

EARLY DEVONIAN TAPHOFLORA RECORD IN PONTA GROSSA ARCH, PARANÁ BASIN (SOUTHERN BRAZIL) AND ITS PALAEOGEOGRAPHIC IMPLICATIONS

INGRID DE MELO MILAGRES¹, EGBERTO PEREIRA^{1*}, SÉRGIO BERGAMASCHI¹, MARIA ANTONIETA DA CONCEIÇÃO RODRIGUES¹ AND PHILIPPE GERRIENNE²

¹ Universidade do Estado do Rio de Janeiro, Faculdade de Geologia, Departamento de Estratigrafia e Paleontologia, Rio de Janeiro, RJ, Brazil.

² Paleobotany Department, Bat. B18, Sart Tilman, Universite de Liege, B-4000 Liege, Belgium.

* CORRESPONDING AUTHOR, egberto@uerj.br

Received on 24 March 2018

Received in revised form on 15 June 2018

Accepted on 27 June 2018

Editor:

Victor Alviras Castillo, Universidad Católica Santo Toribio de Mogrovejo
Chiclayo

Citation:

Milagres, I.M., Pereira, E., Bergamaschi, S., Rodrigues, M.A.C., Gerrienne, P., 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.

Abstract

This work analyzes the taphofloras collected from two Lower Devonian localities (PISA and Ponta Grossa/Carambei) of the eastern border of the Paraná Basin (Southern Brazil). This association is of late Lochkovian age. It includes a large number of records of *Cooksonia paranensis* Gerrienne et al., 2001, as well as of other taxa representative of this age interval. The occurrence of these plants in the Paraná Basin raises questions related to the Early Devonian paleoclimatic and paleogeographic settings, mainly when compared with the coeval floras from Bolivia and Laurasia. According to the most recent paleogeographic reconstructions, the Paraná Basin was located very close to the South Pole during Early Devonian times and was under cold climatic conditions and poor insolation or even darkness during long periods. Some Brazilian primitive

plants possess spine-like emergences, which may indicate protection against cold climatic conditions and desiccation and/or an attempt to increase photosynthetic surfaces. The existence of such diversified taphofloras close to the South Pole during the Early Devonian corroborates the hypothesis of an ice-free pole at this time, which allowed the development of vegetation in terrestrial environments. The taphofloras of the Paraná Basin are strikingly similar to those of probably coeval localities from Euramerica. The implications of these similarities are discussed in a paleogeographic context in this work.

Keywords: *Cooksonia*. Primitive plants. Devonian. Paraná Basin. Gondwana. Paleogeography.

1 Introduction

The initial colonization of the continents by early land plants during the Silurian and Devonian is one of the most instigating themes of Geosciences. Much of this history is known from the analysis of fossiliferous materials obtained in Laurasia (Edwards and Wellman, 2001). In the Gondwana, particularly Western Gondwana, this record only has been recently recognized and studied systematically (Mussa et al., 1996, 2002; Gerrienne et al., 2001; Edwards et al., 2001; Gonez and Gerrienne, 2010a and b).

Discoveries of early land plants in different localities in South America, such as Bolivia, Argentina, Uruguay and Brazil, which were part of the Western Gondwana, have allowed major advances in the study of the evolution of these early land plants. Thus, paleogeographic, paleoclimatic and paleoenvironmental models have been better understood and better evaluated with this new body of information.

This work aims to analyze the taphoflora data obtained in two localities, PISA (acronym of “Papel de Imprensa S/A”) and Ponta Grossa/Carambeí, located in the upper domain of Furnas Formation, at the Ponta Grossa Arch, of the eastern border of the Paraná Basin.

2. Previous record of Devonian taphofloras in the Paraná Basin

Early land plants are known from several Devonian outcrops of the Paraná Basin (Fig. 1A). On the northern border of the basin, Quadros and Melo (1986) recorded plant fragments in sediments of the Furnas Formation, in the Amorinópolis region (Goiás State - GO). The authors identified small remains of so-called “Psilophytas”, and observed that, in the Amorinópolis section, the early land plants have the same stratigraphic position observed in the southern part of the basin, specifically at the upper levels of the Furnas Formation.

At the Chapada dos Guimarães region (northwest of the Paraná Basin), Schubert and Borghi (1991) found small sporangia and axes of early land plants preserved in coastal sediments of the Furnas Formation. According to these authors, the fossiliferous strata in the Amorinópolis and Chapada dos Guimarães (Mato Grosso State - MT) regions are approximately in the same stratigraphic position and are covered by shoreface and offshore deposits belonging to the Ponta Grossa Formation base.

At the southeast border of Paraná Basin, Bigarella et al. (1966) recorded remains of early land plants near Tibagi City (Paraná State - PR), and Rodrigues et al. (1989) found traces of “Psilophytales-related plants” in the Ponta Grossa region. Bolzon et al. (1994) reported a locality with preserved plant remains in the Carambeí region (PR). All these remains are located at the top of the Furnas Formation, close to the Ponta Grossa Formation boundary.

However, all these preliminary records lacked a detailed description of the plant remains. Mussa et al. (1996, 2002), Gerrienne et al. (2001, 2002, 2006), and Gonez and

Gerrienne (2010 a, b) finally provided a broad discussion of the assemblages collected in the Jaguariaíva region (PR).

2.1. Main fossiliferous sites at the Ponta Grossa Arch region

In the Ponta Grossa Arch area, five localities have been reported in the literature (Fig. 1B): (1) Vila 31 de Março, the road to Alagados, Ponta Grossa (PR), described by Rodrigues et al. (1989); (2) Ponta Grossa/Carambeí, PR-151 road, km 317.5, Ponta Grossa (PR), reported by Bolzon et al. (1994) and described by Milagres (2003), Milagres et al. (2007) and Machado et al. (2007); (3) Tibagi, PR-340 road, km 60, Tibagi, PR, reported by Bigarella et al. (1966); (4) PISA, rail access to the PISA Company, Jaguariaíva (PR), initially reported by Mussa et al. (1996, 2002), and reviewed by Milagres (2003) and Milagres et al. (2007) and; (5) Jackson de Figueiredo, Jaguariaíva-Jacarézinho railway extension, km 12.5, Jaguariaíva (PR), described by Mussa et al. (1996, 2002), Gerrienne et al. (2001, 2002, 2006) and Gonez and Gerrienne (2010 a, b).

2.2 Stratigraphic framework of the studied areas

In lithostratigraphic terms, the Devonian sequence includes the Furnas and Ponta Grossa formations, rising along the northern and southeastern borders of the basin that extensively extends across the subsurface. The taphoflora described in this study comes from a second-order sequence cycle in the Furnas Formation (Bergamaschi and Pereira, 2001).

The Furnas Formation consists predominantly of sandstones, grouped in two facies associations: (i) facies that may be related to fluvial processes, in a deltaic context, and (ii) facies interpreted as deposits of one coastal system, with Early Devonian fossil plants (Pereira et al., 1998). According to the latter authors, the Furnas sandstones are associated with shoreface deposits and large braided delta systems, developed as part of a transgressive system tract.

Shoreface and offshore deposits of Ponta Grossa Formation cover transitional and marine deposits found in the upper part of the Furnas Formation. The sandy basal portion of Ponta Grossa Formation shows a succession of tabular bodies of decimetric thicknesses, consisting of fine to very fine sandstones interbedded with pelitic layers. The sandy strata show small wave-ripple cross-lamination, plane-parallel lamination, or most frequently, hummocky cross-stratification (Bergamaschi, 1992).

2.3. Localities and age

The macrofossils from Ponta Grossa/Carambeí were collected from an outcrop located on a section of the same PR-151 road between Ponta Grossa (PR) and Carambeí (PR), at the kilometer 317.5 (Figs 1A and B). The geographical coordinates of this site are: 25° 00'18 "S; 50 ° 08'19"W.

