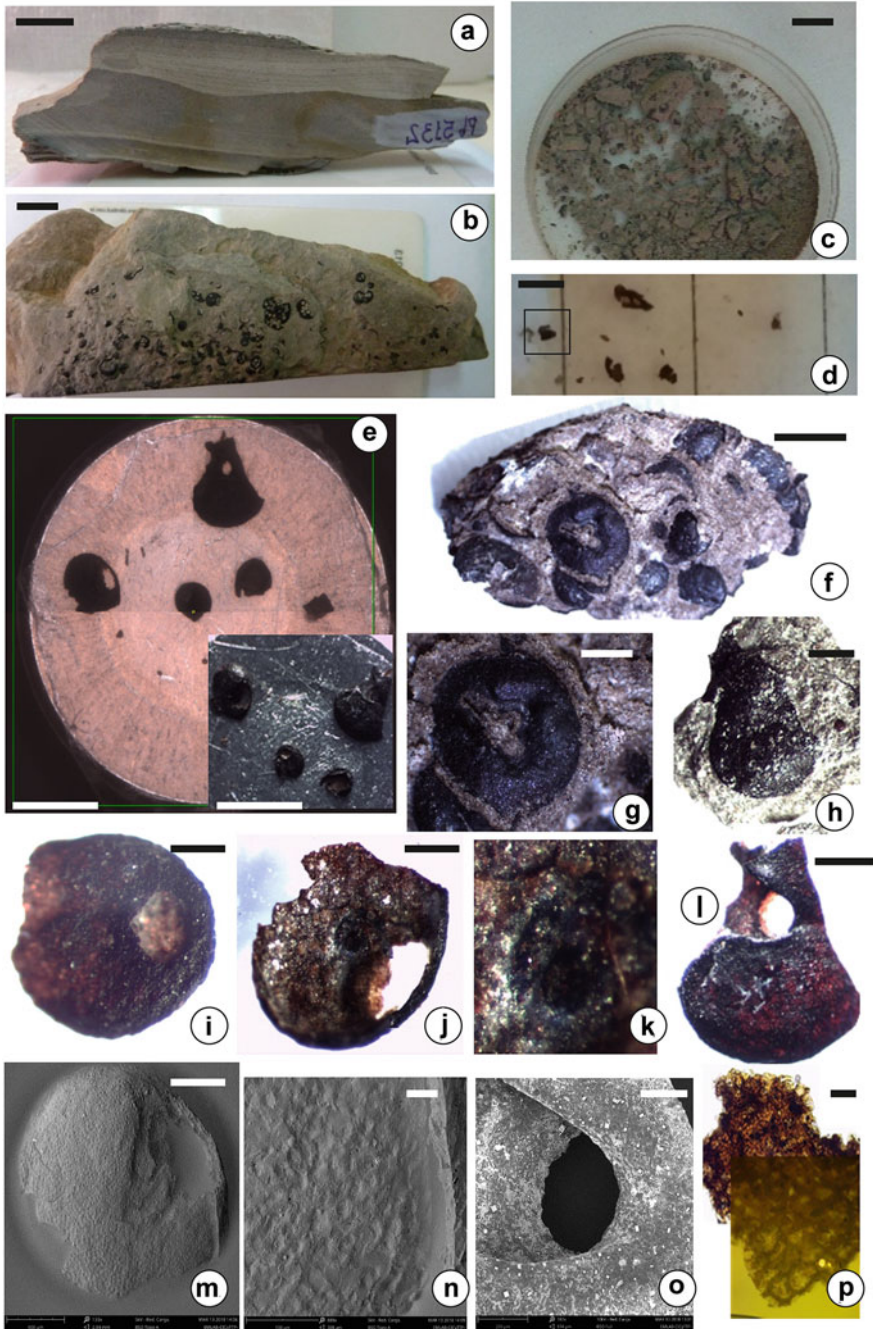


Fig. 17 *Protosalvinia* from the Barreirinha Formation: (a–c) Piece of rock from which two thin shale layers were processed for palynology located at lower (MP-Pb 5132), and (b–c) upper (MP-Pb 5133) surfaces; (d) cuticle fragments of *Protosalvinia* present in the residue of the latter sample; (e) specimens picked from the upper shale (MP-Pb 5133) mounted in stub and pictured with SEM (left)

Cristatisporites imperpetuus (Sennova) Obukhovskaya, *Cymbosporites magnificus* (McGregor) McGregor et Camfield, *Cyrtozpora cristifera* (Luber et Waltz) emend. Van der Zwan, *Geminospora piliformis* Loboziak et al., *Grandispora echinata* Hacquebard, *Leiotriletes* sp. cf. *L. balapucensis* di Pasquo, *Punctatisporites debilis* Hacquebard, *Retusotriletes loboziaki* Rooney et al., and *Verrucosporites depressus* Winslow occurred (Figs. 19, 20, and 21).

Age

Protosalvinia (*Foerstia*) is an important guide fossil (*Protosalvinia*–*Spirophyton* Zone, Niklas et al. 1976; Loboziak et al. 1997), even though it cannot be considered a synchronic floral zone in the USA and Brazil due to its age which varies from the middle to the late (not the latest) Famennian *Diducites versabilis*–*Grandispora cornuta* (VCo)–*A. verrucosa*–*Vallatisporites hystricosus* (VH) palynozones (Fig. 2) and the *marginifera*–*lower expansa* conodont Zones spanning c. 3 m.y. (Ziegler and Sandberg 1990, Gutschick and Sandberg 1991, p. 156, Sandberg et al. 1994, p. 241, Taylor and Taylor 1987, Over et al. 2009, Rooney et al. 2013).

Loboziak et al. (1997) studied the palynologic content of the *Protosalvinia* Zone from the uppermost part of the Barreirinha Formation, tested in 39 core samples from the interval devoid of diamictites and few outcrop samples near the Tapajós River, southern margin of the Amazon Basin. The overlying Curiri Formation containing diamictites displaying the latest Famennian (late “Strunian”) *Retispora lepidophyta* (Rle) Zone following Melo and Loboziak (2003).

Loboziak et al. (1997) attributed the *Protosalvinia*-bearing palynoassemblages to the late Famennian VCo Opperl Zone (Fig. 2) of the Ardenne–Rhenish regions (Streel et al. 1987) due to the occurrence of diagnostic *Rugospora radiata* and *Vallatisporites*, also correlated to the *R. flexuosa*–*G. cornuta* Assemblage Zone Old Red Sandstone Continent and adjacent areas (Richardson and McGregor 1986).

Melo and Loboziak (2003) defined the *Rugospora radiata* Interval Zone (Rad) and the *Vallatisporites hystricosus* Interval Zone (Hys) in the Amazon Basin as characterized by successive appearances of these eponymous taxa. In the former zone, *Auroraspora macra*, *Diaphanospora rugosa*, *Grandispora cornuta*, *Knoxisporites hederatus*, *Leiotriletes struniensis*, and very rare specimens of *Cyrtozpora cristifera* (see Melo et al. 1996) appear. In the Hys Zone, the inception of *Grandispora facilis* and *Spelaotriletes granulatus* (two characteristic species), also possibly *Retusotriletes incohatus* (an accessory form) was documented, whereas *Retusotriletes loboziaki* is exclusive of *Protosalvinia*-bearing beds, establishing their correlation (Fig. 2).

Our assemblages share 25 species of spores and phytoplankton with the palynofloras studied by Loboziak et al. (1997), such as *Auroraspora macra*,



Fig. 17 (continued) and stereoscope (right); (f–i) piece of rock with several fairly complete specimens pictured with stereoscope in the rock surface, later removed with HF (j–l) and pictured with SEM (m–o); (p) detail of a cuticle illustrated using a microscope with white and fluorescent lights (see square in d)

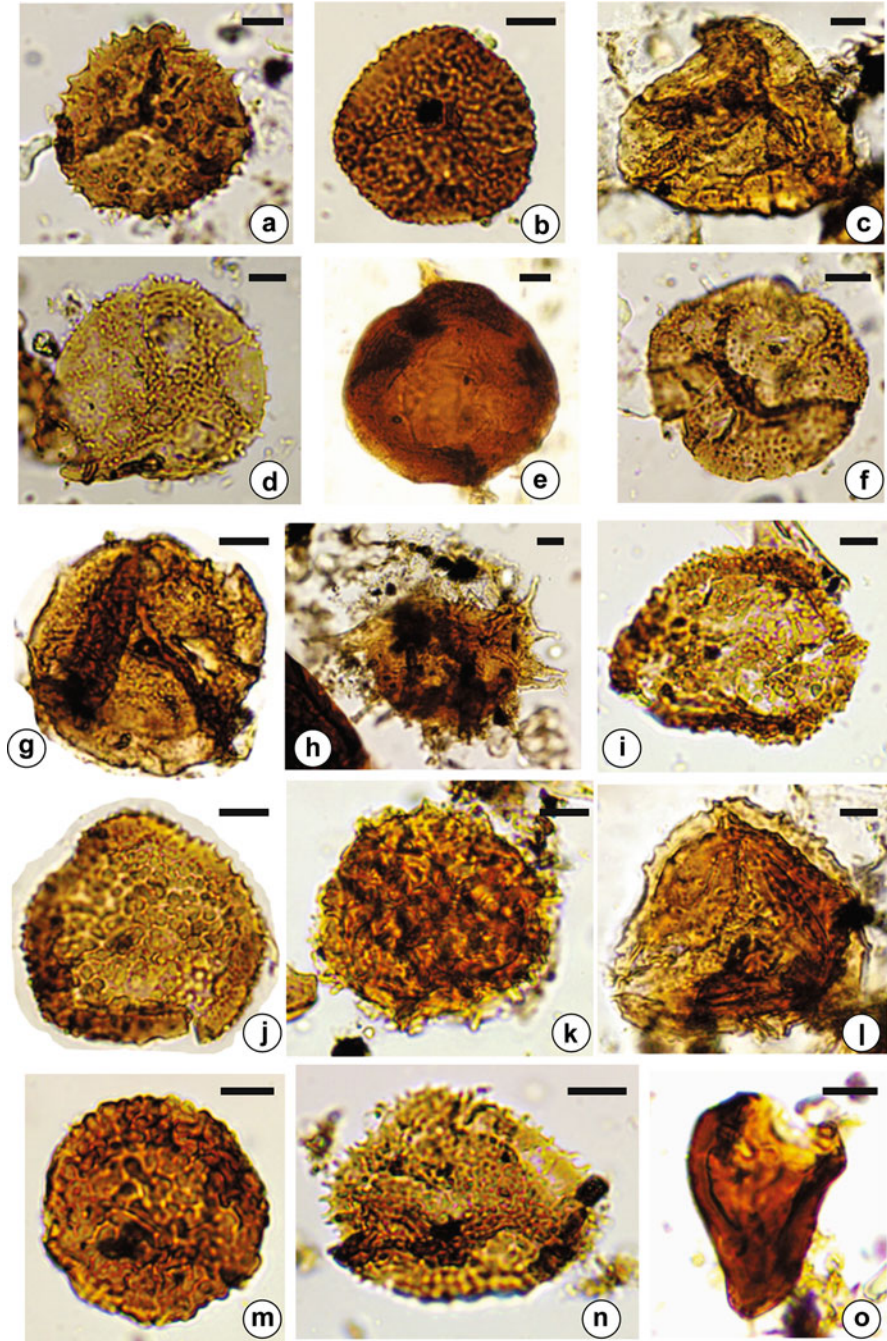


Fig. 18 Palynomorphs associated to *Protosalvinia* remains from the Barreirinha Formation: (a) *Acinosporites eumammillatus* Loboziak, Strel et Burjack. MP-Pb 5132-1 G48; (b) *Acinosporites ledundae* Ottone. MP-Pb 5132-1 R29; (c) *Archaeozonotriletes columnus* Allen. MP-Pb 5133-1

Archaeozonotriletes variabilis, *Chelinospora timanica*, *Cristatisporites imperpetuus*, *Cymbosporites magnificus*, *Geminospora lemurata*, *G. piliformis*, *G. punctata*, *Leiotriletes struniensis*, *Retusotriletes loboziakii*, *Rugospora radiata-flexuosa*, *Samarisporites triangulatus*, *Teichertospora torquata*, *Tumulispora rarituberculata*, various species of *Cymbosporites*, *Lophozonotriletes*, and phytoplankton *Horologinella quadrispina*, *Mediocorpe conspicuo* (still endemic of this basin), *Navifusa bacilla*, *Umbellasphaeridium deflandrei* and *saharicum*, and species of *Maranhites*, *Pterospermella*, and *Verhyachium*. Some species in our assemblages are documented globally in the mid–late Famennian, such as *Grandispora echinata*, *Convolutispora ampla*, *Cordylosporites glumaceus*, *Endoculeospora setaceae*, *Leiotriletes struniensis*, *Retusotriletes loboziakii*, *Rugospora radiata-flexuosa*, *Teichertospora torquata*, *Tumulispora rarituberculata*, and *Verrucosisporites depressus*, whereas others are mostly recorded in Gondwana, e.g., *Umbellasphaeridium deflandrei* and *saharicum*, *Multipliscisphaeridium escobaides*, *Orygmahapsis pachyderma*, *Papulogabata annulata*, *Horologinella quadrispina*, and a few ones from the latest Devonian Rlep Zone of Australia (*Apiculatisporis morbosus*, *Stenozonotriletes forticulus*) and Euramerica (*Microreticulatisporites araneum*) (see Balme and Hassell 1962, Playford and McGregor 1993, Playford and Melo 2012, and di Pasquo et al. 2017).

Therefore, the frequent presence of *Rugospora radiata*, *Retusotriletes loboziaki*, *Apiculiretusispora verrucosa* and rare *Cristatisporites imperpetuus*, *Teichertospora torquata*, and *Mediocorpe conspicuo* in our assemblages would reinforce the constraint of the *Protosalvinia*-bearing assemblages to the Hys Zone, correlated with VH Zone (Maziane et al. 1999), equivalent to the upper VCo Zone Strel et al. (1987) (Fig. 2). It is noted that the absence of *Vallatisporites hystricosus* in our assemblages coincides with the fact that some sections attributed to the Hys Zone also lack this taxon, probably due to *Vallatisporites*-producing plants may have been facies-sensitive in their spatial distribution (cf. Strel and Scheckler 1990, Loboziak et al. 1997, Strel et al. 2000, Melo and Loboziak 2003). Besides, Strel and Marshall (2007) and Rooney et al. (2013) considered that the splitting of the VCo Zone sensu Strel et al. (1987) into VCo–VH zones proposed by Maziane et al.