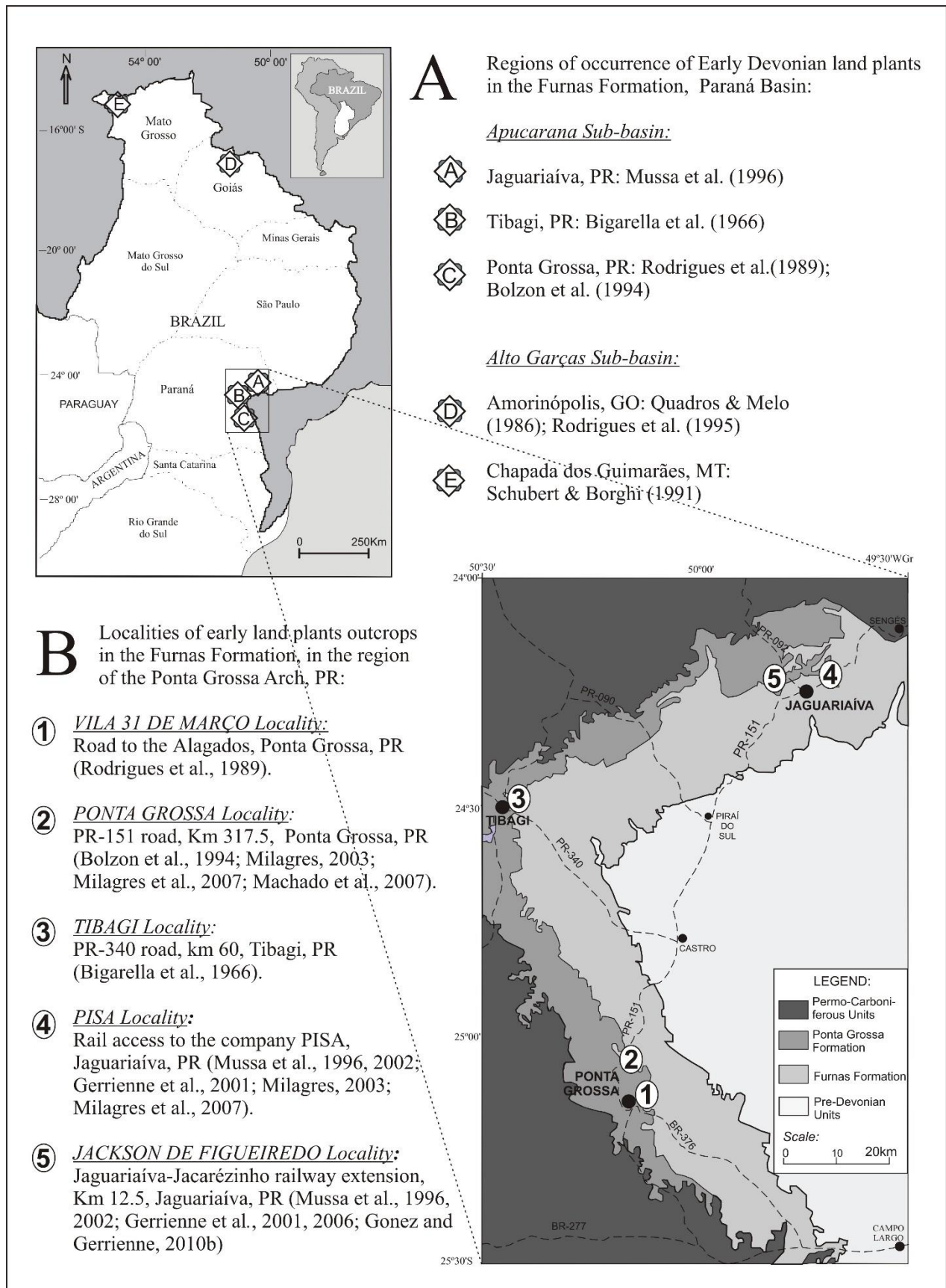


Fig. 1. (A) Occurrence of Early Devonian land plants in the Furnas Formation (Furnas Form.), Paraná Basin. (B) Localities with early land plants in the Furnas Formation, in the region of the Ponta Grossa Arch, PR.

The taphofloristic association observed in PISA was collected from an outcrop located along a small railroad branch in the industrial area of the PISA Company. This area can be accessed at the kilometer 23 of the PR-151 road (Itararé - Ponta Grossa road) and is located about four kilometers northeast of Jaguariá-PR (Figs 1A and B). The geographical coordinates of this point are: 24° 15'23 "S; 49° 40'99"W.

2.3.1. Ponta Grossa/Carambeí locality

Bolzon et al. (1994) first reported the taphofloristic association found at the outcrop of the PR-151 road, km 317.5, between the cities of Ponta Grossa and Carambeí. It is located at least 40 meters below the boundary between the Furnas and Ponta Grossa formations, according to Assine (1996).

Similar plant associations, reported in areas of different outcrops around the Paraná Basin, all occur in transitional deposits to coastal ones located in the upper part of the Furnas Formation. In most cases, plant-bearing sediments are located a few meters below the marine deposits of Ponta Grossa Formation. This arrangement records a well-defined and transgressive event registered by the entire basin in response to rapid flooding of the system caused by the relative sea level rise in the Pragian/Lochkovian. Thus, the inference of the stratigraphic positioning of this locality in the Early Devonian transgressive context, and the morphological characteristics of the described association, indicate a probable Early Devonian age for this association.

2.3.2. PISA locality

This taphofloristic association was collected in an outcrop situated along a small railway branch in the industrial area of the PISA company (Papel de Imprensa S.A.). This area has access by kilometer 206.5 of the PR-151 road (Itararé - Ponta Grossa) and is located about four kilometers northeast of Jaguariá-PR.

The PISA locality is included in the depositional context described by Bergamaschi (1992) for the upper portions of the Furnas Formation. The siltstone bodies, which contain the plant remains, are preserved interbedded with strata of coarse and very coarse sandstone, with tabular geometry and presenting cross stratification. These facies associations have been interpreted differently by a few authors. Bergamaschi (1992) proposed a model of delta-lagoon sedimentation for these deposits, emphasizing the presence, in this association, of sigmoidal sandy lobes interbedded with shale and siltstone, which would register the facies of the delta front. On the other hand, Milani (1997) associated the facies carrying the plant remains to tidal deposits.

According to Rodrigues et al. (1989), this taphoflora is preserved in the upper part of the Furnas Formation and is of Early-Lochkovian age according to Gerrienne et al. (2001). This age attribution was reevaluated by Rubinstein et

al. (2005). Based on the palynological association, these authors attributed the upper Furnas Formation to a late, but not latest, Lockovian age (Si Phylozone of the MN Oppel Zone).

3. Materials and Methods

Approximately 300 specimens of fossil plants, presented as compressions, were collected from two Lower Devonian localities (PISA and Ponta Grossa/Carambeí) of the eastern border of the Paraná Basin (Southern Brazil). They are described and commented below. Classical techniques of plant fossil preparation were applied, among them: "dégagement", "transfer" and macro-photography.

The samples were collected in many expeditions to the Paraná Basin in the period of 1987 to 2001. The specimens were stored in the paleontological collection of Geology Faculty of Universidade do Estado do Rio de Janeiro FGEL-UERJ).

4. Description of the observed association

Superdivision Polysporangiomorpha
Division Eutracheophytes
Subdivision Lycophytina
Genus *Cooksonia* Lang, 1937
***Cooksonia paranensis* Gerrienne et al., 2001**
(Fig. 2 A-E)

Description: Erect plant, showing isotomously branched axes 0.4-1.2 mm wide. When completely preserved, each axis segment ends in one terminal, trumpet shaped sporangium; the transition between the axis and the sporangium is gradual. The sporangium diameter ranges from 0.8 to 2.7 mm and its height approximately from 0.8 to 3.0 mm. The transition between axis and sporangium is characteristically gradual, so the proximal limit of the sporangium is difficult to establish. The proximal limit of the sporangium is located at the place where the sides of the axis are no longer parallel. Spores and anatomy of the plant are unknown.

Localities: PISA and Ponta Grossa/Carambeí.

Comparison and discussion: The characteristics of those specimens are those of the species *Cooksonia paranensis* described by Gerrienne et al. (2001). Gerrienne et al. (2006) reported the discovery of a specimen of *Cooksonia paranensis*, collected from the Jackson de Figueiredo locality, which consists of 4 or 5 axes, fixed at the base on a small organic structure. This structure was interpreted as the trace of a reduced female or even bisexual gametophyte. The presence of sporophytes (axes) yet associated with the gametophyte suggests that these structures would probably be parasitizing the gametophyte, at least at an early stage of development.

Habgood et al. (2002) described the new species *Cooksonia banksii* on the basis of the extremely well-preserved, coalified specimens from a Lochkovian (Lower Devonian) locality in Shropshire, England. *Cooksonia banksii* was compared to *C. paranensis* because both

species show a sunken sporangium and a subtending axis widening into the proximal sporangial wall. In any of the two species, there is no externally visible distinction between the subtending axis and the sporangial wall.

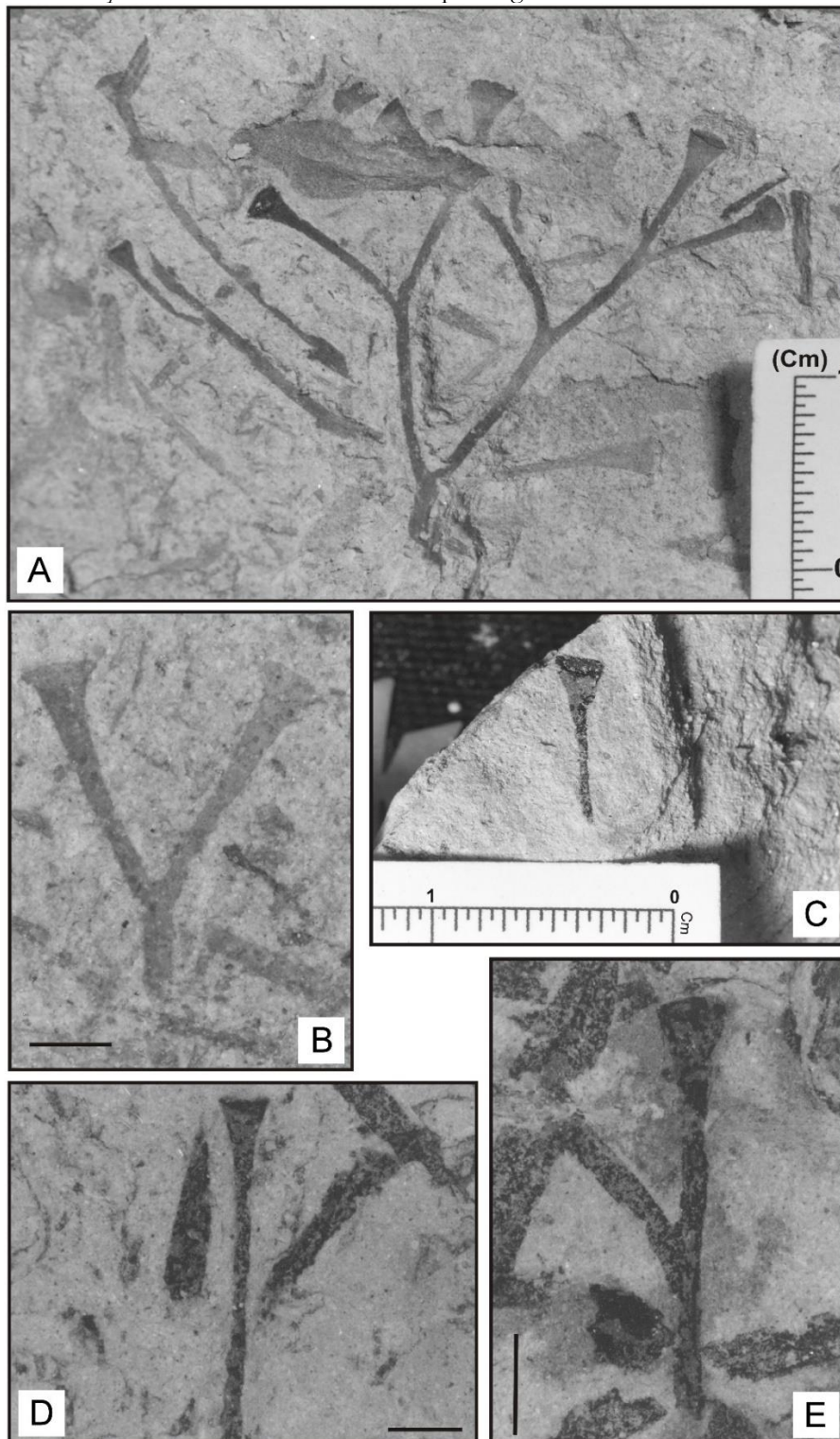


Fig. 2. (A) *Cooksonia paranensis*, Ponta Grossa/Carambeí locality. Specimen showing three levels of branching. (B) *Cooksonia paranensis*, Ponta Grossa/Carambeí locality. Isotomus axis with sporangia at the top, scale bar = 3 mm. (C, D) *Cooksonia paranensis*, PISA locality. Isolated sporangium, scale bar = 5 mm. (E) *Cooksonia paranensis*, PISA locality. Isotomous axis with one preserved sporangium, scale bar = 3 mm.

The specimens identified as *Cooksonia banksii* were later transferred to the new genus *Concavatbeca* by Morris et al. (2012), on the basis of the sporangium structure and spore ultrastructure. *Cooksonia paranensis* was described on the basis of compression fossils lacking anatomy and *in situ* spores. Consequently, no detailed comparison with the English material is possible, and according to the International Code of Nomenclature, Article 11.1 (McNeill et al., 2012), it is recommended to keep them under separate names.

Genus *Aberlemnia* Gonez and Gerrienne, 2010 b
***Aberlemnia caledonica* (Edwards) Gonez and**
Gerrienne, 2010 b
(Fig. 3 A, B)

Description: Two specimens were collected. One shows fertile branching axes, broken proximally (Fig. 3 A); the other is an isolated sporangium (Fig. 2 B). Axes are isotomously branched, with a possible trichotomy (Fig. 3 A); they are 0.8 to 1.2 mm wide. All sporangia are compressed laterally. The sporangium outline ranges from subcircular (Fig. 3 A) to slightly reniform (Fig. 3 B). Sporangium width ranges from 1.0 to 2.0 mm, height from 1.0 to 1.7. The sporangium-bearing axis segment widens just below the sporangial wall. The sporangium is usually darker than the subtending axis, with a clear limit between the two colors (Fig. 3 B). This limit forms a characteristic concave-downward curve, interpreted as the proximal limit of the sporangial wall. The sporangium is composed of two valves of equal size and shows a clear distal mechanism for dehiscence (Fig. 3 B).

Locality: PISA

Discussion and comparison: Those specimens are identical to specimens named *Aberlemnia caledonica* from the Jackson de Figueiredo locality, trichotomy included (Gonez and Gerrienne, 2010 b). Specimens with this sporangial construction were previously called *Cooksonia caledonica* Edwards, 1970, but they have been excluded from the genus *Cooksonia* because of their peculiar sporangium morphology.

Superdivision Polysporangiomorpha
Incertae sedis

Genus *Tarrantia* Fanning, Edwards and Richardson, 1992
***Tarrantia* sp.**
(Fig. 3 C)

Description: Only a few specimens were collected; one is illustrated in Fig. 4 C. The plant shows isotomous naked axes, with a terminal sporangium (about 0.9 mm wide and 1.6 mm high). The sporangium is elliptical and was probably ellipsoidal during life.

Locality: PISA

Discussion and comparison: Only a small number of specimens have been found, but the shape of the sporangium, elliptical and higher than wide, is characteristic: the sporangium, closely resembles those of the fossil named *Tarrantia* and illustrated by Fanning et al. (1992) from the early

Lochkovian of England, and by Gerrienne et al. (2001) from the Jackson de Figueiredo locality. However, more specimens are needed in order to precise the specific attribution of the plant.

Superdivision Bryomorpha
Division Bryophyta
Genus *Sporogonites* (Halle, 1916)
***Sporogonites* sp.**
(Fig. 3 D-F)

Description: Ten specimens were discovered, but only six were sufficiently well preserved to allow a detailed description. The plant is composed of undivided axes, 0.8 to 1.6 mm wide, ending in a large longitudinally elongated sporangium, 2.0 to 4.5 mm wide and 2.2 to 7.0 mm high. The sporangium is composed of two distinct parts: the lower part (which represents 3/4 of the total height) is often striated, while the upper part is sometimes darker and shows numerous small triangular emergences. A specimen from PISA shows sporangia similar to that of *Sporogonites* very close to each other (Fig. 3 F).

Localities: PISA and Ponta Grossa/Carambei.

Discussion and comparison: The aforementioned characteristics were also described by Gerrienne et al. (2001), but there are however some differences. The lower part of the sporangium of their specimens represents 1/4 of the total sporangium height, and the sporangia are almost twice as high as those observed in Ponta Grossa. This suggests that the specimens show intraspecific variation or even that they represent two distinct species. More material is needed to decide.

Superdivision Polysporangiomorpha
Incertae sedis
Genus *Hostinella* (Stur, 1882)
***Hostinella* sp.**
(Fig. 4 A-C)

Description: Most of the sterile axes preserved in the collected material represent naked and undivided vegetative axes. However, we can observe the presence of some dichotomous axes. The main axes have width measurements ranging from 0.4-1.5 mm, while the width of the secondary axes, which are those present after the dichotomy, varies between 0.3-1.0 mm.

Localities: PISA and Ponta Grossa/Carambei.

Discussion: *Hostinella* is a fossil-genus for isotomously branched, naked vegetative axes. The axes may belong to several different natural genera, but it is impossible to know precisely which genus because fertile structures are not preserved. Assuming that those branched axes belong to a sporophyte, and simply because the axis of a bryophyte sporophyte does not branch, the discovery of *Hostinella* at a locality just means that a polysporangiophyte was present.