Fig. 18 (continued) B33–1; **(d)** *Apiculatisporis morbosus* Balme et Hassell. MP-Pb 5133–1 Q62–1; **(e)** *Archaeozonotriletes variabilis* Naumova emend. Allen. MP-Pb 5133–1 M53–3; **(f)** *Apiculiretusispora verrucosa* (*fructicosa*) (Caro-Moniez) Strel in Becker et al. MP-Pb 5132–1 E37–2; **(g)** *Auroraspora macra* Sullivan. MP-Pb 5133–1-roca G23; **(h)** *Ancyrospora langi* (Taugourdeau-Lantz) Allen. MP-Pb 5133–1-roca G21; **(i)** *Bascaudaspora* cf. *collicula* (Playford) Higgs et al. MP-Pb 5133–1 Y18; **(j)** *Cymbosporites cyathus* Allen. MP-Pb 5133–1 H59; **(k)** *Cordylosporites glumaceus* (Byvsheva) Playford et Melo. MP-Pb 5133–2 N15–4; **(l)** *Craspedispora paranensis* Loboziak, Strel et Burjack. MP-Pb 5133–1 Y51–4; **(m)** *Convolutispora ampla* Hoffmeister, Staplin et Malloy. MP-Pb 5133–1 R16; **(n)** *Cristatisporites imperpetuus* (Sennova) Obukhovskaya. MP-Pb 5133–1 X16; and **(o)** *Cyrtoispora cristifera* (Luber et Waltz) emend. Van der Zwan. MP-Pb 5133–2 H20–2. Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 μ m unless specified.

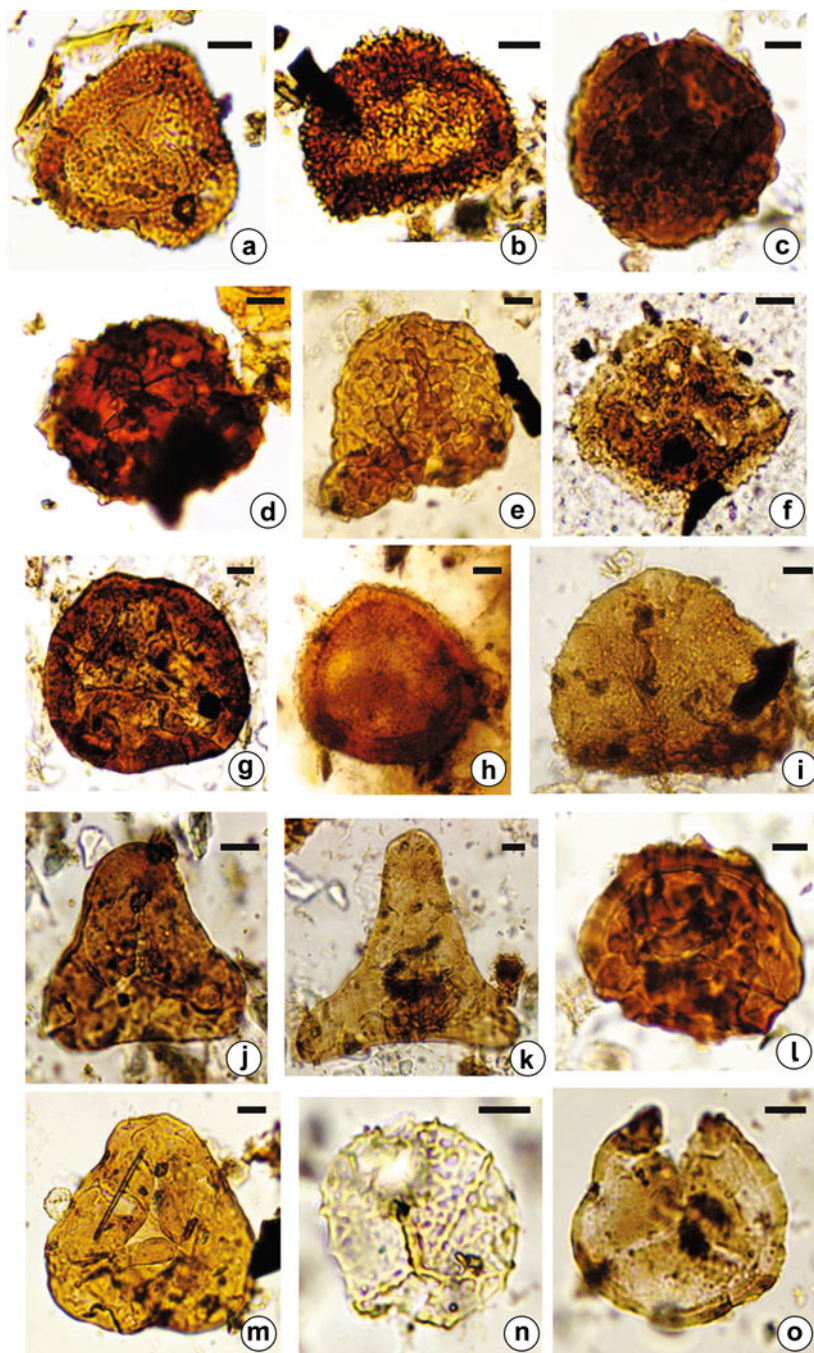


Fig. 19 Palynomorphs associated to *Protosalvinia* remains from the Barreirinha Formation: (a) *Cymbosporites catillus* Allen. MP-Pb 5133-2 G23-2; (b) *Cymbosporites magnificus* (McGregor) McGregor et Camfield. MP-Pb 5133-1 Y25-4; (c) *Chelinospora timanica* (Naumova)

(1999, 2002) is controversial due to a poor correlation at long distances such as between Belgium and North America.

Finally, the Hys Zone was correlated to the *Fungochitina ultima* Zone of Grahn (2005) for Western Gondwana (see also Grahn et al. 2003, 2006), although the lack of chitinozoans in our assemblages does not allow confirming this correlation.

Paleoenvironment Interpretation of the Protosalvinia Interval

Many studies attempted to define the biological affinity of *Protosalvinia* and its paleoecological information for the interpretation of depositional paleoenvironments. Niklas et al. (1976) provided morphological and chemical data from *Protosalvinia* of the Amazon Basin to clarify the ontogeny and taxonomy of the various forms, particularly *P. braziliensis* and *P. bilobata*, which are comparable to those reported from vertical analyses of North American specimens (Phillips et al. 1972, Niklas and Phillips 1976). Their study in the Amazon Basin concluded that all forms of *Protosalvinia* can be interpreted as ontogenetic stages and ecotypes of one single valid species (*P. braziliensis*).

The biological affinity of *Protosalvinia* is still problematic as there are different opinions on whether this is a vascular plant or related to brown algae Phaeophyta (Niklas and Phillips 1976, Romankiw et al. 1988, Mastalerz et al. 1998). The morphology and mode of reproduction of these reproductive structures and organic geochemistry in the fossil record are quite unique. The presence of tetrads of spores does not unequivocally confirm *Protosalvinia* as a land plant because some red and brown algae also produce spores and eggs morphologically similar, but the similarity does not extend to the ultrastructural level. The spores preserved a wall ultrastructure that suggests they result from meiosis, even though they do not appear to have been constructed of sporopollenin (Taylor and Taylor 1987).

Concerning its paleoecological affinity, there is evidence that supports both marine (Schopf 1978) and coastal/littoral habitats (Gray and Boucot 1979, Gutschick and Sandberg 1991). The biomolecular signature is neither distinctly marine nor terrestrial (Mastalerz et al. 1998). Niklas et al. (1976) supported that geometrically changes of *Protosalvinia*, such as radially and bilaterally symmetrical forms, are likely due to paleoecological adaptations to areas of high mechanical activity and areas of low light intensity and/or low nutrient influx, respectively, in littoral



Fig. 19 (continued) Loboziak et Streele. MP-Pb 5132-1 G44; **(d)** *Chelinospora ligurata* Allen. MP-Pb 5133-1 V27-1; **(e)** *Convolutispora tegula* Allen. MP-Pb 5133-1 J23-1; **(f)** *Endoculeospora setaceae* (Kedo) Avkhimovitch et Higgs in Avkhimovitch et al. MP-Pb 5132-1 Z17; **(g)** *Geminospora punctata* Owens. MP-Pb 5132-1 C20; **(h)** *Geminospora piliformis* Loboziak et al. MP-Pb 5133-1-roca N29; **(i)** *Grandispora echinata* Hacquebard. MP-Pb 5133-1 D56; **(j)** *Granulatisporites* sp. MP-Pb 5132-1 K27-3; **(k)** *Leiotriletes struniensis* Moreau-Benoit. MP-Pb 5132-1 R17; **(l)** *Lophozonotriletes media* Taugourdeau-Lantz. MP-Pb 5133-3 55-105 K57; **(m)** *Leiotriletes* sp. cf. *L. balapucensis* di Pasquo. MP-Pb 5133-1 X20; **(n)** *Microreticulatisporites araneum* Higgs et al. MP-Pb 5133-1 G28-3; and **(o)** *Retusotriletes crassus* Clayton et al. MP-Pb 5132-2 K34-4. Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 μ m unless specified.

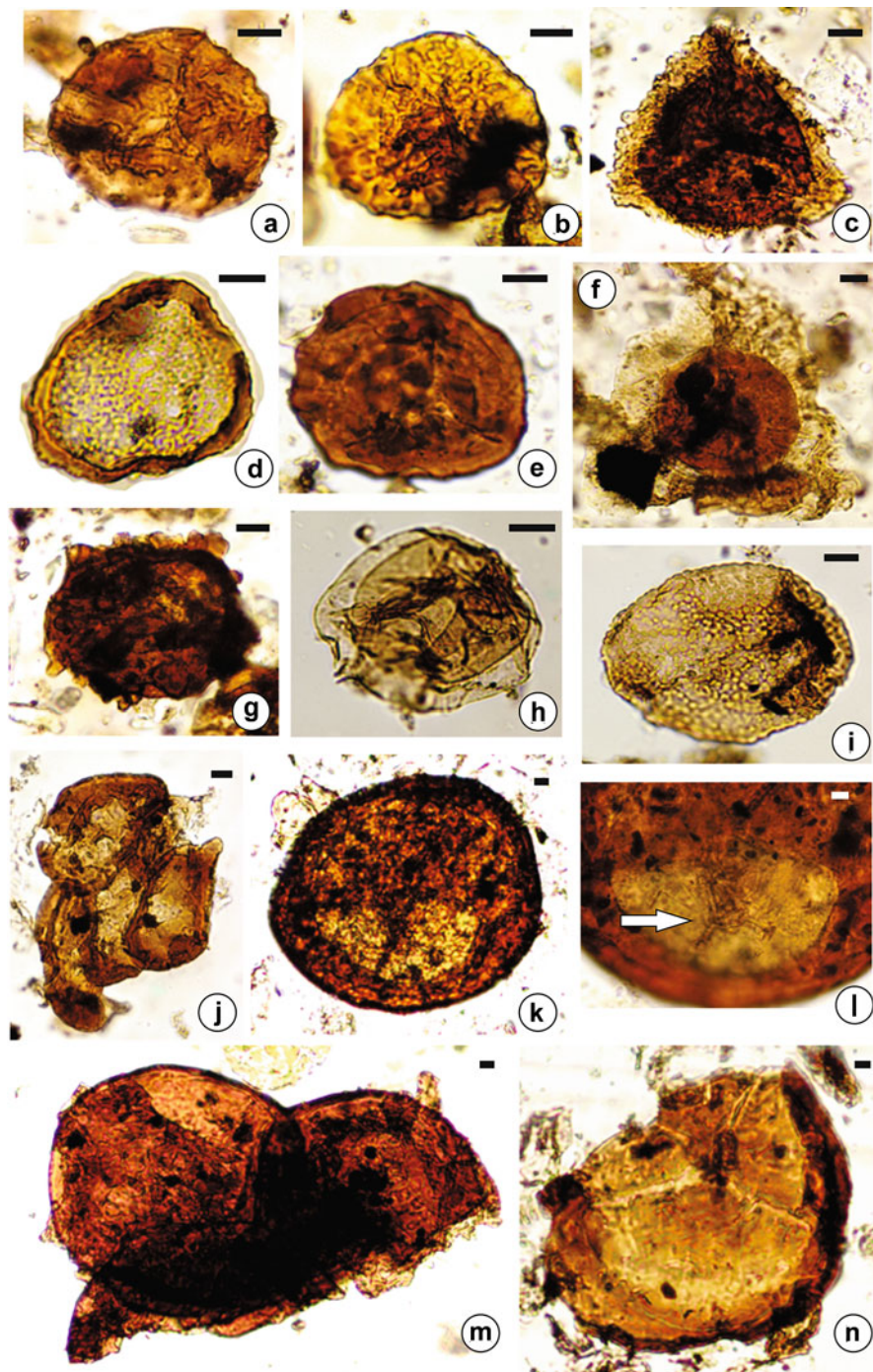


Fig. 20 Palynomorphs associated to *Protosalvinia* remains from the Barreirinha Formation: (a) *Rugospora flexuosa* (Juschko) Bivsheva. MP-Pb 5132-1 K25-5; (b) *Rugospora radiata*

habitats. The heavy exine of the spore *Retusotriletes loboziakii* associated with *Protosalvinia* (see Rooney et al. 2013) was interpreted by Niklas and Phillips (1976) as an adaptation to resist the periodic desiccation of a possible littoral habitat. Gutschick and Sandberg (1991) interpreted that the floating tropical plant *Protosalvinia* occurred in three progressively greater blooms or spikes, associated with correspondingly greater, probable glacio-eustatic sea-level rises related to interglacial stages of Southern Hemisphere glaciation.

The information obtained from our *Protosalvinia* interval composed of an alternation of thin shale layers with fine sandstones bearing current structures allows us to interpret its environment of deposition as follows. *Protosalvinia* remains are mostly preserved as complete and broken compressions. The two palynoassemblages are composed of fairly well-preserved phytoplanktonic and spores species in similar frequency, pyrite in the exines of palynomorphs, AOM (with yellow-light orange fluorescence of algal origin and dark orange to black fluorescence of terrestrial source), and phytoclasts (most derived from *Protosalvinia*). These features support brackish to shallow marine environments of deposition with low oxygen content in the shales at the bottom. *Protosalvinia* remains could be interpreted as a living plant in the depocenter, although short transport across the shelf cannot be discarded from very close areas (brackish coastal swamps) as the terrestrial input is relatively abundant.

The Devonian Paleobotanical Record from Brazil: Historical Review

A historical review of the reports and descriptions of the Devonian plants in Brazil accounts for a total of 25 genera; 18 genera are restricted to Early Devonian, 6 genera occurred in late Early Devonian to early Late Devonian, and 1 occurred in the latest Devonian (Fig. 15). They are unequally distributed among the Paraná, Parnaíba, and Amazon basins (Table 2).

Fig. 20 (continued) (Juschko) Bivsheva. MP-Pb 5133-1 W35-3; (c) *Samarisporites triangulatus* Allen. MP-Pb 5132-2 J27-2; (d) *Stenozonotriletes forticulus* Balme et Hassell. MP-Pb 5133-1 V27-4; (e) *Tumulispota rarituberculata* (Luber) Potonié. MP-Pb 5132-1 O15; (f) *Teichertospora torquata* (Higgs) Foster et Balme. MP-Pb 5132-2 M26-4; (g) *Verrucosisorites scurrus* (Naumova) McGregor et Camfield. MP-Pb 5132-2 N41-4; (h) *Velamisporites perinatus* (Hughes et Playford) Playford. MP-Pb 5133-1-roca T19-4; (i) *Verrucosisorites depressus* Winslow. MP-Pb 5133-1-roca E20-4; (j) *Archaeozonotriletes variabilis* Naumova emend. Allen. MP-Pb 5133-1-roca-Meb C18 (tetrad); (k-n) *Retusotriletes loboziaki* Rooney et al.; (k-l) MP-Pb 5133-1-roca F44; (m) MP-Pb 5133-1 B57; and (n) MP-Pb 5133-1 B13. Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 µm unless specified.

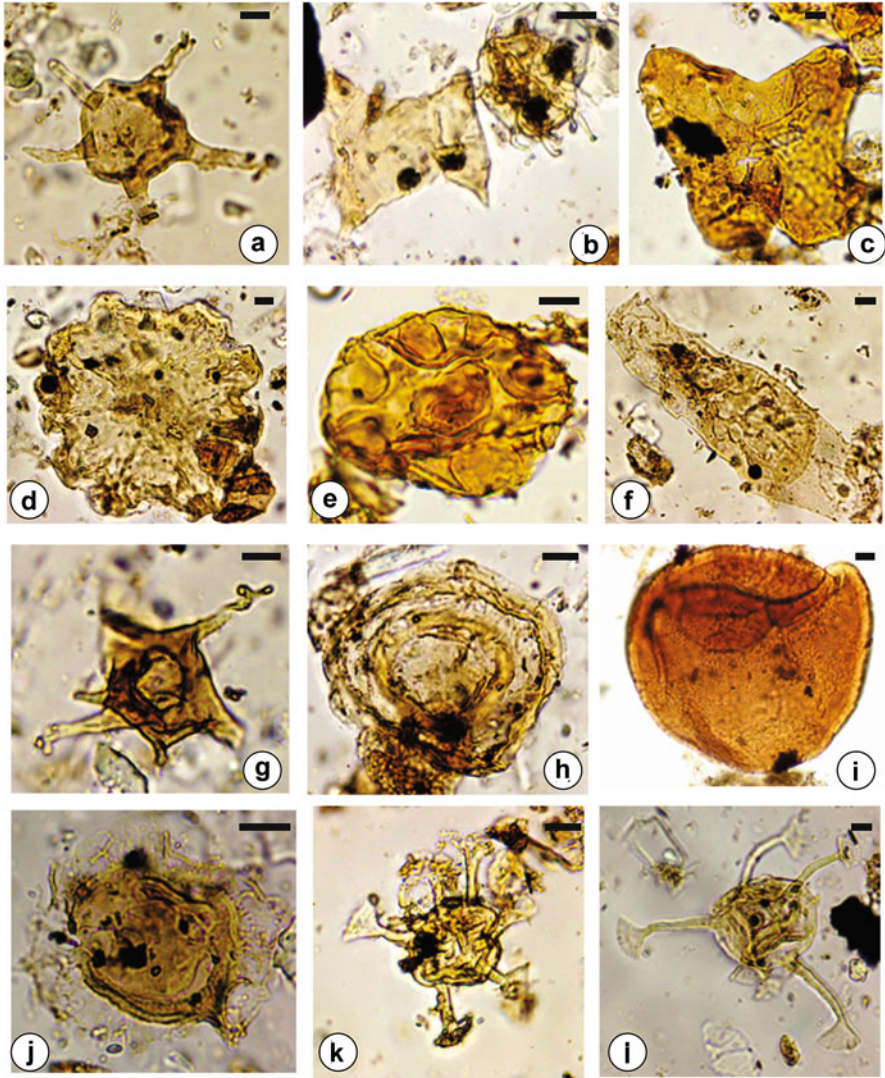


Fig. 21 Palynomorphs associated to *Protosalvinia* remains from the Barreirinha Formation: (a) *Baltisphaeridium* sp. cf. *B. distentum* Playford in Wicander et Playford. MP-Pb 5132-2 Q38-1; (b) *Horologinella quadrispina* Jardiné et al. MP-Pb 5132-1 O16-4; (c) *Horologinella horologia* (Staplin) Jardiné et al. MP-Pb 5133-1 X24; (d) *Maranhites* spp. MP-Pb 5132-2 N44; (e) *Maranhites mosesii* (Sommer) Brito emend. Burjack et Oliveira. MP-Pb 5133-2 J24-2; (f) *Mediacorpe conspicuo* Oliveira ex Loboziak et al. MP-Pb 5132-2 P37; (g) *Multipliscisphaeridium escobaides* (Cramer) Eisenack et Cramer. MP-Pb 5132-1 R19; (h) *Papulogabata annulata* Playford et Dring. MP-Pb 5132-1 E37; (i) *Orygmahapsis pachyderma* Colbath. MP-Pb 5133-1-roca E22-2; (j) *Pterospermella capitata* Wicander. MP-Pb 5132-1 P15; (k-l) *Umbellasphaeridium saharicum* Jardiné et al.; (k) MP-Pb 5133-2 C33; and (l) MP5132-1 N15. Specimens arranged following alphabetical order of genera with England Finder coordinates. Scale bar is 10 μ m unless specified.

Table 2 Plant fossil occurrences in Devonian units in Brazil

Sedimentary basins	Lithostratigraphic units	Ages	Plant fossils	Authors
Amazonas	Barreirinha formation	Late Famennian	<i>Protosabvinia braziliensis</i> ; <i>P. bilobata</i> ; <i>P. arnoldii</i> ; <i>P. ravenna</i> ; <i>P. furcata</i> ; and undetermined plant remains	Rathbun (1874), Dawson (1884, 1886), Sommer (1951, 1962), and Niklas et al. (1976)
	Unnamed	Late Famennian	<i>Protosabvinia arnoldii</i>	Niklas et al. (1976);
Parnaíba	Pimenteira formation	Late Eifelian to early Famennian	<i>Spongiophyton</i> sp.; undetermined plant remains	Andrade Ramos (1957, 1967), Sommer and Van Boekel (1964), and Andrade Ramos and Barbosa (1967)
	Longá formation	Late Famennian	Undetermined plant remains	Duarte (1936), Kegel (1953), and Melo (1988)
	Pimenteira formation	Late Eifelian to early Famennian	<i>Haplostigma</i> sp.; <i>H. furquei</i> ; <i>Protolepidodendron kegelii</i> ; <i>Archaeosigillaria piceensis</i> ; <i>Palaeostigma sewardi</i> ; <i>Spongiophyton</i> sp.; and undetermined plant remains	Kräusel and Dolianiti (1957), Suárez-Riglos (1975), Fonseca and Melo (1987), Melo (1988), Machado and Vasconcelos (2009), Ponciano et al. (2012, and Matsumura et al. 2023 in this chapter)
	Itaim formation	Late Emsian to early Eifelian	<i>Spongiophyton</i> sp.; psilophytes remains	Kegel (1953), Melo (1988), and Souza et al. (2017)
Paraná	Chapada group unit 4	Early Givetian to early Frasnian	<i>Haplostigma</i> sp.; <i>Spongiophyton</i> sp.; and undetermined plant remains	Grahn et al. (2016), Carbonaro and Ghilardi (2016), and Carbonaro et al. (2018)
	Chapada group unit 2	Late Emsian to early Givetian	<i>Spongiophyton nanum</i> ; undetermined plant remains	Melo (1988), Matsumura et al. (2017), and Sedorko et al. (2018b)
	Chapada group unit 1	Lochkovian	Rhyniophyte and psilophyte remains	Quadros and Melo (1986), Schubert and Borghi (1991), and Rodrigues et al. (1995)
Apucarana Sub-Basin	São Domingos formation	Late Emsian to early Frasnian	<i>Haplostigma irregularis</i> ; <i>H. furquei</i> ; <i>H. baldisii</i> ; <i>H. cf. kowiensis</i> ;	Kräusel (1954), Matsumura et al. (2015a, 2016)

(continued)

Table 2 (continued)

Sedimentary basins	Lithostratigraphic units	Ages	Plant fossils	Authors
			<p><i>Spongiophyton lenticulare</i>; <i>S. nanum</i>; <i>S. minutissimum</i>; <i>S. articulatum</i>; <i>Aculeophyton? hirsutum</i>; and undetermined plant remains</p>	
	Ponta Grossa formation	Late Pragian to early Emsian	<p><i>Euzebiola clarkei</i>; <i>Octaviona petrii</i>; <i>Spongiophyton lenticulare</i>; and undetermined plant remains</p>	Barbosa (1949), Sommer (1954)
	Furnas formation	Lochkovian	<p><i>Cooksonia paranensis</i>; <i>C. cf. cambrensis</i>; <i>Aberlemnia caledonica</i>; <i>Pertonella</i> sp. A; <i>Pertonella</i> sp. <i>Psilophyities</i> sp.; <i>Hosinella</i> sp.; <i>Sporogonites</i> sp. A; <i>Tarrantia</i> sp.; <i>Horneophyton</i> sp.; <i>Edwardsnella campanulata</i>; <i>Salopella brasilitana</i>; <i>Sphaerulophyton originalis</i>; and <i>psilophytes</i> remains</p>	Bigarella et al. (1966), Rodrigues et al. (1989), Mussa and Borghi (1993), Mussa et al. (1996, 2002), Gerrienne et al. (2001, 2006, 2022, in this volume), Milagres et al. (2007, 2018), Machado et al. (2007), Grahn et al. (2010a), and Gonez and Gerrienne (2010).

Paraná Basin

In the Paraná Basin (Apucarana Sub-Basin), the first mention of a putative plant fossil “problematicum” was made by Clarke (1913). After, Sommer (1954) redescribed this specimen as an alga *Euzebiola clarkei*. Currently, the plant affinity is not acceptable, and the material is considered a medusozoan cnidarian, *Sphenothallus sica* (see Van Iten et al. 1992, 2019). The other algae also described by Sommer (1954), *Octaviona petrii*, remains valid. Oppenheim (1935) collected and illustrated some Devonian plant remains from Ponta Grossa and Tibagi municipalities and included a brief description of them. Oliveira (1937) illustrated a putative *Lepidodendron* specimen from Ponta Grossa municipality but did not describe it. In the same municipality, Read (1941) cited *Psilophyton* but did not illustrate it. Barbosa (1949) described *Haplostigma lenticulare* from material collected in eastern Bolivia (La Torre Formation, now Limoncito Formation) and pointed out its distribution also in Paraná Basin (Paraná and Mato Grosso states). Kräusel (1954), studying new material from Ponta Grossa municipality, redescribed *Haplostigma lenticulare* as *Spongiophyton lenticulare* (Barbosa) Kräusel 1954, including the species *S. nanum*, *S. minutissimum*, *S. articulatum*, and *S. hirsutum* (now *Aculeophyton? hirsutum* Kräusel and Venkatachala 1966); and also recorded *Haplostigma irregulare*. The subsequent studies focused on plant remains on top of the Furnas Formation in several localities in Paraná state, mainly in Ponta Grossa and Tibagi municipality (Petri 1948, Bigarella et al. 1966). Rodrigues et al. (1989) reported the remains of Psilophytales in Ponta Grossa. Mussa and Borghi (1993) cited a possible occurrence of *Horneophyton*-like plant in Furnas Formation. Bolzon et al. (1994) reported the presence of *Cooksonia* in Ponta Grossa municipality but did not illustrate it. Mussa et al. (1996, 2002) described new taxa of sporophytes, i.e., *Jaguariaivia melloii* Mussa, Borghi, Bergamaschi, Schubert, Pereira et Rodrigues 2002, *Salopella brasiliiana* Mussa, Borghi, Bergamaschi, Schubert, Pereira et Rodrigues 2002 and *Sphaerullophyton originalis* Mussa, Borghi, Bergamaschi, Schubert, Pereira et Rodrigues 2002, a gametangiophore *Edwardsnella campanulata* Mussa, Borghi, Bergamaschi, Schubert, Pereira et Rodrigues 2002, and sterile branched axes (*Sulculiphyton furnasensis* Mussa et al. 2002) from Furnas Formation in Jaguariaíva municipality. Gerrienne et al. (2001) described a new species of *Cooksonia*, named *Cooksonia paranensis*, besides *Pertonella* sp. A, and *Sporogonites* sp. A, among other occurrences. Machado et al. (2007) recorded *C. paranensis* and described some undetermined sterile and fertile stems from new localities of Furnas Formation. Milagres et al. (2007, 2018) described new specimens of *C. paranensis*, *C. cf. cambrensis*, *Edwardsnella campanulata*, *Tarrantia* sp., *Sporogonites* sp., *Hostinella* sp., and *Psilophytites* sp. from Furnas Formation. Gonez and Gerrienne (2010) redescribed *Cooksonia caledonica* as *Aberlemnia caledonica* (Edwards) Gonez et Gerrienne 2010 based on original materials from the UK and Furnas Formation.

Matsumura et al. (2015a) identified several species of *Haplostigma* (*H. irregulare*, *H. furquei*, *H. baldissi*, and *H. cf. kowiensis*) in a new locality from São Domingos Formation (sensu Grahn et al. 2013). Finally, Matsumura et al. (2016)

provided chemical analysis using FTIR in *Spongiophyton lenticulare*, *S. nanum*, and *S. minutissimum* and discussed their biological affinities.

In the northern and northwestern border of the Paraná Basin (Alto Garças Sub-Basin), Quadros and Melo (1986) recorded plant remains probably attributed to the Psilophytales in Goiás state. Schubert and Borghi (1991) also recorded undetermined plant remains and ichnofossils in Chapada dos Guimarães region, Mato Grosso state. Rodrigues et al. (1995) reported new plant remains perhaps attributed to the Rhyniophyta group in southwestern Goiás State. All these plant remains were collected from deposits named Furnas Formation but now named Chapada Group Unit 1. In the Chapada Group Unit 2, Sedorko et al. (2018b) described several ichnoassemblages and reported plant fragments from Mato Grosso do Sul State. Matsumura et al. (2017) reported *Spongiophyton nanum* from the Mato Grosso State. In Chapada Goup Unit 4, Grahn et al. (2016), Carbonaro and Ghilardi (2016), and Carbonaro et al. (2018) recorded *Haplostigma* sp. and undetermined plant remains from Goiás State.

Parnaíba Basin

On the eastern border of the Parnaíba Basin (Piauí state), Kegel (1953) and Melo (1988) reported Psilophytales-like remains from the Itaim Formation. In the same unit, Souza et al. (2017) identified *Spongiophyton* sp. in the Pimenteria Formation, and Kräusel and Dolianiti (1957) described *Palaeostigma seawardii*, *Archaeosigillaria picosensis*, *Protolpidodendron kegeli*, and *Spongiophyton* sp., whereas Suárez-Riglos (1975) reported *Haplostigma* sp. without illustration. Machado and Vasconcellos (2009) and Ponciano et al. (2012) also reported *Spongiophyton* sp. and plant debris in the Pimenteira Formation. Duarte (1936), Kegel (1953), and Melo (1988) reported undetermined plant remains from the Longá Formation.