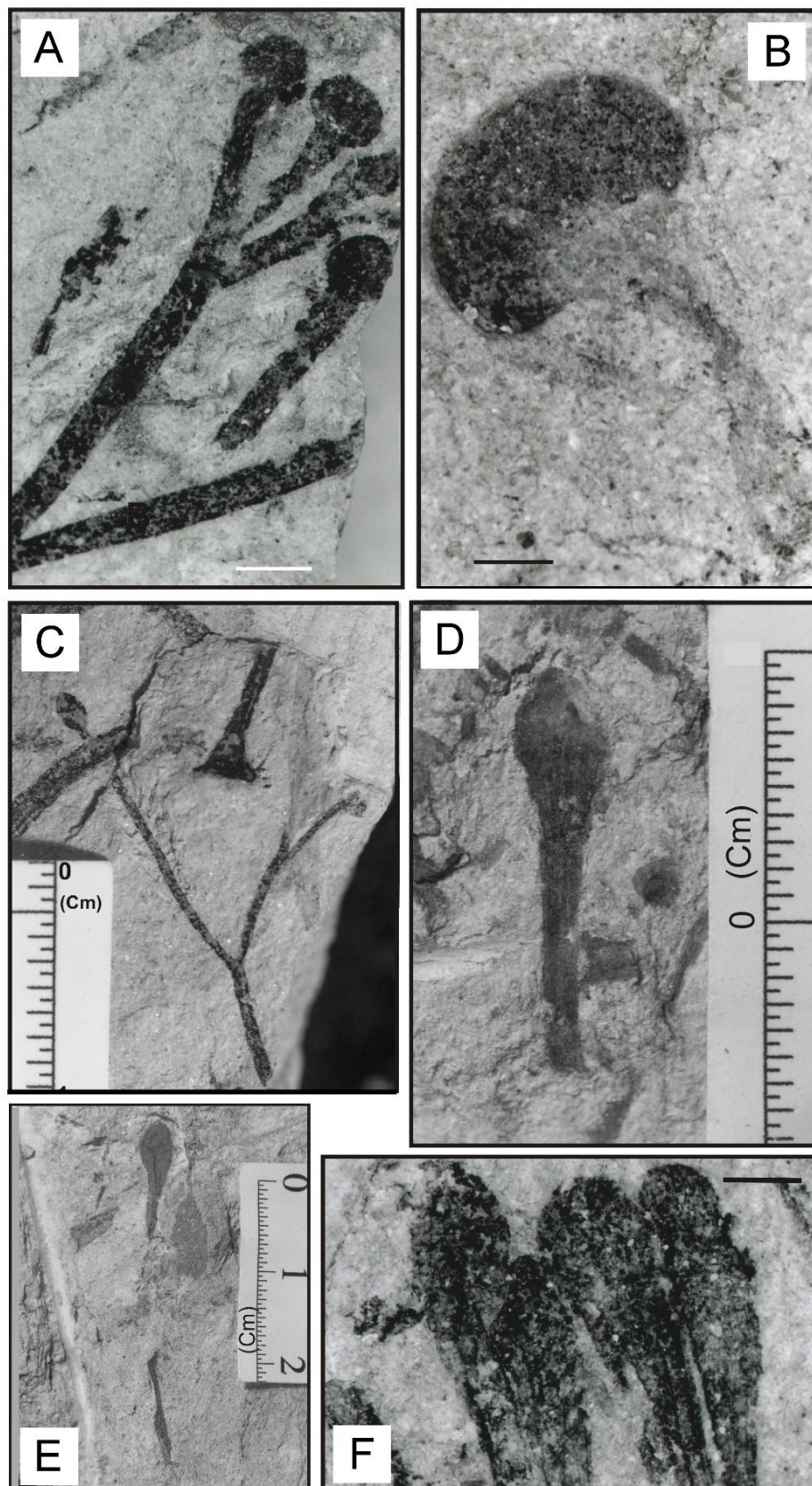


Fig. 3. (A, B) *Aberlemnia caledonica*, PISA locality. (A) Detail of four sporangia belonging most probably from the same specimen. Note the possible trichotomy, scale bar = 2 mm. (B) Isolated sporangium, scale bar = 0.5 mm. (C) *Tarrantia* sp., PISA locality. Dichotomous axis with a terminal sporangium. (D, E) *Sporogonites*, Ponta Grossa/Carambeí locality. Isolated sporangium. (F) *Sporogonites* sp., PISA locality. Four sporangia very close to each other, scale bar = 1 cm.

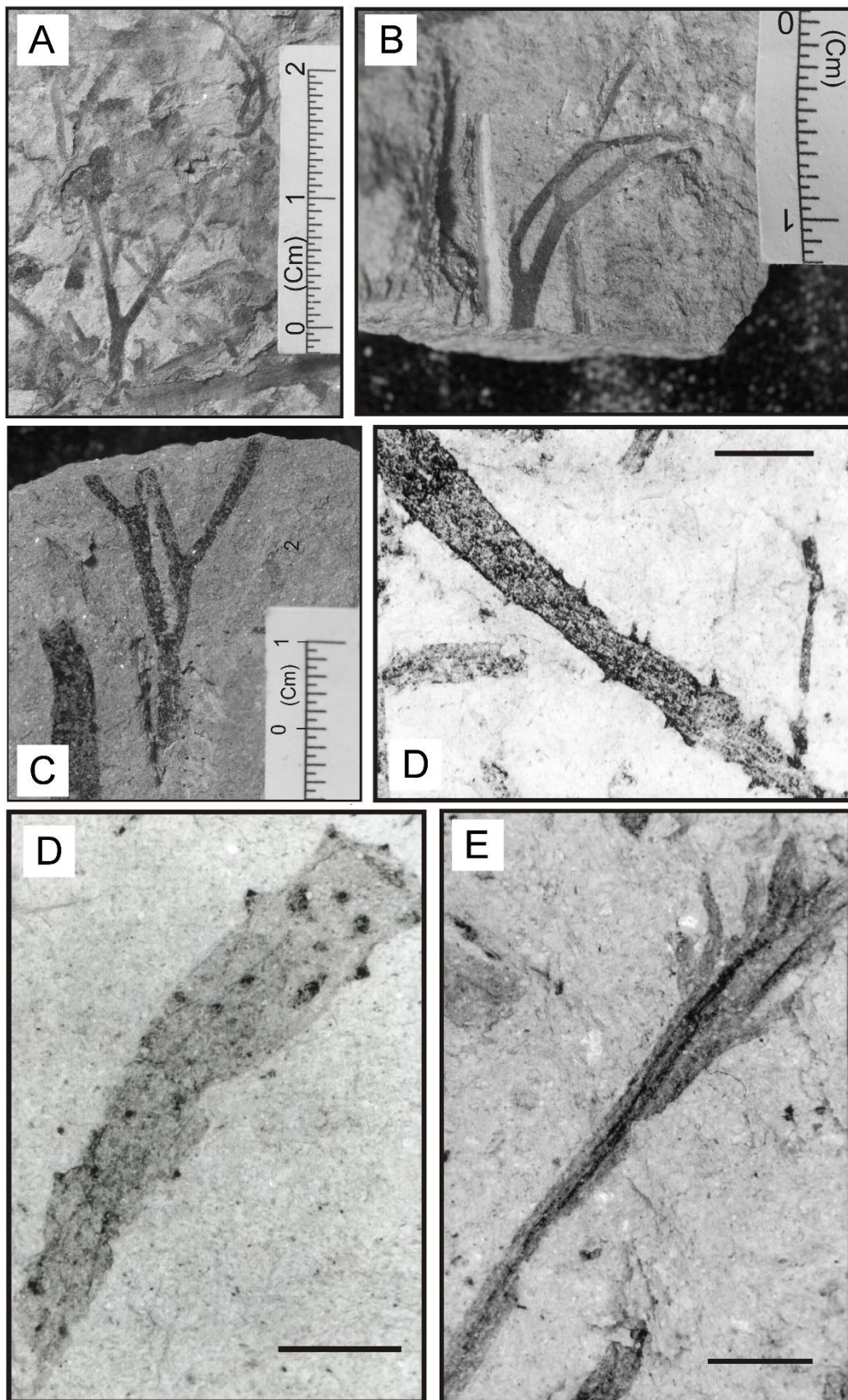


Fig. 4. (A-C) *Hostinella*, from Ponta Grossa/Carambeí locality (A, B) and from PISA locality (C). Naked dichotomous axes. (D) *Psilophytites* sp., PISA locality. Axis with emergences, scale bar = 1mm. (E) *Psilophytites* sp., PISA locality. Dichotomous axis with emergences, scale bar = 3 mm. (F) *Edwardsnella campanulata*, PISA locality. Striated axis with apical long, proximally decurrent emergences, scale bar = 4 mm.

Superdivision Polysporangiomorpha

Incertae sedis

Genus *Psilophytites* Höeg, 1952

Psilophytites sp.

(Fig. 4 D, E)

Description: The specimens are vegetative axes, 0.5 to 2.0 mm wide, bearing triangular emergences, 0.1 to 0.3 mm wide (at their base) and high; they are relatively common in the PISA locality. The axes are mostly undivided, but a single branched specimen has also been observed.

Locality: PISA

Discussion and comparison: The abundance of such axes with spiniform emergences is unusual in Early Devonian taphofloras. It has been interpreting as a possible morphological adaptation to cold climate (Gerrienne et al., 2001).

Incertae sedis

Edwardsnella campanulata Mussa et al., 1996

(Fig. 4 F)

Description: This species is represented by several undivided vegetative. The specimens consist of undivided axes, 0.6 to 1.0 mm wide, tapering in their proximal part. Axes are markedly longitudinally striated. In the apical portion, the plant bears several long, proximally decurrent, emergences, up to 2.5 mm long. Emergences are inserted on the axis with an angle close to 60°. No fertile parts have been discovered.

Locality: PISA

Discussion and comparison: Mussa et al. (1996, 2002) collected similar specimens and interpreted them as being a stem fragment with rhizomorphs (here called emergences) at its base. The nature of the emergences is unknown. However, Gerrienne et al. (2001), who also illustrated similar specimens, considered these extensions to be distal, and being possible pre-leaves or leaves.

The affinities of the plant are unknown, but Gerrienne et al. (2001) tentatively interpreted them as (i) a young lycopsids sporophyte or (ii) a leafy gametophyte of bryophyte. The specimens illustrated here are fragmentary and do not bring any further indication of the affinities of the species.

5. Discussion

5.1. Comparison between the studied localities

Table 1 presents a summary of the occurrences of macrofossils in PISA and Ponta Grossa/Carambeí localities. Even though the Ponta Grossa/Carambeí taphoflora is less well-preserved and less diversified, it can be assumed that the two localities were colonized by similar and very close plant associations. The PISA assemblages are strikingly similar to that of Jackson de Figueiredo described by Mussa et al. (1996), Gerrienne et al. (2001) and to that described for

the Ponta Grossa locality by Milagres et al. (2007). As already pointed out by Gerrienne et al. (2001), those diversified fossiliferous association observed in the Paraná Basin illustrates the amplitude of the radiation of the primitive plants of the Siluro-Devonian.

The macrofossils found in PISA and Ponta Grossa/Carambeí, located in coastal environments, may have suffered a rapid transport to the deposition zone, being removed from their coastal habitats by catastrophic flooding in transitional zones, or by large tidal waves increased by storms in coastal areas.

Tab. 1. Fossil plants collected at PISA and Ponta Grossa/Carambeí localities.

Species/ Taxa	PISA	Ponta Grossa/Carambeí
<i>Aberlemnia caledonica</i>	X	
<i>Cooksonia paranensis</i>	X	X
<i>Edwardsnella campanulata</i>	X	
<i>Hostinella</i> sp.	X	X
<i>Psilophytites</i> sp.	X	
<i>Sporogonites</i> sp.	X	X
<i>Tarrantia</i> sp.	X	

These elements acted as taphonomic agents, responsible for the erosion of the plants in the coastal zone and for their rapid transport by suspension to the deposition region before the decomposition and disarticulation of the axes and sporangia. The reworking was possibly minimal, in spite of the high level of energy, as indicated by the excellent degree of preservation of some specimens.

5.2. Palaeogeographic context

The occurrence of early land plants in the Paraná Basin (Brazil) is known since the pioneer works of Quadros and Melo (1986), Rodrigues et al. (1989), Bolzon et al. (1994) and Mussa et al. (1996). Since then, several other works have contributed to the knowledge of those early floras (Gerrienne et al., 2001, 2002 and 2006; Milagres et al., 2007; Gonez and Gerrienne, 2010 a, b). The presence of an early land plant flora dispersed over extensive areas of the Gondwana has important implications for the palaeogeographic and palaeoclimatic configuration of Western Gondwana.

The fossiliferous association registered in the localities presented in this work and others (see references above) includes several hundred specimens of a species of *Cooksonia*, among others taxa. This emblematic early land plant was first reported by W. H Lang in the 1930s in southern Brittany's Pridolian sediments from England (on the Euramerica paleocontinent). The genus *Cooksonia* was later recognized in Ireland, Scotland, Wales, Czech Republic, and other

localities in the Northern Hemisphere (mostly from Euramerica).

One of the first occurrences of this genus in high paleolatitudes (60° S) in Gondwana was recorded by Morel et al. (1995) in Bolivia. More complete and diverse assemblages were later described by Edwards et al. (2001), from the same area. The presence of *Cooksonia* (now *Aberlemnia*) cf. *caledonica* was noted. As already discussed, Gerrienne et al. (2001 and 2006) and Milagres (2003) also recorded new occurrences of the genus *Cooksonia* in the Ponta Grossa Arch region. Beside at least two different *Cooksonia* species, the rich assemblage described by Gerrienne et al. (2001) at Jackson de Figueiredo includes several other taxa (*Aberlemnia*, *Tarrantia*, *Pertonella*) that are all found both in Great Britain (Euramerica) and in the Paraná Basin (Gondwana). In a paleogeographical context, it is important to emphasize that the species *Aberlemnia* (*Cooksonia*) *caledonica* is present in Great Britain, as well as in Brazil and most probably in Bolivia.

According to the paleogeographic reconstructions of Scotese (2000a), during the Lochkovian, the Paraná Basin was located in southern Gondwana, within the polar circle. The occurrence of this rich association of plants gives support to the hypothesis of a "Warm Mode" during the Early Devonian and corroborates the model of an ice-free south pole as proposed by Scotese (2000a). These authors proposed a paleoclimatic reconstruction that implies the existence of an extensive cold temperate zone that extends from the south pole to the mid latitude bands (Fig. 5A).

The presence of those plants observed in Brazil has some deep paleogeographic implications when they are compared with related assemblages of Bolivia and of Euramerica. Indeed, the similarities between the Euromerican and the Gondwanan assemblages are striking and it seems unlikely that they could be the result of parallel evolution in both region. We consequently suggest that the presence of almost identical floras both in Euramerica and in Gondwana clearly indicate a migration of the floras, which is however difficult to explain.

The plants described in Euramerica occur in a very distinct climatic zone and are slightly older (Late Silurian to early Lochkovian) than the Brazilian plants (Late Lochkovian). It would therefore relatively easy to build a model in which the plants migrated from Northern hemisphere to Gondwana as soon as both continents were close enough. However, this explanation does not hold for the Bolivian plants. Although there are still doubts about the age of the Bolivian association, the Lipeón Formation is considered of Late Silurian age (Edwards et al., 2001). The Bolivian plants would be roughly contemporaneous with the early land plants described from Euramerica (Wales, England and Scotland), but (i) with no time to migrate from one place to the other, and (ii) according to most recent paleogeographic reconstructions (Torsvik and Cocks, 2013; Scotese, 2014), with the Rheic Ocean separating Euramerica

and Gondwana. On the other hand, the Bolivian plants occur in a climatic zone near the one in which the Brazilian plants occur. But in the Bolivian forms, no morphological adaptations to the cold climate conditions, similar to those observed by Gerrienne et al. (2001) in the plants of the Paraná Basin, have been described so far. Furthermore, as observed by Milagres (2003), the taphofloristic associations described in the region of Tarija - Bolivia differ from those analyzed in the Paraná Basin, both in terms of the identified species and the characteristics of the most common species. Finally, as expressed above, the species *Aberlemnia* (*Cooksonia*) *caledonica* is present in Great Britain as well as in Brazil and most probably in Bolivia, where the plant was described under the name *Cooksonia* cf. *caledonica*.

In this context, a Silurian radiation where early land plants were developing simultaneously in distinct climatic areas of Euramerica and Gondwana respectively, when the two paleocontinents were separated by the Rheic ocean, is really puzzling. A part of the answer might be in the reconstruction proposed by Scotese (2000c) (Fig. 5B) for Early Devonian (400 Ma), which is more compatible with the distribution of plants in both hemispheres. However, the Late Silurian age of the Bolivian (Gondwanan) plant remains is incompatible with a migration from or towards Euramerica because there was no connexion between the two paleocontinents during Silurian times.

All these data are contradictory and can hardly be compiled in a single model. Indeed, differences between the Brazilian and the Bolivian associations, as well as similarities of the Bolivian association with those present in Euramerica, indicate that the mode of propagation of those floras occurred in a complex way. From a biological viewpoint, we exclude the possibility that the plants identified as *Aberlemnia* (*Cooksonia*) *caledonica* from Scotland and Brazil could be different biological entities with the same morphological characters. The latter are so specific (especially those related to the dehiscence mechanism) that a convergent evolution is extremely unlikely. Accordingly, some questions arise. (a) How can we explain such dispersion of this plants, together with other genera, when paleogeographic reconstructions demonstrate climatic and geographical barriers? (b) Is the Brazilian plant named *Aberlemnia* (*Cooksonia*) cf. *caledonica* biologically very close to the *Aberlemnia* (*Cooksonia*) *caledonica* from Scotland and Brazil or does it represent another genus, having evolved independently? (c) Is the age of the Bolivian localities correct? (d) The Bolivian plants would have had some "hidden" (physiological) adaptations to the cold? (e) Could, against all odds, a plant assemblage with at least four identical genera cross a rather large ocean thanks to the spore dispersal only? (f) Is the closing age of the beginning of the Rheic ocean correct, in other words: are the currently accepted paleogeographic reconstructions of Late Silurian trustful? These questions definitely highlight the need for a more detailed analysis of the dispersal mode of these early land plants.