In western border of the Parnaíba Basin, Andrade Ramos (1957, 1967), Sommer and Van Boekel (1964), and Andrade Ramos and Barbosa (1967) reported *Spongiophyton* sp. and plant fragments from Pimenteira Formation in Tocantins state. Niklas et al. (1976) reported *Protosalvinia arnoldii* in radioactive black shales in undesignated core samples from well 2-SL-1-MA.

Amazon Basin

In the Amazon Basin, Dawson (1884, 1886) described *Protosalvinia braziliensis* and *P. bilobata* from Barreirinha Formation (Early Famennian, Curuá Group). Sommer (1962) redescribed and revalidated the species *P. bilobata*. Niklas et al. (1976) described the morphology of all *Protosalvinia* species (*P. braziliensis*, *P. bilobata*, *P. arnoldii*, *P. ravenna*, and *P. furcata*) and interpreted the paleoecology of the *Protosalvinia*. According to those authors, all forms of *Protosalvinia* are ontogenetic stages and/or ecotypes of *P. braziliensis*. Dolianiti (1967) described a new species of lycopsid from Curuá Group, named *Lycopodites amazonica*. The material was found

between 2041 and 2044 m deep in the 1-RX-4-AM borehole. However, the later biostratigraphic reassessment by Melo and Loboziak (2003) repositioned this interval in the upper part of the Oriximiná Formation (Early Carboniferous).

Phytostratigraphy and Floral Stages in the Devonian of Brazil

Up to now, only herbaceous plants have been described in the Devonian of Brazil. The lycopsid *Haplostigma* and the enigmatic land plants *Spongiophyton lenticulare* (sensu Matsumura et al. 2016) and *Protosalvinia* (sensu Gray and Boucot 1979) seem to withstand cool temperatures at high to medium latitude, where terrestrial environments were free of ice (Gerrienne et al. 2001, 2006, Milagres et al. 2018).

The type of preservation (taphonomic) of the Devonian paleobotanical record of Brazil is similar to other South American occurrences (Di Pasquo and Noetinger 2008, Di Pasquo et al. 2009, Edwards et al. 2001, 2009). In general, they are preserved as highly fragmented plant debris deposited in shallow marine environments, where the wave energy contributed to their reworking and transport to deeper zones (Martins et al. 2018). This fact, associated with the low preservation potential of early land plants, prevents a reliable taxonomic identification, even at the generic level (Matsumura and Iannuzzi 2013).

Despite this preservation bias, the high biostratigraphic resolution based on the palynological record of the Devonian lithostratigraphic units allowed a reliable correlation among the three sedimentary basins, as well as the stratigraphic positioning of the fossil plants (Loboziak and Melo 2002, Melo and Loboziak 2003, Mendlowicz Mauller et al. 2009, Breuer and Grahn 2011, Grahn et al. 2006, 2008, 2010a, b, 2013, 2016). Our palynologic results corroborate the age of the *Haplostigma*–*Spongiophyton* and *Protosalvinia* depicted in Fig. 2. Berry and Fairon-Demaret (2001) provided a synthesis of the Middle–early Late Devonian Flora from Laurussia, including North America, Europe, and Northwest Venezuela. According to the authors, the Middle Devonian plant community was composed of bushy aneurophytalean (*Aneurophyton*) and archaeopteridalean (*Svalbardia*) progymnosperms, herbaceous lycopsids (*Haskinsia* and *Leclercqia*), cladoxylopsids (*Cladoxylon* and *Pseudosporochnus*), iridopteridaleans (*Anapaulia* and *Ibyka*), and zosterophylls (*Serrulacaulis*). This association of plants is an intermediary between the Siluro–Devonian dominated by zosterophyll, rhyniophyte, and trimerophyte groups and Late Devonian composed of rhizomorphic lycopsids, sphenopsids, early putative ferns, and first seed plants as proposed by DiMichele and Bateman (1996).

Therefore, qualitative differences and similarities of the plant assemblages and palynofloras described herein compared to those from Gondwana and Euroamerica corroborate the existence of a wide variety of highly diversified paleofloras worldwide reasonably similar to the record in other periods (e.g., Melo and Loboziak 2003, di Pasquo et al. 2009, Grahn et al. 2013, 2016). The dynamic evolution of the floras is a consequence of several factors that triggered paleogeographic and paleobiogeographic changes along the Devonian (e.g., Scotese et al. 1999).

As observed in the abovementioned review, the Devonian plants from Brazil exhibit differences with respect to North American and European records, and even with Venezuela. In this way, based on Matsumura and Iannuzzi (2015) and this compilation, it is possible to recognize three stratigraphic intervals, i.e., the earliest Devonian, late Early Devonian to early Late Devonian, and the Latest Devonian, which correspond to three distinct floristic stages in Brazil: *Cooksonia–Hostinella*, *Spongiophyton–Haplostigma*, and *Protosalvinia*. The stratigraphic range of the 25 genera of plant fossils recorded in Devonian deposits of Brazil (Table 2) supports the recognition of these three floral stages tentatively correlated (Fig. 2) to Devonian plant biozones (Edwards et al. 2000) and spore zonations (Streel et al. 1987, Steemans 1989, Melo and Loboziak 2003).

Floral stage *Cooksonia–Hostinella* (sensu Matsumura and Iannuzzi 2015): Characterized by *Cooksonia*, *Aberlemnia*, *Hostinella*, *Pertonella*, *Psilophyrites*, *Sporogonites*, *Tarrantia*, *Edwardsnella*, *Salopella*, and *Sphaerullophyton*. It comprises avascular (bryophyte) and vascular (tracheophyte) plants bearing simple and herbaceous organization, having leafless stems with dichotomous branching bearing terminal sporangia (polysporangiophytes). This stage is recorded as the earliest Devonian (Lochkovian) age, and plant fossils come from the Furnas Formation and Chapada Group Unit 1 of the Paraná Basin. In South America, some elements (cooksonioid-like axes and *Hostinella*) were also recorded in Argentina (Edwards et al. 2001, 2009, Di Pasquo and Noetinger 2008) and Uruguay (Sprechmann et al. 1993). Also, this stage is equivalent to *Zosterophyllum* and earliest *Gosslingia* (+*Zosterophyllum*) plant zones of Edwards et al. (2000) and equivalent in terms of spore zonation to MN Oppel Zone (Streel et al. 1987, Steemans 1989) and NsZ and earliest Ems Interval Zones (Melo and Loboziak 2003, Di Pasquo and Noetinger 2008).

Floral stage *Spongiophyton–Haplostigma* (sensu Matsumura and Iannuzzi 2015): Characterized by the presence of *Spongiophyton*, *Haplostigma*, *Octaviona*, *Palaeostigma*, *Protolepidodendron*, and *Archaeosigillaria*. It comprises vascular and avascular (thallophytes and nematophytes) plants, which present prostrate, decumbent, or aerial stems, herbaceous or shrub-like habits, and stems bearing microphylls (i.e., lycopsids). This stage spans from late Early Devonian to early Late Devonian (Late Emsian to Early Frasnian) times, being recorded in Ponta Grossa and São Domingos formations and Chapada Group Units 2 and 4 of Paraná Basin (Fig. 2). It also occurs in the Pimenteira and Cabeças formations from Parnaíba Basin. *Haplostigma* is an important Gondwanan element in this stage and has the widest geographic distribution in Argentina (Cingolani et al. 2002, Di Pasquo et al. 2009, 2013, 2015, Noetinger et al. 2018), Bolivia (Di Pasquo et al. 2009, 2015), Chile (Moisan et al. 2011), South Africa (Seward 1932, Plumstead 1967, Anderson and Anderson 1985), Antarctica (Mildenhall and Schopf 1980, McLoughlin and Long 1994), and Australia (McLoughlin and Long 1994). Due to its long stratigraphic amplitude, a future subdivision of this stage would be expected. Lastly, this stage is equivalent to upper *Psilophyton* to lower *Archaeopteris* plant zones of Edwards et al. (2000) and spore zonations from Euramerican upper PoW to BM Oppel Zones (Streel et al. 1987, Steemans 1989), and Brazilian Upper Ems to BPi Interval Zones (Melo and Loboziak 2003).

Floral stage *Protosalvinia*: Characterized by a wide variety of *Protosalvinia* remains with clavate, bilobate, furcate, or rounded shapes bearing rounded reproductive structures enclosing tetrads of spores. This stage is recorded in the latest Devonian, late Famennian, in the Barreirinha Formation (sensu Cunha et al. 2007) of Amazon Basin, and Pimenteira Formation of Parnaíba Basin, recognized but not named by Matsumura and Iannuzzi (2015). Up to now, *Protosalvinia* represents the only record of fossil plants in the Famennian of Brazil, and it is essential to expand its knowledge by exploring new deposits of well-dated lithostratigraphic units (Loboziak et al. 1997, Melo and Loboziak 2003, Over et al. 2009, Rooney et al. 2013). Loboziak et al. (1997) proposed the *Protosalvinia* Zone for late Famennian age based on co-occurrences of *Protosalvinia* sp., and miospores *Rugospora radiata*, *Vallatisporites hystricosus*, *Grandispora facilis*, *Spelaotriletes granulatus*, and *Retusotriletes incohatus* also correlated with the *Protosalvinia* black shale deposits at different localities in eastern USA (Appalachian, Illinois and Michigan basins, Fig. 16) ranging from the VCo Zone (Streel et al. 1987) and VH Zone (Maziane et al. 1999) and the uppermost *marginifera* to Lower *expansa* conodont Zones of Middle to Late Famennian (Over et al. 2009, Rooney et al. 2013). The large-sized, thick wall exine spore illustrated as *Retusotriletes* sp. by Loboziak et al. (1997), recently named *Retusotriletes loboziakii* (Rooney et al. 2013), is documented in all those palynoassemblages as in our study herein, because it derives from *Protosalvinia*. Finally, the floral stage *Protosalvinia* corresponds to the *Protosalvinia* Zone (Loboziak et al. 1997) and the *Vallatisporites hystricosus* Interval Zone of Melo and Loboziak (2003) also equivalent to the lower *Cyclostigma* + *Rhacophyton* plant zone of Edwards et al. (2000) (Figs. 2 and 16).

Paleophytogeographic Considerations

Wnuk (1996) distinguished three great phytogeographic realms through the Devonian, from the northern to the southern Hemisphere: (i) Angara, (ii) Euramerica, and (iii) Gondwana. The Gondwanan Realm was subdivided into the Australian Region (Late Silurian to Late Devonian) and South Gondwanan Region (late Early Devonian to Late Devonian).

During the Early Devonian (Lochkovian), the record of *Cooksonia*, Cooksonioids, and other plant remains occurring in Brazil (Gerrienne et al. 2001, 2006 and this work), Argentina (Edwards et al. 2001, 2009), Bolivia (Di Pasquo and Noetinger 2008), and Uruguay (Sprechmann et al. 1993) demonstrate their appearance in the realm of western Gondwana whereas different floras characterize the Euramerican Realm (Laurussia Region) with *Zosterophyllum* and *Baragwanathia* assemblage from Australia and South China (Hao and Gensel 1998). Based on the similarity between plant assemblages from Laurussia (Wales and Scotland) and Western Gondwana (Bolivia, Argentina, and Brazil), Raymond et al. (2006) proposed a single paleophytogeographic unit called the South Laurussian-Northwest Gondwanan during the Late Silurian to Early Devonian.

In the Middle Devonian, Wnuk (1996) distinguished three Realms based on six phytogeographic units: (i) Kazakhstan Region in Angaran Realm; (ii) Tunguskan, Laurussian, and South China regions in Euramerican Realm; and (iii) Australian and South Gondwanan regions in Gondwana Realm. Based on miospores, Streele and Loboziak (1996) defined three phytogeographical provinces for the Middle and Late Devonian: (i) Northern Euramerica; (ii) Southern Euramerica–Western Gondwana; and (iii) a possible Eastern Gondwana.

Di Pasquo et al. (2009), based on endemic miospores (at the specific level) and distribution of the “*Haplostigma* flora,” proposed the Afro–South American (ASA) Subrealm for the southwestern part of the South Gondwana Realm during the Middle and early Late Devonian. The ASA Subrealm differs from Laurussia and North-western Gondwana including Venezuela and Colombia plant assemblages in bearing lycophytes *Haskinsia*, *Colpodexylon*, *Gilboaphyton*, *Drepanophycus*, and *Leclercqia* as the most typical elements. In contrast, the high-latitude deposits from southwestern Gondwana, including Argentina, South Bolivia, Brazil, Ghana, South Africa, and Antarctica, are characterized by the presence of the herbaceous lycopsid *Haplostigma* (Di Pasquo et al. 2015, Matsumura et al. 2015a) and some *Spongiophyton*, evidenced from South Bolivia, Brazil, and Ghana. Therefore, Middle–early Late Devonian Brazilian floras show more similarities to other Gondwana regions, such as South America, South Africa, and Antarctica (Fig. 16).

Protosalvinia is the only plant element recorded during the Late Devonian (Famennian) in the Amazon and Parnaíba basins of Brazil and Michigan, Illinois, and Appalachian basins of North America, possibly representing one single floral stage. Although the *Protosalvinia* assemblages could be allochthonous in their deposits (sensu Gray and Boucot 1979), its high abundance, limited stratigraphic range, and wide regional distribution are often associated with the trace fossil *Spirophyton* (= *Zoophycos* isp.) and similar palynological composition bearing the miospore *Retusotriletes loboziakii* (Loboziak et al. 1997, Rooney et al. 2009) and make possible to consider the floral stage *Protosalvinia* as a distinct paleophytogeographic unit (Fig. 16) for Eastern North America–Northwest Gondwana (only Northern Brazil). The closure of the Rheic ocean in Early Devonian times (di Pasquo et al. 2009) triggered the exchange of floras between the Northern and Southern Hemispheres, and this feature is reinforced by the worldwide distribution of Mid–Late Devonian terrestrial palynomorphs, for example, the latest Famennian spore *Retispora lepidophyta* (e.g., McGregor and Playford 1992, Wicander and Playford 2013, and di Pasquo et al. 2017).

Conclusion

The literature revision showed the scarcity of paleobotanical studies in the Devonian of Brazil. Despite recent contributions about Early and Middle Devonian plants, these works are concentrated chiefly on the eastern border of the Paraná Basin. We strongly encourage further study of the plant fossil record in all Devonian units of the Paraná, Parnaíba, and Amazon basins because of the potential already known for

paleofloras from eastern Gondwana (Australia and China), Euramerica, and Kazakhstan areas. We compiled 25 genera of plant fossils from the Devonian of Brazil; some genera are shared at least in two sedimentary basins. The stratigraphic range of the plant fossils allied to palynological zonations allowed the recognition of three floral stages, named *Cooksonia–Hostinella*, *Haplostigma–Spongiophyton*, and *Protosalvinia*. The former shares several taxa with Euramerican and western Gondwanan areas, whereas the *Haplostigma–Spongiophyton* stage seems to be more restricted to the Gondwanan areas. Finally, more palynological studies are needed to have a more comprehensive list of plant groups represented in the floral stages, a better constraint of their stratigraphic intervals, and verify their occurrences in not well explored Brazilian intracratonic basins, such as Parecis, Alto Tapajós, and Jatoba.