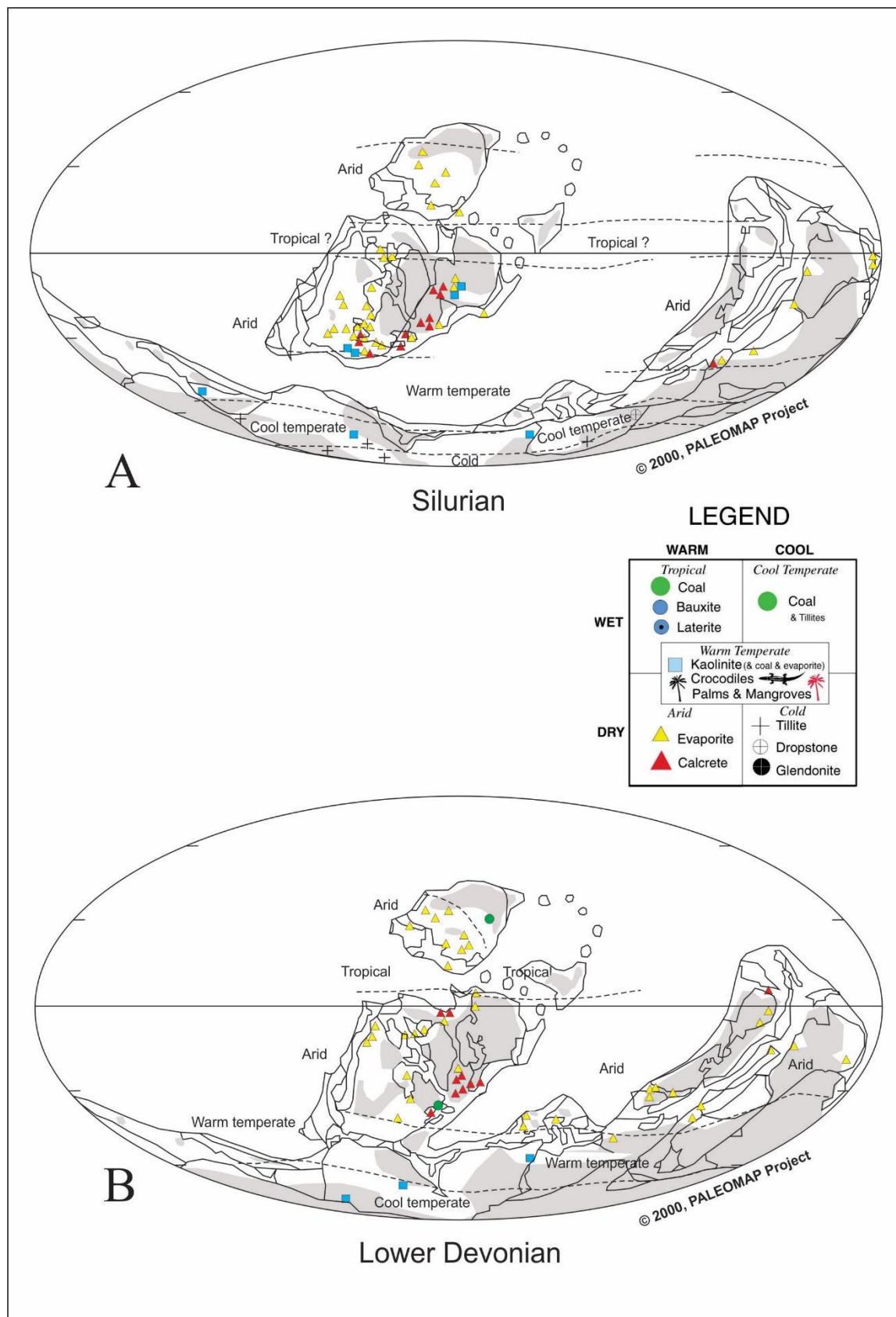


Fig. 5. Palaeoclimatic maps proposed by Scotese (2000a). (A) Palaeoclimatic proposal for the Silurian (420 M.a) (Source: Scotese, 2000b). (B) Palaeoclimatic proposal for the Early Devonian (400 Ma) (Source: Scotese, 2000c).

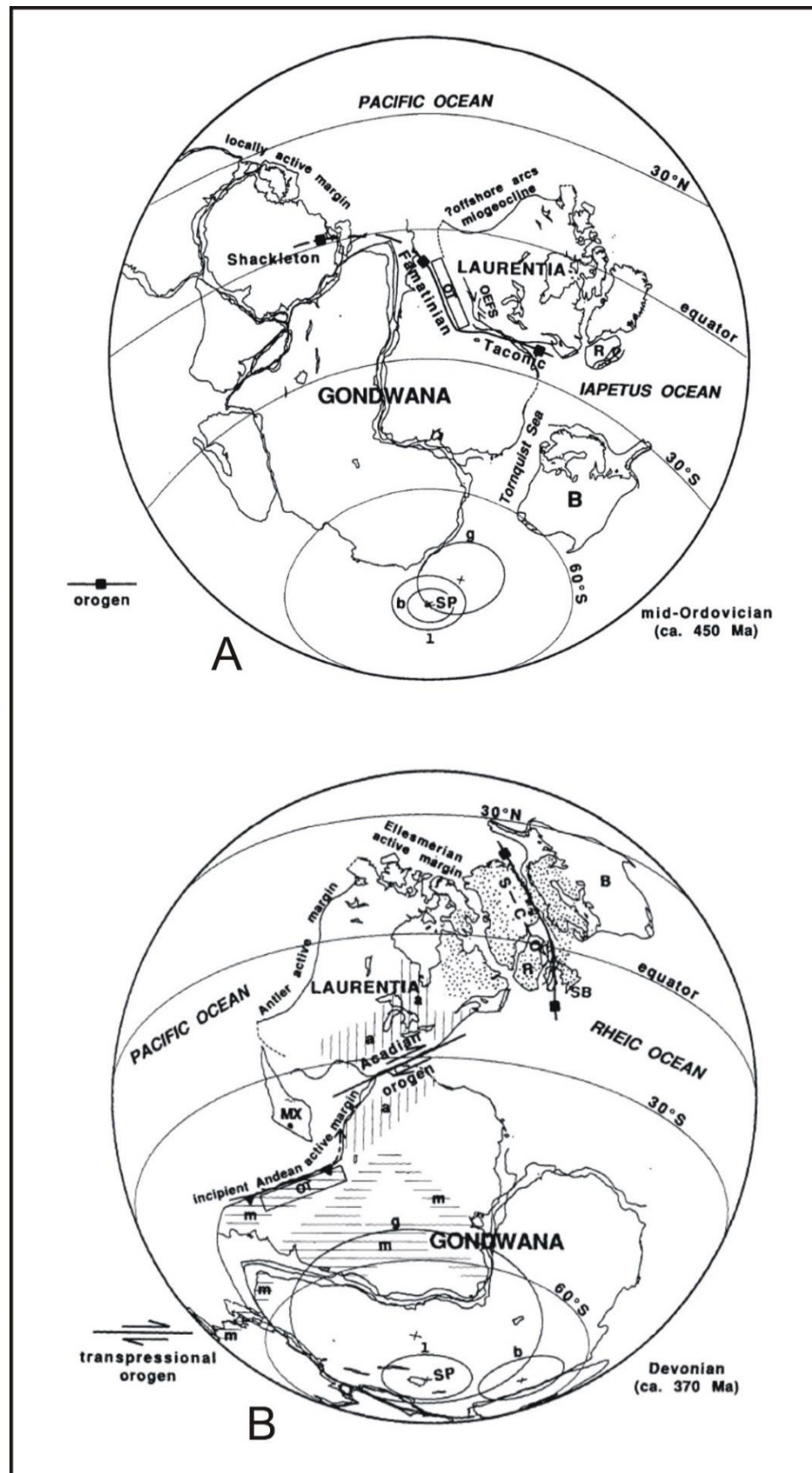


Fig. 6. Paleogeographic maps proposed by Dalziel et al. (1994) (A) for the Middle Ordovician (450 Ma) and (B) for the Devonian (370 Ma). (Source: Dalziel et al., 1994).

5.3 Plant propagation model

The questions proposed above are partly elucidated if we use, as a paleogeographic model, the maps referring to the Middle Ordovician (450 Ma) and the Devonian (370 Ma) proposed by Dalziel et al. (1994) (Fig. 6). They show geographical conditions favorable to the propagation of these plants in the considered period. Already in the Middle Ordovician, this paleogeographic model shows that the convergence between the Euramerica and Gondwana cratons result in the closing of the Rheic ocean, and finally, in the Euramerica - Gondwana collision. This is consistent with a possible first evolution of the early land plant assemblage studied here first either in England/Wales/Scotland or in Bolivia during Late Silurian and with a subsequent Early Devonian migration towards to the Paraná Basin, following the coastline as shown by Pereira et al. (2012)

This model is partly used by Gerrienne et al. (2002) (Fig. 7). In the Early Ordovician, Brazil, located on the South American plate, was positioned at approximately 50° south latitude. During the Ordovician and the Silurian, South America slowly migrates towards the south. Most paleogeographic reconstructions (Boucot, 1999; Scotese, 2000a; Torsvik and Cocks, 2011) agree to locate South America very close to the South Pole in the Early Devonian.