Cross-References

► [Earliest Evidence of Land Plants in Brazil](#)

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References

- Albuquerque OR, Dequech V (1946) Contribuição para a geologia do Meio-Norte, especialmente Piauí e Maranhão. Paper presented at the 2nd Congresso Panamericano de Engenharia de Minas e Geologia, Petrópolis, 12–28 October 1946
- Algeo TJ, Scheckler SE, Maynard JB (2001) Effects of the middle to late Devonian spread of vascular land plants on weathering regimes, marine biotas, and global climate. In: Gensel P, Edwards D (eds) *Plants invade the land: evolutionary & environmental perspectives*, Critical moments & perspectives in paleobiology and earth history series. Columbia University Press, New York, pp 213–236
- Anderson JM, Anderson HM (1985) Palaeofloras of southern Africa. *Prodromus of South Africa megafloras, Devonian to lower cretaceous*. Balkema, Rotterdam
- Andrade SM, Camarço PEN (1980) Estratigrafia dos sedimentos devonianos do flanco nordeste da Bacia do Paraná. Paper presented at the 31th Congresso Brasileiro de Geologia, Camboriú, 17–28 October 1980

- Andrade Ramos JR (1957) Novas localidades fossilíferas no setentrão goiano. *Divisão de Geologia e Mineralogia, Notas preliminares e estudos* 99:1–8
- Andrade Ramos JR (1967) Estratigrafia da região Xingú–Tocantina. Paper presented at the 1st Simpósio sobre a Biota Amazônica, Belém, 6–11 June 1966
- Andrade Ramos JR, Barbosa O (1967) Geologia e Petrografia de Porto Nacional a Miracema do Norte, Rio Tocantins. Paper presented at the 1st Simpósio sobre a Biota Amazônica, Belém, 6–11 June 1966
- Assine ML (1999) Fácies, icnofósseis, paleocorrentes e sistemas deposicionais da Formação Furnas no flanco sudeste da Bacia do Paraná. *Revista Brasileira de Geociências* 29(3):357–370
- Assine ML (2001) O ciclo Devoniano na Bacia do Paraná e correlações com outras Bacias Gondwânicas. In: Melo JHG, Terra GJS (eds) *Correlação de seqüências paleozóicas sulamericanas, Ciência-Técnica-Petróleo, Seção Exploração de Petróleo*, vol 20, pp 55–62
- Balme BE, Hassell CW (1962) Upper Devonian spores from the Canning Basin, Western Australia. *Micropaleontology* 8:1–28
- Barbosa O (1949) Vegetais fósseis do Devoniano do Brasil e da Bolívia. *Mineração e Metalurgia* 15:81–84
- Barbosa RCM, Nogueira ACR, Domingos FHG (2015) Famennian glaciation in the eastern side of Parnaíba Basin, Brazil: evidence of advance and retreat of glacier in Cabeças formation. *Brazilian Journal of Geology* 45(Suppl 1):13–27. <https://doi.org/10.1590/2317-4889201530147>
- Becker RT, House MR (2000) Devonian ammonoid zones and their correlation with established series and stage boundaries. In: Bultynck P (ed) *Subcommission on Devonian stratigraphy: fossil groups important for boundary definition*. Courier Forschungsinstitut Senckenberg, vol 220. E. Schweizerbart Science Publishers, Stuttgart, pp 113–151
- Becker RT, Gradstein FM, Hammer O (2012) The Devonian period. In: Gradstein FM, Ogg JG, Schmitz M, Ogg G (eds) *The geologic time scale 2012*. Elsevier, Amsterdam, pp 559–601. <https://doi.org/10.1016/B978-0-444-59425-9.00022-6>
- Bergamaschi S, Pereira E (2001) Caracterização de seqüências deposicionais de 3ª ordem para o Siluro–Devoniano na Sub-Bacia de Apucarana, Bacia do Paraná, Brasil. In: Melo JHG, Terra GJS (eds) *Correlação de seqüências paleozóicas sulamericanas, Ciência-Técnica-Petróleo, Seção Exploração de Petróleo*, vol 20, pp 63–72
- Berry CM, Fairon-Demaret M (2001) The middle Devonian Flora revisited. In: Gensel P, Edwards D (eds) *Plants invade the land: evolutionary & environmental perspectives, Critical moments & perspectives in paleobiology and earth history series*. Columbia University Press, New York, pp 120–139
- Bigarella JJ, Salamuni R, Marques Filho PL (1966) Estruturas e texturas da Formação Furnas e sua significação paleogeográfica. *Boletim da Universidade Federal do Paraná. Geologia* 18:1–119
- Blom H, Clack JA, Ahlberg PE et al (2007) Devonian vertebrates from East Greenland: a review of faunal composition and distribution. *Geodiversitas* 29(1):119–141
- Bolzon RT, Assine ML, Guerra-Sommer M (1994) Ocorrência de *Cooksonia* Lang, 1937 na Formação Furnas, Estado do Paraná. In: *Abstract of the 8th Reunião de Paleobotânicos e Palinólogos*, São Paulo. 5–9 Dezembro 1994
- Bosetti EP, Grahn Y, Horodyski RS et al (2011) An earliest Givetian “Lilliput Effect” in the Paraná Basin, and the collapse of the Malvinokaffric shelly fauna. *Paläontol Z* 85(1):49–65. <https://doi.org/10.1007/s12542-010-0075-8>
- Bosetti EP, Grahn Y, Horodyski RS et al (2012) The first recorded decline of the Malvinokaffric Devonian fauna in the Paraná Basin (southern Brazil) and its cause: taphonomic and fossil evidences. *J S Am Earth Sci* 37:228–241. <https://doi.org/10.1016/j.jsames.2012.02.006>
- Boucot AJ, Rowell AJ, Racheboeuf P, Pereira E, Gonçalves de Melo JH, Peixoto de Siqueira L (2001) Position of the Malvinokaffric Realm’s northern boundary (Early Devonian) based on newly discovered brachiopods from the Parecis Basin (Brazil). *J Czech Geol Soc* 46:109–120
- Boureau ME, Pons D (1973) Sur des empreintes végétales devoniennes du Sud de La Bolivie. *Compte Rendus de l’Académie Sciences de Paris, Série D* 276:2151–2153
- Breuer P, Grahn Y (2011) Middle Devonian spore stratigraphy in the eastern outcrop belt of the Parnaíba Basin, northeastern Brazil. *Rev Esp Micropaleontol* 43:19–38

- Brice D, Carls P, Cocks LRM et al (2000) Brachiopoda. In: Bultynck P (ed) Subcommission on Devonian stratigraphy: fossil groups important for boundary definition, Courier Forschungsinstitut Senckenberg, vol 220. E. Schweizerbart Science Publishers, Stuttgart, pp 65–86
- Bultynck P (2007) Limitations on the application of the Devonian standard conodont zonation. *Geological Quarterly* 51(4):339–344
- Caplan ML, Bustin RM (1999) Devonian–Carboniferous Hangenberg mass extinction event, widespread organic-rich mudrock and anoxia: causes and consequences. *Palaeogeogr Palaeoclimatol Palaeoecol* 148:187–207. [https://doi.org/10.1016/S0031-0182\(98\)00218-1](https://doi.org/10.1016/S0031-0182(98)00218-1)
- Caputo MV (1985) Late Devonian glaciation in South America. *Palaeogeogr Palaeoclimatol Palaeoecol* 51:291–317. [https://doi.org/10.1016/0031-0182\(85\)90090-2](https://doi.org/10.1016/0031-0182(85)90090-2)
- Caputo MV, Melo JHG, Streef M et al (2008) Late Devonian and early carboniferous glacial records of South America. In: Fielding CR, Frank TD, Isbell JL (eds) Resolving the late Paleozoic ice age in time and space, Geological Society of America special publication, vol 441, pp 161–173. [https://doi.org/10.1130/2008.2441\(11\)](https://doi.org/10.1130/2008.2441(11))
- Carbonaro FA, Ghilardi RP (2016) Fósseis do devoniano de Goiás, Brasil (Sub-Bacia Alto Garças, Bacia do Paraná). *Papéis Avulsos de Zoologia (São Paulo)* 56(11):135–149. <https://doi.org/10.11606/0031-1049.2016.56.11>
- Carbonaro FA, Meira FVE, Leme JDM et al (2016) *Metacryphaeus tuberculatus* and *Metacryphaeus australis* (Trilobita, Phacopida) from the Devonian of the Paraná Basin: taxonomy and paleobiogeography. *Ameghiniana* 53(5):552–564. <https://doi.org/10.5710/amgh.23.06.2016.2966>
- Carbonaro FA, Comniskey JC, Corral HS et al (2018) *Orbiculoidea baini* and *Orbiculoidea excentrica* (Brachiopoda, Discinidae) from the middle Devonian (Alto Garças Sub-Basin, Paraná Basin) of Caiapônia, Goiás (Brazil). *Geologia USP, Série científica* 18(4):11–20. <https://doi.org/10.11606/issn.2316-9095.v18-137847>
- Carozzi VC, Falkenheim FUH, Carneiro RG et al (1975) Análise ambiental e evolução tectônica sinsedimentar da seção siluro–eocarbonífera da bacia do Maranhão. In: *Ciência-Técnica-Petróleo*, vol 7. Seção Exploração de Petróleo, Rio de Janeiro, pp 1–89
- Carrizo HA, Azcuy CL (2015) Floras neodevónicas-eocarboníferas de Argentina. Consideraciones sobre las Fitozonas del Carbonífero Tardío del centro oeste argentino. *Opera Lilloana*, 49:1–292
- Carvalho R (1975) Braquiópodes devonianos da bacia Amazônica: Orthida, Strophomenida, Spiriferida e Terebratulida. *Boletim do Museu Paraense Emílio Goeldi, Geologia* 21:1–35
- Carvalho MGP, Ponciano LCMO (2015) The Devonian trilobites of Brazil: a summary. *J S Am Earth Sci* 64(1):217–228. <https://doi.org/10.1016/j.jsames.2015.10.010>
- Caster KE (1948) Excursão geológica ao Estado do Piauí. *Mineração e Metalurgia* 72:271–272
- Chaloner WG, Mensah MK, Crane MD (1974) Non-vascular land plants from the Devonian of Ghana. *Palaeontology* 17:925–947
- Chlupac I, Feist R, Morzadec P (2000) Trilobites and standard Devonian stage boundaries. In: Bultynck P (ed) Subcommission on Devonian stratigraphy: fossil groups important for boundary definition, Courier Forschungsinstitut Senckenberg, vol 220. E. Schweizerbart Science Publishers, Stuttgart, pp 87–98
- Cingolani CA, Berry CM, Morel E et al (2002) Middle Devonian lycopsids from high southern palaeolatitudes of Gondwana (Argentina). *Geol Mag* 139:641–649. <https://doi.org/10.1017/S0016756802006957>
- Clarke JM (1899) Moluscos devonianos do Estado do Pará, Brasil. *Archivos do Museu Nacional* 10:49–174
- Clarke JM (1913) Fósseis devonianos do Paraná, vol 1. *Monographias do Serviço Geológico e Mineralógico do Brasil*, Rio de Janeiro, pp 1–353
- Cohen KM, Finney SC, Gibbard PL et al (2013) The ICS international chronostratigraphic chart. *Episodes* 36:199–204
- Comniskey JC, Bosetti EP (2017) Discinoids of the Malvinokaffric realm: stratigraphic. *Paleogeographical Distribution and Systematic Review Terr@Plural* 11:175–192. <https://doi.org/10.5212/TerraPlural.v.11i2.0001>
- Comniskey JC, Ghilardi RP (2018) Devonian Tentaculitoidea of the Malvinokaffric realm of Brazil, Paraná Basin. *Palaeontol Electron* 21.2.21A:1–14. <https://doi.org/10.26879/712>

- Costa NMM (1978) Palinologia e correlação estratigráfica de sedimentos paleozoicos do extremo noroeste do estado de Mato Grosso. Paper presented at the 30th Congresso Brasileiro de Geologia, 1–10 November 1978
- Cunha PRC, Melo JHG, Silva OB (2007) Bacia do Amazonas. Boletim de Geociências da Petrobras 15:227–251
- Dawson JW (1884) On rhizocarps in the Paleozoic period. Canadian Record of Science 1:19–27
- Dawson JW (1886) On rhizocarps in the Erian (Devonian) period in America. Bull Chicago Acad Sci 1(9):105–118
- Della Fávera JC (1990) Tempestitos da Bacia do Parnaíba: um ensaio holístico. Phd Thesis., Universidade Federal do Rio Grande do Sul
- Derby OA (1877) Contribuições para a geologia do Baixo Amazonas. Archivos do Museu Nacional 2:77–104
- Derby OA (1879) A contribution to the geology of the lower Amazonas. Proc Am Philos Soc 18 (103):155–178
- di Pasquo MM (2007) Asociaciones palinológicas presentes en las Formaciones Los Monos (Devónico) e Itacua (Carbonífero Inferior) en el perfil de Balapuca, sur de Bolivia. Parte 1. Formación Los Monos. Revista Geológica de Chile 34(1):98–137
- di Pasquo M, Noetinger S (2008) First record of early Devonian (Lochkovian) flora from the Santa Rosa formation – Alarache. Southern Bolivia Geologica Acta 6(2):191–210
- di Pasquo MM, Silvestri L (2014) Las colecciones de Palinología y Paleobotánica del Laboratorio de Palinoestratigrafía y Paleobotánica del Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICYTTP), Entre Ríos, Argentina. Contribuição à RESEPPP “Rede Sul-americana de Coleções e Ensino em Paleobotânica e Palinologia”. Boletín de la Asociación Latinoamericana de Paleobotánica y Palinología 14:39–47
- di Pasquo MM, Vilá J (2019) SEM observation of non-metallized samples in Paleopalynology. M&M-Microscopy & MicroAnalysis Journal 26:149–150
- di Pasquo M, Amenábar CR, Noetinger S (2009) Middle Devonian microfloras and megaflores from western Argentina and southern Bolivia: their importance in the palaeobiogeographical and palaeoclimatic evolution of western Gondwana. In: Königshof P (ed) Devonian change: case studies in palaeogeography and palaeoecology. Geological Society (Special Publications, 314), London, pp 193–213. <https://doi.org/10.1144/SP314.11>
- di Pasquo M, Noetinger S, Starck D et al (2013) Devonian plants – *Haplostigma* Seward – of Argentina and Bolivia: new records, palynoassemblages, and ages. In: Abstract of the 23th Congresso Brasileiro de Paleontologia, Gramado, 13–18 October 2013
- di Pasquo M, Noetinger S, Isaacson P et al (2015) Mid–late Devonian assemblages of herbaceous lycophytes from northern Argentina and Bolivia: Age assessment with palynomorphs and invertebrates and paleobiogeographic importance. J S Am Earth Sci 63:70–83. <https://doi.org/10.1016/j.jsames.2015.06.010>
- di Pasquo MM, Grader GW, Warren A et al (2017) Palynological delineation of the Devonian–Carboniferous boundary, west-central Montana. Palynology, Special Issue in honor of Gordon Wood 41(sup1):189–220. <https://doi.org/10.1080/01916122.2017.1366180>
- DiMichele WA, Bateman RM (1996) Plant palaeoecology and evolutionary inference: two examples from the Paleozoic. Rev Palaeobot Palynol 90(3–4):223–247. [https://doi.org/10.1016/0034-6667\(95\)00085-2](https://doi.org/10.1016/0034-6667(95)00085-2)
- Dolianiti E (1967) Uma licopodiácea do Devoniano do Amazonas. Paper presented at the 1st Simpósio sobre a Biota Amazônica, Belém, 6–11 June 1966
- Driese SG, Mora CI (2001) Diversification of Siluro–Devonian plant traces in paleosols and influence on estimates of paleoatmospheric CO₂ levels. In: Gensel P, Edwards D (eds) Plants invade the land: evolutionary & environmental perspectives, Critical moments & perspectives in paleobiology and earth history series. Columbia University Press, New York, pp 237–253
- Duarte A (1936) Fósseis da sondagem de Therezina, estado do Piauí. Serviço Geológico e Mineralógico, Notas preliminares e Estudos 2:1–16
- Edwards D (1990) Constraints on silurian and early devonian phytogeographic analysis based on megafossils. Palaeozoic Palaeogeography and Biogeography. In: McKerrow WS, Scotese CR (Eds.), Geol Soc Lond Mem 12:233–242