Thus, the similarities between the Early Devonian floras of Brazil and of the Great Britain can be explained by the following scenario:

(1) The earliest land plants probably evolved on Gondwana (Strother et al., 1996; Rubinstein et al., 2010) during the first half of Ordovician.

(2) Since the first half of the Ordovician, the earliest land plants colonized eastern Avalonia, which was close to Gondwana at that time.

(3) As it migrated northward, East Avalonia carried these early land plants.

(4) During the second part of the Silurian, after the junction of the Scotland / Avalonian East plates, the plants were able to colonize the Scotland terrane.

(5) In the Late Silurian, South America and the northernmost continents, among others Laurentia (North America), Baltic (Northern Europe), Scotland and Avalonia (Fig. 7) were close to each other (Scotese, 2000a). There was probably a more or less uninterrupted coastal zone between Great Britain and South America. This fact allowed the *Cooksonia*-type plants, shortly after their appearance in Britain, to migrate southward during Late Silurian/earliest Devonian. Migrating towards the south (to Bolivia first and then to Brazil), these plants encountered increasingly severe climatic conditions, which forced them to develop morphological adaptations to low temperatures.

This scenario, however, requires two conditions: (i) western Gondwana and Euramerica became very close as soon as during latest Silurian times (as proposed by Scotese, 2000a, 2014), and (ii) the age of the Bolivian locality should be slightly younger than proposed by Ewdards et al. (2001).

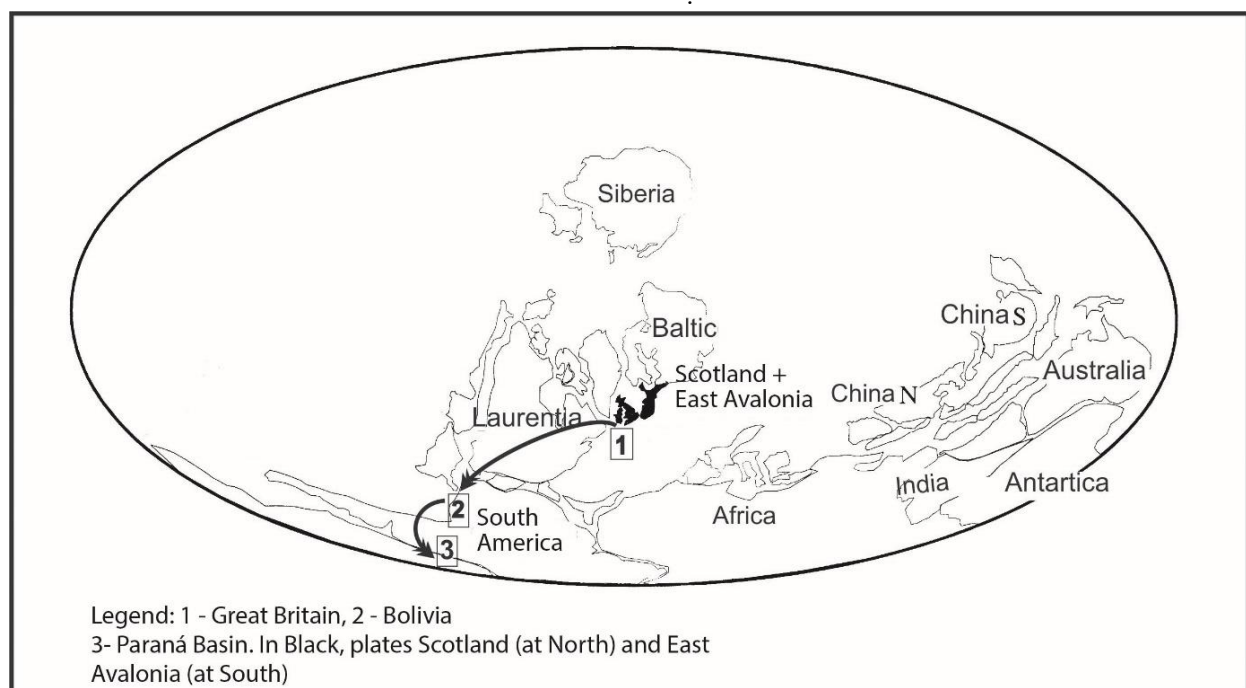


Fig. 7. Scheme of dispersion of early land plants from Great Britain (Avalonia) to West Gondwana, modified from Gerrienne et al. (2002). Palaeogeographic basis from Early Devonian map of Scotese (2000a). (Source: Gerrienne et al., 2002).

6. Conclusion

This work describes two early land plant assemblages collected from two Lower Devonian localities (PISA and Ponta Grossa/Carambeí) of the eastern border of the Paraná Basin (Southern Brazil). The two taphofloras present an impressive diversity, both with taxa already known from Euramerica localities and other with unusual morphologies and hence difficult to correlate with genera and species already described in the literature for the Early Devonian.

The associations studied in this work are very similar to that previously described for the Jackson de Figueiredo locality. In the PISA locality, many specimens show small spiniform emergences, and others have sporangia deeply sunken in their subtending axis, a range of morphological characters that suggests possible adaptations to bad climatic conditions, similar to those found in Jackson de Figueiredo locality. Those characters could also indicate specific adaptation against desiccation; the presence of spine-like emergences might also be explained by the need of increasing the photosynthetic surfaces in polar areas where insolation is poor during long periods of time.

The taphoflora of the Ponta Grossa/Carambeí locality is probably very similar to those described in PISA and Jackson de Figueiredo, but more fossils are necessary for a better comparison with the aforementioned localities. The paleoposition of these areas situated near the south pole during the beginning of the Devonian corroborates the hypothesis of an ice-free pole (warm mode), which explain that the plants could survive and reproduce.

The taphofloras from the Paraná Basin (Gondwana) share several genera or even species with the Late-Silurian/early Lochkovian plant assemblages from Great Britain (Euramerica). Based on the late Lochkovian ages of the Brazilian associations, it is tentatively suggested that these taxa first evolved on Euramerica and then, soon after the collision of Euramerica and Gondwana in earliest Devonian times, that they migrated towards higher latitudes on Gondwana.

Acknowledgments

The authors would like to thank CNPq and FAPERJ for the financial support that enabled the development of this research.

References

- Assine, M.L. 1996. Aspectos da estratigrafia das seqüências pré-carboníferas da Bacia do Paraná no Brasil. Programa de Pós-Graduação em Geologia Sedimentar, Universidade de São Paulo, PhD Thesis, 207p.
- 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, J.H.G. and Terra, G.J.S. (eds.). Correlações de Seqüências Paleozóicas Sul-Americanas. Ciência Técnica Petróleo, Seção Exploração de Petróleo, p. 63-72.
- Bergamaschi, S., 1992. Análise sedimentológica da Formação Furnas na faixa de afloramentos do flanco norte do arco estrutural de Ponta Grossa, Bacia do Paraná. MsD Thesis, Universidade Federal do Rio de Janeiro, 172 p.
- Bigarella, J.J., Marques Filho, P.L., Salamuni, R., 1966. Estruturas e texturas da Formação Furnas e sua significação paleogeográfica. Boletim da Universidade Federal do Paraná 18, 114 p.
- Bolzon, R.T., Assine, M.L., Guerra-Sommer, M., 1994. Ocorrência de *Cooksonia* Lang, 1937 na Formação Furnas, Estado do Paraná. In: Reunião de Paleobotânicos e Palinólogos, 8, São Paulo, 1994. Resumo das Comunicações, São Paulo, USP, p.11.
- Boucot, A.J., 1999. Southern African phanerozoic marine invertebrates: biogeography, paleoecology, climatology and comments on adjacent regions. Journal of African Earth Sciences 28, 129-143.
- Dalziel, I.W.D., Dalla Salda, L.H., Gahagan, L.M., 1994. Paleozoic Laurentia-Gondwana interection and the origin of the andean-appalachian mountains system. Geological Society of America Bulletin 106, 243-252.
- Edwards, D., 1970. Fertile Rhyniophytina from Lower Devonian of Britain. Paleontology 13, 451-461.
- Edwards, D., Morel, E.M., Paredes, F., Ganuza, D.G. and Zuniga, A. 2001. Plant assemblages from the Silurian of Southern Bolivia and their Paleogeographic significance. Botanical Journal of the Linnean Society 135, 229-250.
- Edwards, D., Wellman, C.H., 2001. Embryophytes on land: the Ordovician to Lochkovian (Lower Devonian) record. In: Gensel, P.G. and Edwards, D. (Eds.), Plants Invade the Land: Evolutionary and Environmental Perspectives. Columbia University Press, New York, pp. 3-28.
- Fanning, U., Edwards, D., Richardson, J.B., 1992. A diverse assemblage of early land plants from the Lower Devonian of the Welsh Boderland. Botanical Journal of the Linnean Society 109, 161-188.
- Gerrienne, P., Dilcher, D., Bergamaschi, S., Milagres, I.M., Pereira, E. and Rodrigues, M.A.C. 2006. An exceptional specimen of the early land plant *Cooksonia* paranensis, and a hypothesis on the life cycle of the earliest eutracheophytes. Review of Palaeobotany and Palynology 142 (3-4), 123-130.
- Gerrienne, P., Milagres, I.M., Bergamaschi, S., Pereira, E., Rodrigues, M.A.C., Steemans, P., 2002. Quelques specimens exceptionnels de premieres plantes terrestres decouvertes au Brésil (Bassin du Parana, Devonien basal). Geo-eco-trop 25, 65-74.
- Gerrienne, P., Bergamaschi, S., Pereira, E., Rodrigues, M.A.C., Steemans, P., 2001. An Early Devonian flora, including *Cooksonia*, from the Paraná Basin (Brazil). Review of Palaeobotany and Palynology 116, 19-38.
- Gonez, P., Gerrienne, P., 2010 a. A New Definition and a Lectotypification of the Genus *Cooksonia* Lang 1937. International Journal of Plant Sciences 171 (2), 199-215.
- Gonez, P., Gerrienne, P., 2010 b. *Aberlemnia caledonica* gen. et comb. nov., a new name for *Cooksonia caledonica* Edwards 1970. Review of Palaeobotany and Palynology 163 64-72.
- Habgood, K.S., Edwards, D., Axe, L., 2002. New perspectives on *Cooksonia* from the Lower Devonian of the Welsh Borderland. Botanical Journal of the Linnean Society 139, 339-359.