- Edwards D, Berry CM (1991) Silurian and Devonian. In: Cleal CJ (ed) Plant fossils in geological investigation: the Palaeozoic. Ellis Horwood, Chichester, pp 117–153
- Edwards D, Richardson JB (2004) Silurian and lower Devonian plant assemblages from the Anglo-Welsh Basin: a palaeobotanical and palynological synthesis. *Geol J* 39:375–402. <https://doi.org/10.1002/gj.997>
- Edwards D, Fairon-Demaret M, Berry CM (2000) Plant megafossils in Devonian stratigraphy: a progress report. In: Bultynck P (ed) Subcommission on Devonian stratigraphy: fossil groups important for boundary definition, Courier Forschungsinstitut Senckenberg, vol 220. E. Schweizerbart Science Publishers, Stuttgart, pp 25–37
- Edwards D, Morel E, Poiré DG et al (2001) Land plants in the Devonian Villavicencio formation, Mendoza Province, Argentina. *Review of Palaeobotany and Palynology* 116(1–2):1–18. [https://doi.org/10.1016/S0034-6667\(01\)00059-8](https://doi.org/10.1016/S0034-6667(01)00059-8)
- Edwards D, Poiré DG, Morel E et al (2009) Plant assemblages from SW Gondwana: further evidence for high-latitude vegetation in the Devonian of Argentina. In: Basset MG (ed) Early Palaeozoic Peri-Gondwana Terranes: new insights from tectonics and biogeography. Geological Society (Special Publications, 325), London, pp 233–255. <https://doi.org/10.1144/SP325.12>
- Figueroa RT, Machado DMC (2016) Paleoictiofauna da Formação Pimenteira (Devoniano), Bacia do Parnaíba, PI. *Brasil Revista Brasileira de Paleontologia* 19(3):491–504. <https://doi.org/10.4072/rbp.2016.3.13>
- Fonseca VMM, Melo JHG (1987) Ocorrência de *Tropidoleptus carinatus* (Conrad) (Braquiopoda, Orthida) na Formação Pimenteira, e sua importância paleobiogeográfica. Paper presented at the 10th Congresso Brasileiro de Paleontologia, Rio de Janeiro, 19–25 July 1987
- Gensel P, Edwards D (eds) (2001) Plants invade the land: evolutionary & environmental perspectives, Critical moments & perspectives in paleobiology and earth history series. Columbia University Press, New York
- Gensel PG, Chaloner WG, Forbes WH (1991) *Spongiophyton* from the late lower Devonian of New Brunswick and Quebec, Canada. *Palaeontology* 34:149–168
- Gerrienne P, Bergamaschi S, Pereira E et al (2001) An early Devonian flora, including *Cooksonia*, from the Paraná Basin (Brazil). *Rev Palaeobot Palynol* 116:19–38. [https://doi.org/10.1016/S0034-6667\(01\)00060-4](https://doi.org/10.1016/S0034-6667(01)00060-4)
- Gerrienne P, Araújo-Júnior H. de, Bergamaschi S, Milagres I, Oliveira Martins G. de, Pereira E, Rodrigues MA, Rodrigues-Francisco V, Steemans P (2022) Earliest evidence of land plants in Brazil. In: Iannuzzi R, Rößler R, Kunzmann L (Eds.), Brazilian Paleofloras. From Paleozoic to Holocene. Springer Nature Switzerland AG, Print ISBN 978-3-030-22525-4, eReference ISBN 978-3-030-22526-1. https://doi.org/10.1007/978-3-319-90913-4_2-1
- Gerrienne P, Dilcher DL, Bergamaschi S et al (2006) An exceptional specimen of the early land plant *Cooksonia paranensis*, and a hypothesis on the life cycle of the earliest Eutracheophytes. *Rev Palaeobot Palynol* 142:123–130. <https://doi.org/10.1016/j.revpalbo.2006.05.005>
- Góes A, Feijó FJ (1994) Bacia do Parnaíba. *Boletim de Geociências da Petrobras* 8(1):57–67
- Gonez P, Gerrienne P (2010) *Aberlemnia caledonica* gen. et comb. Nov., a new name for *Cooksonia caledonica* Edwards 1970. *Rev Palaeobot Palynol* 163:64–72. <https://doi.org/10.1016/j.revpalbo.2010.09.005>
- Grahn Y (1992) Revision of Silurian and Devonian strata of Brazil. *Palynology* 16:35–61. <https://doi.org/10.1080/01916122.1992.9989406>
- Grahn Y (2005) Devonian chitinozoan biozones of Western Gondwana. *Acta Geol Pol* 55:211–227
- Grahn Y, Bosetti EP (2010) Storm deposited pebble and cobble-sized particles in the early Emsian of the Ponta Grossa formation, Paraná Basin (state of Paraná, Brazil). *Revista Brasileira de Geociências* 40(1):236–241. <https://doi.org/10.25249/0375-7536.2010402236241>
- Grahn Y, Pereira E, Bergamaschi S (2000) Silurian and lower Devonian chitinozoan biostratigraphy of the Paraná Basin in Brazil and Paraguay. *Palynology* 24:143–172. <https://doi.org/10.1080/01916122.2000.9989542>

- Grahn Y, Loboziak S, Melo JHG (2003) Integrated correlation of late Silurian (Pridoli s.l.)–Devonian chitinozoans and miospores in the Solimões Basin, northern Brazil. *Acta Geol Pol* 53:283–300
- Grahn Y, Melo JHG, Steemans P (2005) Integrated chitinozoan and miospore zonation of the Serra Grande group (Silurian–lower Devonian), Parnaíba Basin, Northeast Brazil. *Rev Esp Micro-paleontol* 37:183–204
- Grahn Y, Melo JHG, Loboziak S (2006) Integrated middle and late Devonian miospore and chitinozoan zonation of the Parnaíba Basin, Brazil: an update. *Revista Brasileira de Paleontologia* 9(3):283–294
- Grahn Y, Young C, Borghi L (2008) Middle Devonian chitinozoan biostratigraphy and sedimentology in the eastern outcrop belt of the Parnaíba Basin, northeastern Brazil. *Revista Brasileira de Paleontologia* 11(3):137–146. <https://doi.org/10.4072/rbp.2008.3.01>
- Grahn Y, Mendlowicz Mauller P, Breuer P et al (2010a) The Furnas/Ponta Grossa contact and the age of the lowermost Ponta Grossa formation in the Apucarana Sub-Basin (Paraná Basin, Brazil): integrated palynological age determination. *Revista Brasileira de Paleontologia* 13: 89–102. <https://doi.org/10.4072/rbp.2010.2.02>
- Grahn Y, Mendlowicz Mauller P, Pereira E et al (2010b) Palynostratigraphy of the Chapada group and its significance in the Devonian stratigraphy of the Paraná Basin, South Brazil. *J S Am Earth Sci* 29:354–370. <https://doi.org/10.1016/j.jsames.2009.09.001>
- Grahn Y, Mendlowicz Mauller P, Bergamaschi S et al (2013) Palynology and sequence stratigraphy of three Devonian rock units in the Apucarana Sub-Basin (Paraná Basin, South Brazil): additional data and correlation. *Review of Paleobotany and Palynology* 198:27–44. <https://doi.org/10.1016/j.revpalbo.2011.10.006>
- Grahn Y, Horodyski SC, Mendlowicz Mauller P et al (2016) A marine connection between Parnaíba and Paraná basins during the Eifelian/Givetian transition: review and new data. *Revista Brasileira de Paleontologia* 19(3):357–366. <https://doi.org/10.4072/rbp.2016.3.01>
- Gray J, Boucot AJ (1979) The Devonian land plant *Protosalvinia*. *Lethaia* 12:57–63. <https://doi.org/10.1111/j.1502-3931.1979.tb01243.x>
- Groos-Uffenorde H, Lethiers F, Blumenstengel H (2000) Ostracodes and Devonian stratigraphy. In: Bultynck P (ed) Subcommission on Devonian stratigraphy: fossil groups important for boundary definition, Courier Forschungsinstitut Senckenberg, vol 220. E. Schweizerbart Science Publishers, Stuttgart, pp 99–111
- Gutiérrez PR (1996) Revisión de las licopidas de la Argentina 2. *Malanzania Archangelsky*, Azcuy et Wagner y *Haplostigma* Seward; con notas sobre *Cyclostigma* Haughton. *Ameghiniana* 32 (29):127–144
- Gutiérrez PR, Archangelsky S (1997) *Haplostigma baldisii* sp. nov. (Lycophyta) del Devónico de La Precordillera de San Juan. *Argentina Ameghiniana* 34:275–282
- Gutschick RC, Sandberg CA (1991) Upper Devonian biostratigraphy of Michigan Basin. *Geol Soc Am Spec Pap* 256:155–179
- Hao S, Gensel PG (1998) Some new plant finds from the Posongchong formation of Yunnan, and consideration of a phytogeographic similarity between South China and Australia during the early Devonian. *Sci China Ser D Earth Sci* 41(1):1–13. <https://doi.org/10.1007/BF02932414>
- Hartt CF, Rathbun R (1875) On the Devonian trilobites and mollusks of Eréré, province of Pará, Brazil. *Annals of the Lyceum of Natural History* 11:110–127
- Horodyski RS, Holz M, Grahn Y et al (2014) Remarks on sequence stratigraphy and taphonomy of the Malvinokaffric shelly fauna during the KACÁK event in the Apucarana subbasin (Paraná Basin), Brazil. *Int J Earth Sci* 103:367–380. <https://doi.org/10.1007/s00531-013-0954-9>
- Horodyski RS, Brett CE, Sedorko D et al (2019) Storm-related taphofacies and paleoenvironments of Malvinokaffric assemblages from the lower/middle Devonian in southwestern Gondwana. *Palaeogeogr Palaeoclimatol Palaeoecol* 514:706–722. <https://doi.org/10.1016/j.palaeo.2018.10.001>
- Jaeger H (1979) Devonian Graptolithina. In: House MR (ed) The Devonian system, Special papers in palaeontology, vol 23, pp 335–340
- Jurina AL (2009) Middle Devonian lycophyte *Protolepidodendron scharianum*: history of study and description of the holotype. *Paleontol J* 43:1253–1261

- Katzer F (1897) A fauna devônica do rio Maecurú e as suas relações com a fauna dos outros terrenos devônicos do globo. *Boletim do Museu Paraense* 2:204–246
- Kegel W (1953) Contribuição para o estudo do Devoniano da Bacia do Parnaíba, Brasil. *Boletim da Divisão de Geologia e Mineralogia* 141:1–48
- Kegel W (1961) Restos de um trilobita (?*Homalonotus*) do Devoniano Inferior do Piauí. *An Acad Bras Cienc* 33(2):163–167
- Kräusel R (1954) *Spongyophyton* nov. gen. (Tallophyta) und *Haplostigma* Seward (Pteridophyta) im unter-Devon von Paraná. In: Lange FW (ed) *Paleontologia do Paraná: Comissão de Comemorações do Centenário do Paraná*, Curitiba, pp 195–210
- Kräusel R, Dolianiti E (1957) Restos vegetais das Camadas Picos, Devoniano Inferior do Piauí. *Boletim do Ministério da Agricultura. Departamento Nacional da Produção Mineral, Divisão de Geologia e Mineralogia* 173:7–19
- Kräusel R, Venkatachala BS (1966) Devonische Spongiophytaceen aus Destnud. West-Asien *Senckenbergiana Lethaia* 47:215–251
- Kuglitsch JJ, Taylor WA, Gray J (1998) Non-marine Devonian plants from southeastern Wisconsin. *Geol Soc Am Abstr Programs* 30(7):31
- Leclercq S (1960) Refendage d'une roche fossilifère et dégagement de ses fossiles sous binoculaire. *Senckenb Lethaea* 41:483–487
- Loboziak S, Melo JHG (2002) Devonian miospore successions of Western Gondwana: update and correlation with southern Euramerican miospore zones. *Review of Paleobotany and Palynology* 121:133–148. [https://doi.org/10.1016/S0034-6667\(01\)00098-7](https://doi.org/10.1016/S0034-6667(01)00098-7)
- Loboziak S, Melo JHG, Quadros LP et al (1997) Palynological evaluation of the Famennian *Protosalvinia* (*Foerstia*) zone in the Amazon Basin, northern Brazil: a preliminary study. *Rev Palaeobot Palynol* 96:31–45. [https://doi.org/10.1016/S0034-6667\(96\)00049-8](https://doi.org/10.1016/S0034-6667(96)00049-8)
- Machado LG, Vasconcellos FM (2009) Novas ocorrências de restos vegetais na Formação Pimenteira (Bacia do Parnaíba, Devoniano) do estado do Piauí. Abstract of the 21th Congresso Brasileiro de Paleontologia, Belém, 13–18 September 2009
- Machado LG, Bolzon RT, Azevedo I et al (2007) Primeiras plantas terrestres no Eodevoniano (Formação Furnas) do estado do Paraná, Brasil. In: Carvalho IS, Rodrigues MAC, Cassab RCT (eds) *Paleontologia: cenários de vida*. Interciência, Rio de Janeiro, pp 49–59
- Maisey JG, Melo JHG (2005) Some middle Devonian (Eifelian–Givetian) fossil fish remains from the Pimenteira formation of the Parnaiba Basin, Northeast Brazil. *Arquivos do Museu Nacional* 63:495–505
- Marshall J (2016) Palynological calibration of Devonian events at near-polar palaeolatitudes in The Falkland Islands, South Atlantic. In: Becker RT, Koenigshof P, Brett CE (eds) *Devonian climate, sea level and evolutionary events*. Geological society. Special Publications, London, pp 423–435. <https://doi.org/10.1144/SP423.13>
- Marshall J, Miller MA, Filatoff J et al (2007) Two new middle Devonian megaspores from Saudi Arabia. *Rev Micropaleontol* 50:73–79
- Martins GPO, Rodrigues-Francisco VMC, Rodrigues MAC et al (2018) Are early plants significant as paleogeographic indicators of past coastlines? Insights from the taphonomy and sedimentology of a Devonian taphoflora of Paraná Basin, Brazil. *Palaeogeogr Palaeoclimatol Palaeoecol* 505:234–242. <https://doi.org/10.1016/j.palaeo.2018.05.047>
- Mastalerz M, Hower J, Carmo A (1998) In situ FTIR and flash pyrolysis/GC-MS characterization of *Protosalvinia* (upper Devonian, Kentucky, USA): implications for maceral classification. *Org Geochem* 28:57–66
- Matsumura WMK, Iannuzzi R (2013) Descrição das Bases foliares e micrófilos de *Haplostigma irregularis* (Lycophyta) no Devoniano Médio da Bacia do Paraná. In: Abstract of the 14th Simpósio Brasileiro de Paleobotânica e Palinologia, Rio de Janeiro 13–16 May 2013
- Matsumura WMK, Iannuzzi R (2015) Plantas devonianas do Brasil e seu significado bioestratigráfico. *Boletim do Museu Paraense Emílio Goeldi, Ciências Naturais* 10(1):19–36
- Matsumura WMK, Iannuzzi R, Bosetti EP (2013) Histórico e evolução do conhecimento sobre a paleoflora do Devoniano na Bacia do Paraná. *Terra@Plural* v. 7:25–42. <https://doi.org/10.5212/TerraPlural.v.7iEspecial.0003>

- Matsumura WMK, Iannuzzi R, Bosetti EP (2015a) Middle Devonian herbaceous lycopsid *Haplostigma* from the Paraná Basin, Brazil: taxonomy, biostratigraphy and phytogeography. *Geobios* 48:397–415. <https://doi.org/10.1016/j.geobios.2015.07.001>
- Matsumura WMK, di Pasquo MM, Iannuzzi R (2015b) New paleobotanical and palynological data from Early Givetian in Paraná Basin, southern Brazil. XVI Simposio Argentino de Paleobotánica y Palinología (La Plata, mayo 2015). *Ameghiniana* 52((4) Suplemento 2015, Resúmenes):24
- Matsumura WMK, Iannuzzi R, di Pasquo MM et al (2015c). An early Givetian land plant and palynoassemblage and its biostratigraphical significance. IX Simpósio Sul-Brasileiro de Geologia- II workshop de Recursos Minerais da Região Sul, Florianópolis, Santa Catarina. Abstracts, p 24
- Matsumura WMK, Balzaretto NM, Iannuzzi R (2016) Fourier transform infrared characterization of the middle Devonian non-vascular plant *Spongiophyton*. *Palaeontology* 59(3):365–386. <https://doi.org/10.1111/pala.12230>
- Matsumura WMK, Ghilardi RP, Ribeiro VR et al (2017) Novos registros de *Spongiophyton* no Devoniano do Mato Grosso, MT (sub-Bacia de Alto Garças). In: Abstracts of the 25th Congresso Brasileiro de Paleontologia, Ribeirão Preto, 17–21 July 2017
- Matthews RD (1983) *Foerstia* from the Antrim shale (Devonian) of Michigan. *Geology* 2:327–330. [https://doi.org/10.1130/0091-7613\(1983\)11<327:FFTASD>2.0.CO;2](https://doi.org/10.1130/0091-7613(1983)11<327:FFTASD>2.0.CO;2)
- Maziane N, Higgs K, Strel M (1999) Revision of the late Famennian miospore zonation scheme in eastern Belgium. *J Micropalaeontol* 18:17–25
- Maziane N, Higgs KT, Strel M (2002) Biometry and paleoenvironment of *Retispora lepidophyta* (Kedo) Playford 1976 and associated miospores in the latest Famennian nearshore marine facies, eastern Ardenne (Belgium). *Rev Palaeobot Palynol* 118:211–226
- McGhee GR (2013) When the invasion of land failed: the legacy of the Devonian extinctions. Columbia University Press, New York
- McGregor DC, Playford G (1992) Canadian and Australian Devonian spores: zonation and correlation. *Bulletin of the Geological Survey of Canada* 438:1–125
- McLoughlin S, Long JA (1994) New records of Devonian plants from southern Victoria land, Antarctica. *Geol Mag* 131:81–90. <https://doi.org/10.1017/S0016756800010517>
- Melo JHG (1988) The Malvinokaffric realm in the Devonian of Brazil. In: Mc Millan NJ, Embry AF, Glass DJ (eds) Devonian of the world. Canadian Society of Petroleum Geologists Memoires 1:669–703
- Melo JHG, Loboziak S (2003) Devonian early carboniferous miospore biostratigraphy of the Amazon Basin, northern Brazil. *Rev Palaeobot Palynol* 124:131–202. [https://doi.org/10.1016/S0034-6667\(02\)00184-7](https://doi.org/10.1016/S0034-6667(02)00184-7)
- Melo JHG, Grahn Y, Loboziak S et al (1996) First record of *Fungochitina fenestrata* (Taugourdeau & Jekhowsky 1960) (Chitinozoa) in the Devonian of Brazil and its biostratigraphic significance. *Anais do Simpósio Sul Americano do Siluro–Devoniano: Estratigrafia e Paleontologia*, Ponta Grossa, Paraná, Brasil 1996:263–288
- Mendlowicz Mauller P, Grahn Y, Cardoso TRM (2009) Palynostratigraphy from the lower Devonian of the Paraná Basin, South Brazil, and a revision of contemporary chitinozoan biozones from Western Gondwana. *Stratigraphy* 6:313–332
- Meyer-Berthaud B, Soria A, Decombeix A-L (2010) The land plant cover in the Devonian: a reassessment of the evolution of the tree habit. In: Vecoli M, Clément G, Meyer-Berthaud B (eds) *The Terrestrialization process: modelling Complex Interactions at the biosphere-geosphere Interface*, Geological Society of London special publications, vol 339, pp 59–70. <https://doi.org/10.1144/SP339.6>
- Milagres IM, Pereira E, Bergamaschi S et al (2007) O registro da tafloflora devoniana observada no arco de Ponta Grossa, Bacia do Paraná, e suas implicações paleogeográficas. In: Carvalho IS, Rodrigues MAC, Cassab RCT (eds) *Paleontologia: cenários de vida*. Interciência, Rio de Janeiro, pp 25–48
- Milagres IM, Pereira E, Bergamaschi S et al (2018) Early Devonian Taphoflora record in Ponta Grossa arch, Paraná Basin (southern Brazil) and its palaeogeographic implications. *Journal of Sedimentary Environments* 3(2):93–107. <https://doi.org/10.12957/jse.2018.35405>

- Milani EJ, Faccini UF, Scherer CMS et al (1998) Sequences and stratigraphic hierarchy of the Parana Basin (Ordovician to cretaceous), southern Brazil. *Boletim IG/USP, Série Científica* 29: 125–173
- Milani EJ, Melo JHG, Souza PA et al (2007) Bacia do Paraná. *Boletim de Geociências da Petrobrás* 15(2):265–287
- Mildenhall DC, Schopf JM (1980) A mid-late Devonian flora from the Ruppert Coast, Marie Byrd Land, West Antarctica. *J R Soc N Z* 10:271–285. <https://doi.org/10.1080/03036758.1980.10415333>
- Moisan P, Niemeyer H, Kerp H (2011) Lycopsids from the upper Devonian of northern Chile with remarks on the geographical distribution of the morphogenus *Haplostigma* Seward. *Paläontol Z* 85(3):231–240. <https://doi.org/10.1007/s12542-010-0093-6>
- Morel E, Edwards D, Rodriguez MI (1995) The first record of *Cooksonia* from South America in Silurian rocks from Bolivia. *Geol Mag* 132(4):449–452. <https://doi.org/10.1017/S0016756800021506>
- Mussa D, Borghi L (1993) A presença do gênero *Horneophyton* Barghoorn & Darrah na Formação Furnas, Bacia do Paraná. *An Acad Bras Cienc* 65(2):214–215
- Mussa D, Carvalho IS, Roesler O (1994) Ocorrência de uma planta devoniana na Bacia de Jatobá. In: Abstract of the 8th Reunião de Paleobotânicos e Palinólogos, São Paulo. 5–9 Dezember 1994
- Mussa D, Borghi L, Bergamaschi S et al (1996) Estudo preliminar da tafloflora da Formação Furnas, Bacia do Paraná, Brasil. *An Acad Bras Cienc* 68(1):65–89
- Mussa D, Borghi L, Bergamaschi S et al (2002) New taxa from the Furnas formation, Paraná Basin, Brazil – an approach and revalidation of names. *Bradea* 8(45):303–309
- Niklas KJ, Phillips TL (1976) Morphology of *Protosalvinia* from the upper Devonian of Ohio and Kentucky. *Am J Bot* 63:9–29. <https://doi.org/10.2307/2441665>
- Niklas KJ, Phillips TL, Carozzi AV (1976) Morphology and paleoecology of *Protosalvinia* from the upper Devonian (Famennian) of the middle Amazon Basin of Brazil. *Palaeontographica B* 155: 1–30
- Noetinger S (2015) Spore diversity trends in the middle Devonian of the Chaco-Salteño plain, northwestern Argentina. *Palaeogeogr Palaeoclimatol Palaeoecol* 417:151–163
- Noetinger S, di Pasquo MM, Starck D (2018) Middle–upper Devonian palynofloras from Argentina, systematic and correlation. *Rev Palaeobot Palynol* 257:95–116
- Ogg JG, Ogg GM, Gradstein FM (2016) Devonian. In: Ogg JG, Ogg GM, Gradstein FM (eds) *A concise geologic time scale*. Elsevier, Amsterdam, pp 85–98. <https://doi.org/10.1016/B978-0-444-59467-9.00008-X>
- Oliveira E (1937) Estado actual da Paleobotânica brasileira. *Mineração e Metalurgia* 2(7):7–17
- Oppenheim V (1935) Fósseis devonianos do Paraná. *An Acad Bras Cienc* 7(4):345–348
- Over DJ, Lazar R, Baird GC et al (2009) *Protosalvinia* Dawson and associated conodonts of the upper *Trachytera* zone, Famennian, upper Devonian, in the eastern United States. *J Paleontol* 83 (1):70–79. <https://doi.org/10.1017/S0022336000058133>
- Paris F, Winchester-Seeto T, Boumendjel K et al (2000) Towards a global biozonation of Devonian chitinozoans. In: Bultynck P (ed) *Subcommission on Devonian stratigraphy: fossil groups important for boundary definition*. Courier Forschungsinstitut Senckenberg, vol 220. E. Schweizerbart Science Publishers, Stuttgart, pp 39–55
- Petri S (1948) Contribuição ao estudo do Devoniano paranaense. *Boletim do Departamento Nacional de Produção Mineral, Divisão de Geologia e Mineralogia* 129:1–125
- Phillips TL, Niklas KL, Andrews HN (1972) Morphology and vertical distribution of *Protosalvinia* (*Foerstia*) from the New Albany shale (upper Devonian). *Rev Palaeobot Palynol* 14:171–196
- Playford G, McGregor DC (1993) Miospores and organic-walled microphytoplankton of Devonian-Carboniferous boundary beds (Bakken Formation), southern Saskatchewan: a systematic and stratigraphic appraisal. *Geol Surv Can, Bulletin* 445:1–107
- Playford G, Melo JHG (2012) Miospore palynology and biostratigraphy of Mississippian strata, Amazonas Basin, Brazil (Part One–Part Two). *AASP Foundation Contributions Series No 47*:1–201

- Playford G, Borghi L, Lobato G et al (2012) Palynological dating and correlation of early Mississippian (Tournaisian) diamictite sections, Parnaíba Basin, northeastern Brazil. *Rev Esp Micropaleontol* 44(1–3):1–22
- Plummer FB (1948) Estados do Maranhão e Piauí [States of Maranhão and Piauí]. Brasil, Conselho Nacional do Petróleo, Relatório de 1946. Rio de Janeiro, 87–134
- Plumstead EP (1967) A general review of the Devonian fossil plants found in the cape system of South Africa. *Palaeontol Afr* 10:1–83
- Ponciano LCMO, Della Fávera JC (2009) Flood-dominated fluvio–deltaic system: a new depositional model for the Devonian Cabeças formation, Parnaíba Basin, Piauí, Brazil. *An Acad Bras Cienc* 81(4):769–780. <https://doi.org/10.1590/S0001-37652009000400014>
- Ponciano LCMO, Fonseca VMM, Machado DMC (2012) Taphofacies analysis of late early Givetian fossil assemblages of the Parnaíba Basin (state of Piauí, Northeast Brazil). *Palaeogeogr Palaeoclimatol Palaeoecol* 326–328:95–108. <https://doi.org/10.1016/j.palaeo.2012.02.008>
- Quadros LP, Melo JHG (1986) Ocorrência de restos vegetais em sedimentos continentais do Paleozóico Médio do estado de Goiás. *An Acad Bras Cienc* 58(4):611
- Quijada M, Riboulleau A, Ströther P et al (2016) *Protosalvinia* revisited, new evidence for a land plant affinity. *Rev Palaeobot Palynol* 227:52–64. <https://doi.org/10.1016/j.revpalbo.2015.10.008>
- Racheboeuf PR, Casier J-G, Plusquellec Y, Toro M, Mendoza D, Pires de Carvalho M. da Gloria, Le Hérisse, Paris F, Fernández-Martínez E, Tourneur F, Crasquin S, Janvier P (2012) New data on the Silurian-Devonian paleontology and biostratigraphy of Bolivia. *Bull Geosci* 87(2):269–314
- Rathbun R (1874) On the Devonian Brachiopoda of Ererê, province of Pará, Brazil. *Buffalo Society of Natural Sciences, Bulletin* 1:236–261
- Rathbun R (1879) The Devonian Brachiopoda of the province of Pará, Brazil. *Boston Society of Natural History, Proceedings* 20:14–39
- Raymond A (1987) Paleogeographic distribution of early Devonian plant traits. *PALAIOS* 2(2): 113–132. <https://doi.org/10.2307/3514640>
- Raymond A, Gensel P, Stein WE (2006) Phytogeography of late Silurian macrofloras. *Rev Palaeobot Palynol* 142:165–192. <https://doi.org/10.1016/j.revpalbo.2006.02.005>
- Read CB (1941) Plantas fósseis do Neopaleozóico do Paraná e Santa Catarina. *Monographias do Serviço Geológico e Mineralógico do Brasil* 12:1–102
- Richardson JB, McGregor DC (1986) Silurian and Devonian spore zones of the old red sandstone continent and adjacent regions. *Bulletin of the Geological Survey of Canada* 364:1–79
- Richter M, Bosetti EP, Horodyski RS (2017) Early Devonian (late Emsian) shark fin remains (Chondrichthyes) from the Paraná Basin, southern Brazil. *An Acad Bras Cienc* 89(1):103–118. <https://doi.org/10.1590/0001-3765201720160458>
- Rodrigues MAC, Pereira E, Bergamaschi S (1989) Ocorrência de Psilophytales na Formação Furnas, bordo leste da Bacia do Paraná. *Boletim IG-USP* 7:35–43
- Rodrigues MAC, Dino R, Laranjeira NPF (1995) Nova ocorrência de Rhyniophyta na Formação Furnas no sudoeste de Goiás. *An Acad Bras Cienc* 67(3):384–385
- Romankiw LA, Hatcher PG, Roen JB (1988) Evidence of land plant affinity for the Devonian fossil *Protosalvinia* (*Foerstia*). *Lethaia* 21:417–423. <https://doi.org/10.1111/j.1502-3931.1988.tb01772.x>
- Rooney A, Clayton G, Goodhue R (2013) The dispersed spore *Retusotriletes loboziakii* sp. nov., affiliated with the enigmatic late Devonian alga *Protosalvinia* Dawson 1884. *Palynology* 37(2): 196–201. <https://doi.org/10.1080/01916122.2013.774959>
- Russell DJ (1985) Depositional analysis of a black shale by using gamma-ray stratigraphy: the upper Devonian kettle point formation of Ontario. *Bull Can Petrol Geol* 33:236–253
- Sandberg CA, Hassenmueller NR, Rexroad CB (1994) Conodont biochronology, biostratigraphy, and biofacies of upper Devonian part of the New Albany shale, Indiana. *Cour Forschungsinst Senck* 168:227–253
- Santiago AF, Santos JOS, Maia RGN (1980) Estratigrafia preliminar da Bacia sedimentar do Alto Tapajós. Paper presented at the 31th Congresso Brasileiro de Geologia, Camboriú, 17–28 October 1980