- Halle, T.G., 1916. Lower Devonian plants from Rörägen, in Norway. *Kungliga Svenska Vetenskapakademiens Handlingar* 57(1), 1-46.
- Höeg, O.A., 1952. Psilophyrites, a new form genus of Devonian plants, *Paleobotanist* 1, 212-214.
- Lang, W.H., 1937. On the plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London, Series B*, 227, 245-291.
- Machado, L.G., Bolzon, R.T., Azevedo, I., Carvalho, M.A., Souza, A.F., 2007. Primeiras plantas terrestres do Eodoniano (Formação Furnas) do Estado do Paraná, Brasil. *In: Carvalho, I.S., Rodrigues, M.A.C., Tardin, R.C.S. (Org.). Paleontologia - Cenários de Vida*. Rio de Janeiro: Interciência, 2007, v. 1, p. 49-59.
- McNeill, J., Barrie F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D., Turland, N.J., 2012. International Code of Nomenclature for Algae, Fungi and Plants (Melbourne Code) adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, 140 p.
- Milagres, I.M., 2003. Caracterização das taofloras de plantas vasculares primitivas registradas na região do Arco de Ponta Grossa (Bacia do Paraná, Brasil) e na região de Tarija (Subandino da Bolívia) e suas implicações paleogeográficas. MsD thesis, Universidade do Estado do Rio de Janeiro, 70 p.
- Milagres, I., Pereira, E., Bergamaschi, S., Rodrigues, M.A.C., Gerrienne, P., 2007. O registro da taoflora devoniana observada no arco de Ponta Grossa, Bacia do Paraná, e suas implicações paleogeográficas. *In: Carvalho, I.S., Rodrigues, M.A.C., Tardin, R.C.S. (Org.), Paleontologia - Cenários de Vida*, Rio de Janeiro: Interciência, 2007, v. 1, p. 25-48.
- Milani, E.J., 1997. Evolução tectono-estratigráfica da Bacia do Paraná e seu relacionamento com a geodinâmica fanerozoica do Gondwana Sul-Occidental. Programa de Pós-Graduação em Geociências. PhD Thesis, Universidade Federal do Rio Grande do Sul, 255 p.
- Morel, E., Edwards, D., Rodriguez, M.I., 1995. The first record of *Cooksonia* from South America in Silurian rocks from Bolivia. *Geological Magazine* 132, 449-452.
- Morris, J.L., Edwards, D., Richardson, J.B., Axe, L., Davies, K.L., 2012. Further insights into trilete spore producers from the Early Devonian (Lochkovian) of the Welsh Borderland, UK. *Review of Palaeobotany and Palynology* 185, 35-63. <https://doi.org/10.1016/j.revpalbo.2012.08.001>
- Mussa, D., Borghi, L., Bergamaschi, S., Schubert, G., Pereira, E., Rodrigues, M.A.C., Pereira, J.F., Emmerich, M., 2002. New taxa from the Furnas Formation, Paraná Basin, Brazil - an approach and revalidation of names. *Bradea* 8 (45), 303-309.
- Mussa, D., Borghi, L., Bergamaschi, S., Schubert, G., Pereira, E., Rodrigues, M.A., 1996. Estudo preliminar da taoflora da Formação Furnas, Bacia do Paraná, Brasil. *Anais da Academia Brasileira de Ciências*, 68 (1): 65-89.
- Pereira, E., Carneiro, C.D.R., Bergamaschi, S., de Almeida, F.F.M., 2012. Evolução das sinéclises Paleozoicas: Províncias Solimões, Amazonas, Parnaíba e Paraná. *In: Hasui, Y. et al. (Org.). Geologia do Brasil*. São Paulo, Beca.
- Pereira, E., Bergamaschi, S., Rodrigues, M.A. 1998. Sedimentary evolution of the Ordovician, Silurian and Devonian sequences of Paraná Basin in Brasil. *Zentralblatt für Geologie und Paläontologie, Teil 1*, 1997 (3/6), 779-792.
- Quadros, L.P., Melo, J.H.G., 1986. Ocorrência de restos vegetais em sedimentos continentais do Paleozóico Médio do Estado de Goiás. *Anais da Academia Brasileira de Ciências* 58 (4), 611.
- Rodrigues, M.A.C., Dino, R., Laranjeira, N.P.F., 1995. Nova ocorrência de Rhyniophyta na Formação Furnas no Sudoeste de Goiás. *Anais da Academia Brasileira de Ciências* 67 (3), 384-385.
- Rodrigues, M.A.C., Pereira, E., Bergamaschi, S., 1989. Ocorrência de psilophytales na Formação Furnas, borda leste da Bacia do Paraná. *Boletim IG-USP, Publicação Especial* 7, 35-43.
- Rubinstein, C.V., Gerrienne, P., de la Puente, G.S., Astini, R. A., Steemans, P., 2010. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist, Special Issue: Featured papers on 'Pollinator-mediated selection and floral evolution'*, 188 (2), 365-369. <https://doi.org/10.1111/j.1469-8137.2010.03433.x>
- Rubinstein, C., Melo, J.H.G., Steemans, P., 2005. Lochkovian (earliest Devonian) miospores from the Solimões Basin, northwestern Brazil. *Review of Palaeobotany and Palynology* 133, 91-113.
- Schubert, G., Borghi, L., 1991. Sobre a ocorrência inédita de uma taoflora devoniana na região da Chapada dos Guimarães (Bacia do Paraná, MT). *Anais da Academia Brasileira de Ciências* 63 (1), 96-97
- Scotese, C.R., 2000a. Paleomap Project 2000. Available in: <http://www.scotese.com/pzanim.htm>. Access on March 27, 2018.
- Scotese, C.R., 2000b. Silurian climate. Paleomap Project. Available in: www.scotese.com/silclim.htm. Access on March 27, 2018.
- Scotese, C.R., 2000c. Devonian climate. Paleomap Project. Available in: <http://www.scotese.com/edevclim.htm>. Access on March 27, 2018.
- Scotese, C.R., 2014. Atlas of Devonian Paleogeographic Maps, PALEOMAP Atlas for ArcGIS, volume 4, The Late Paleozoic, Maps 65-72, Mollweide Projection, PALEOMAP Project, Evanston, IL.
- Strother, P., Al-Hajri, S., Traverse, A., 1996. New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. *Geology* 24, 55-58.
- Stur, M.D., 1882. Die Silur-flora der Etage H-h1 in Böhmen. *Sitzungsber. Kais. Akad. Wiss., Naturw. Cl.*, 84, 330-391.
- Torsvik, T.H., Cocks, L.R.M. 2011. The Palaeozoic palaeogeography of central Gondwan. In: Van Hinsbergen, D.J.J., Buiter, S.J.H., Torsvik, T.H., Gaina, C. and Webb, S.J. (eds) *The Formation and Evolution of Africa: A Synopsis of 3.8 Ga of Earth History*. Geological Society, London, Special Publications, 357, 137-166.
- Torsvik, T.H., Cocks, L.R.M., 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. *Geological Society, London, Memoirs*, 38(1), 5-24.