- Scheffler SM (2015) Stalked echinoderms of the Brazilian Devonian and their palaeobiogeographical affinities. *Boletim do Museu Paraense Emílio Goeldi Ciências Naturais* 10(1):63–81
- Scheffler SM, Silva CF, Fernandes ACS et al (2010) Crinóides da borda leste da bacia do Parnaíba (Formação Cabeças, Devoniano Médio). *Boletim do Museu Paraense Emílio Goeldi* 5(2):165–173
- Scheffler SM, Fonseca VMM, Fernandes ACS (2015) New crinoids from the Maecuru formation (middle Eifelian, Amazon Basin, state of Pará, Brazil). 48:57–69. <https://doi.org/10.1016/j.geobios.2014.11.002>
- Scheffler SM, Horodyski RS, Bosetti EP (2018) Morphology, palaeoecology and taphonomy of the Devonian mitrate *Placocystella langei* from Paraná Basin, Brazil. *Alcheringa* 43:228–240. <https://doi.org/10.1080/03115518.2018.1528507>
- Schopf JM (1975) Modes of fossil preservation. *Rev Palaeobot Palynol* 20:27–53. [https://doi.org/10.1016/0034-6667\(75\)90005-6](https://doi.org/10.1016/0034-6667(75)90005-6)
- Schopf JM (1978) *Foerstia* and recent interpretations of early, vascular land plants. *Lethaia* 11:139–143
- Schopf JM, Schwietering JF (1970) The *Foerstia* zone of the Ohio and Chattanooga shales. Contributions to stratigraphy. US Geol Surv Bull 1294-H:1–15
- Schubert G, Borghi L (1991) Sobre a ocorrência inédita de uma tafloflora devoniana na região de Chapada dos Guimarães (Bacia do Paraná – MT). *An Acad Bras Cienc* 63(1):95–96
- Scotese CR, McKerrow WS (1990) Revised world maps and introduction. In: McKerrow WS, Scotese CR (eds) Palaeozoic palaeogeography and biogeography. *Geol Soc Lond Mem* 12:1–21. <https://doi.org/10.1144/GSL.MEM.1990.012.01.01>
- Scotese CR, Boucot AJ, McKerrow WS (1999) Gondwanan palaeogeography and palaeoclimatology. *J Afr Earth Sci* 28:99–114. [https://doi.org/10.1016/S0899-5362\(98\)00084-0](https://doi.org/10.1016/S0899-5362(98)00084-0)
- Sedgwick A, Murchison RI (1836) A classification of the old slate rocks of the north of Devonshire. Report of the British Association for the Advancement of science (Bristol meeting, 1836), p 95–96
- Sedgwick A, Murchison RI (1839) Stratification of the older stratified deposits of Devonshire and Cornwall. *The London and Edinburgh Philosophical Magazine and Journal of Science* 14:241–260
- Sedgwick A, Murchison RI (1840) On the physical structure of Devonshire, and on the subdivisions and geological relations of its older stratified deposits. *Transactions of the Geological Society of London* 5:633–704
- Sedoroko D, Netto RG, Savrda CE et al (2017) Chronostratigraphy and environment of Furnas formation by trace fossil analysis: calibrating the lower Paleozoic Gondwana realm in the Paraná Basin (Brazil). *Palaeogeogr Palaeoclimatol Palaeoecol* 487:307–320. <https://doi.org/10.1016/j.palaeo.2017.09.016>
- Sedoroko D, Netto RG, Savrda CE (2018a) Ichnology applied to sequence stratigraphic analysis of Siluro–Devonian mud-dominated shelf deposits, Parana Basin, Brazil. *J S Am Earth Sci* 83:81–95. doi: <https://doi.org/10.1016/j.jsames.2018.02.008>
- Sedoroko D, Bosetti EP, Ghilardi RP et al (2018b) Palaeoenvironments of a regressive Devonian section from Paraná Basin (Mato Grosso do Sul state) by integration of ichnologic, taphonomic and sedimentologic analyses. *Brazilian Journal of Geology* 48(4):805–820. <https://doi.org/10.1590/2317-4889201820180021>
- Seward AC (1932) Fossil plants from the Bokkeveld and Witteberg beds of South Africa. *Q J Geol Soc Lond* 88:358–369. <https://doi.org/10.1144/GSL.JGS.1932.088.01-04.15>
- Shear WA, Selden PA (2001) Rustling in the undergrowth: animals in early terrestrial ecosystems. In: Gensel P, Edwards D (eds) *Plants invade the land: evolutionary & environmental perspectives, Critical moments & perspectives in Paleobiology and Earth History Series*. Columbia University Press, New York, pp 29–51
- Silva RC, Dominato VG, Fernandes ACS (2012) Novos registros e aspectos paleoambientais dos icnofósseis da Formação Pimenteira, Devoniano da Bacia do Parnaíba, Piauí. *Brasil Gaea* 8(1): 33–41. <https://doi.org/10.4013/gaea.2012.81.05>

- Simões MG, Leme JM, Soares SP (2009) Systematics, taphonomy, and paleoecology of homalonotid trilobites (Phacopida) from Ponta Grossa formation (Devonian), Paraná Basin. *Brazil Revista Brasileira de Paleontologia* 12(1):27–42. <https://doi.org/10.4072/rbp.2009.1.03>
- Sommer FW (1951) O problema de *Protosalvinia braziliensis* Dawson. *An Acad Bras Cienc* 23: 415–419
- Sommer FW (1954) Contribuição a Paleofitogeografia do Paraná. In: Lange FW (ed) *Paleontologia do Paraná: Comissão de Comemorações do Centenário do Paraná*, Curitiba, 175–194
- Sommer FW (1962) On *Protosalvinia bilobata* DAWSON from the Devonian of Pará and its taxonomic situation. *An Acad Bras Cienc* 34:465–475
- Sommer FW, Van Boekel NM (1964) Quitinozoários do Devoniano de Goiás. *An Acad Bras Cienc* 36(4):423–431
- Souza IR, Santos JM, Rodrigues KC et al (2017) Primeira ocorrência de *Spongiophyton* sp. na Formação Itaim (Devoniano), da Bacia do Parnaíba em Itainópolis, Piauí. In: Abstracts of the 25th Congresso Brasileiro de Paleontologia, Ribeirão Preto, 17–21 July 2017
- Sprechmann P, Montaña J, Gaucher C (1993) Devónico. In: Bossi J (ed) *Geología y recursos minerales del departamento de Durazno*. Intendencia Municipal de Durazno, Montevideo, pp 25–55
- Stemans P (1989) Palynostratigraphie de l'Eodévien dans l'ouest de l'Europe. Mémoires Explicatifs pour les Cartes Géologiques & Minéralogiques de la Belgique. Service Géologique de Belgique 27. 453 pp
- Strel M, Loboziak S (1996) Middle to upper Devonian miospores. In: Jansonius JJ, McGregor DC (eds) *Palynology: principles and applications*. AASP Foundation, Salt Lake City, pp 575–587
- Strel M, Marshall JEA (2007) Devonian–carboniferous boundary global correlations and their paleogeographic implications for the assembly of Pangaea. In: The W (ed) *Proceedings XVth Int. congress on carboniferous and Permian stratigraphy*, Utrecht, 2003. Royal Netherlands Academy of Arts and Sciences, pp 481–496
- Strel M, Scheckler SE (1990) Miospore lateral distribution in upper Famennian alluvial, lagoonal to tidal facies from eastern United States and Belgium. *Rev Palaeobot Palynol* 64:315–324
- Strel M, Higgs K, Loboziak S et al (1987) Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne–Rhenish regions. *Rev Palaeobot Palynol* 50(3): 211–229. [https://doi.org/10.1016/0034-6667\(87\)90001-7](https://doi.org/10.1016/0034-6667(87)90001-7)
- Strel M, Loboziak S, Stemans P et al (2000) Devonian miospore stratigraphy and correlation with the global stratotype sections and points. In: Bultynck P (ed) *Subcommission on Devonian stratigraphy: fossil groups important for boundary definition*. Courier Forschungsinstitut Senckenberg, vol 220. E. Schweizerbart Science Publishers, Stuttgart, pp 9–23
- Ströther PK, Servais T, Vecoli M (2010) The effects of terrestrialization on marine ecosystems: the fall of CO₂. In: Vecoli M, Clément G, Meyer-Berthaud B (eds) *The terrestrialization process: modelling complex interactions at the biosphere–geosphere Interface*. *Geol Soc Lond, Spec Publ* 339:37–48. <https://doi.org/10.1144/SP339.4>
- Suárez-Riglos M (1975) Algunas consideraciones biocronostratigráficas del Silúrico–Devónico en Bolivia. Paper presented at the 1st Congreso Argentino de Paleontología y Bioestratigrafía, Universidad Nacional de Tucumán, 12–16 August 1974
- Taylor TN, Osborn JM (1996) The importance of fungi in shaping the paleoecosystem. *Rev Palaeobot Palynol* 90:249–262. [https://doi.org/10.1016/0034-6667\(95\)00086-0](https://doi.org/10.1016/0034-6667(95)00086-0)
- Taylor WA, Taylor TN (1987) Spore wall ultrastructure of *Protosalvinia*. *Am J Bot* 74:437–443
- Tiffney BH (ed) (1985) *Geological factors and the evolution of plants*. Yale University Press, New Haven
- Torsvik TH, Cocks LRM (2004) Earth geography from 400 to 250 Ma: a palaeomagnetic, faunal and facies review. *J Geol Soc* 161(4):555–572. <https://doi.org/10.1144/0016-764903-098>
- Trindade VSF, Carvalho MA (2018) Paleoenvironment reconstruction of Parnaíba Basin (north, Brazil) using indicator species analysis (IndVal) of Devonian microphytoplankton. *Mar Micro-paleontol* 140:69–80. <https://doi.org/10.1016/j.marmicro.2018.02.003>

- Trindade VSF, Carvalho MA, Borghi L (2015) Palynofacies patterns of the Devonian of the Parnaíba Basin, Brazil: Paleoenvironmental implications. *J S Am Earth Sci* 62:164–175. <https://doi.org/10.1016/j.jsames.2015.06.001>
- Van Iten H, Cox RS, Mapes RH (1992) New data on the morphology of *Sphenothallus* hall: implications for its affinities. *Lethaia* 25:135–144. <https://doi.org/10.1111/j.1502-3931.1992.tb01378.x>
- Van Iten H, Leme JM, Simões MG et al (2019) Clonal colony in the early Devonian cnidarian *Sphenothallus* from Brazil. *Acta Palaeontol Pol* 64(2):409–416. <https://doi.org/10.4202/app.00576.2018>
- Vaz PT, Rezende NGAM, Wanderley Filho JR et al (2007) Bacia do Parnaíba. *Boletim de Geociências da Petrobras* 15(2):253–263
- Wicander R, Playford G (2013) Marine and terrestrial Palynoforas from transitional Devonian–Mississippian strata, Illinois Basin, USA. *Boletín Geológico y Minero de España* 124:589–637
- Willis KJ, McElwain JC (2002) The evolution of plants. Oxford University Press, New York
- Wnuk C (1996) The development of floristic provinciality during the middle and late Paleozoic. *Rev Palaeobot Palynol* 90(1–2):5–40. [https://doi.org/10.1016/0034-6667\(95\)00022-4](https://doi.org/10.1016/0034-6667(95)00022-4)
- Young GC (1990) Devonian vertebrate distribution patterns and cladistic analysis of palaeogeographic hypotheses. In: WC MK, Scotese CR (eds) *Palaeozoic palaeogeography and biogeography*, vol 12. Geological Society of London Memoir, pp 243–255. <https://doi.org/10.1144/GSL.MEM.1990.012.01.23>
- Zabini C, Holz M, Bosetti EP (2010) Taphonomy and taphofacies analysis of lingulid brachiopods from the Devonian sequences of the Paraná Basin, Brazil. *Palaeogeogr Palaeoclimatol Palaeoecol* 292:44–56. <https://doi.org/10.1016/j.palaeo.2010.03.025>
- Zabini C, Holz M, Bosetti EP et al (2012) Sequence stratigraphy and taphonomic signatures of marine invertebrates: a Devonian (Pragian/Eifelian) example of the Paraná Basin. *J S Am Earth Sci* 33:8–20. <https://doi.org/10.1016/j.jsames.2011.08.001>
- Ziegler W, Sandberg CA (1990) The late Devonian standard conodont zonation. *Cour Forschungsinstit Senck* 121:1–115