Journal of Paleontology, 90(4), 2016, p. 632–639

0022-3360/16/0088-0906
doi: 10.1017/jpa.2016.82

Journal of
PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

Hepaticites iporangae Ricardi-Branco, Faria, Jasper, and Guerra-Sommer, 2011 from the early Permian of the Paraná Basin, Brazil, is not a liverwort but a tracheophyte

Dieter Uhl,[1,2,3] André Jasper,[1,2,3] Talyssa Valerius,[1] Joseline Manfroi,[1,2] Margot Guerra-Sommer,[4] and Fresia Soledad Ricardi-Branco[5]

[1]Setor de Botânica e Paleobotânica do Museu de Ciências Naturais da UNIVATES, Centro Universitário UNIVATES, 95.900-000, Lajeado, Rio Grande do Sul, Brazil ⟨ajasper@univates.br⟩, ⟨tvalerius@universo.univates.br⟩, ⟨joselinemanfroi@universo.univates.br⟩
[2]Programa de Pós-Graduação em Ambiente e Desenvolvimento (PPGAD), Centro Universitário UNIVATES, 95.900-000, Lajeado, Rio Grande do Sul, Brazil
[3]Senckenberg Forschungsinstitut und Naturmuseum, 60325, Frankfurt am Main, Germany. Senckenberg Center for Human Evolution and Palaeoenvironment, Institut für Geowissenschaften, Universität Tübingen, 72076, Tübingen, Germany ⟨dieter.uhl@senckenberg.de⟩
[4]Programa de Pós-Graduação em Geociências (PPGGeo), Universidade Federal do Rio Grande do Sul, UFRGS, 91.509-900, Porto Alegre, Rio Grande do Sul, Brazil ⟨margot.sommer@ufrgs.br⟩
[5]Departmento de Geologia e Recursos Naturais, Instituto de Geociências, Universidade Estadual de Campinas, UNICAMP, 13.083-970, Campinas, São Paulo, Brazil ⟨fresia@ige.unicamp.br⟩

Abstract.—From new and more complete material, which includes frond fragments with casts of tracheid remains of the rachis, it can be demonstrated that the putative liverwort *Hepaticites iporangae* Ricardi-Branco, Faria, Jasper, and Guerra-Sommer, 2011, from the early Permian Rio Bonito Formation (Sakmarian) of the Paraná Basin, Brazil, is not a bryophyte but a tracheophyte. The new material was collected from the same locality and layer as the type material, in the Quitéria outcrop in the municipality of Encruzilhada do Sul, state of Rio Grande do Sul, Brazil. From the morphology of the deeply dissected pinnatifid pinnules with narrow laminar lobes, the taxon is provisionally reassigned to the genus *Rhodeopteridium*. Thus we propose the new combination '*Rhodeopteridium*' *iporangae* new combination for this taxon. This new systematic interpretation contributes to our understanding of early liverworts (by removing *Hepaticites iporangae* as a possible taxon thereof) and clarifies an issue of diversity of the flora of the early Permian Rio Bonito Formation resulting from the original misidentification.

Introduction

During the late Paleozoic, the global climate changed from the 'icehouse-climate' of the Carboniferous to the 'greenhouse climate' of the middle and late Permian, and these climatic changes were accompanied by changes and shifts in the vegetation (e.g., Gastaldo et al., 1996; Montañez et al., 2007). Such changes occurred also on western Gondwana, e.g., in the Paraná Basin, where glaciers existed into the early Permian followed by a transition to a semiarid climate in the late Permian (e.g., Christiano-de-Souza and Ricardi-Branco, 2015). These climatic changes resulted in severe paleoenvironmental and floristic changes in this region (Iannuzzi, 2010, 2013; Christiano-de-Souza and Ricardi-Branco, 2015). However, to be able to interpret relationships between climate and vegetation change and even possible evolutionary consequences, it is necessary to have solid taxonomic data concerning the vegetation, especially when dealing with plant groups that are usually underrepresented in the fossil record.

The Quitéria outcrop, located in the municipality of Encruzilhada do Sul, Rio Grande do Sul, Brazil, is one of the most important sources of information about vegetation from wet biomes in the early Permian Rio Bonito Formation in the southern part of the Paraná Basin (e.g., Jasper et al., 2006, 2008; Guerra-Sommer et al., 2008; Boardman et al., 2012). Several taxonomical studies dealing with lycophytes (Jasper and Guerra-Sommer, 1999; Salvi et al., 2008), conifers (Jasper et al., 2005), glossopterids (Boardman et al., 2006), and the putative liverwort *Hepaticites iporangae* Ricardi-Branco, Faria, Jasper, and Guerra-Sommer, 2011 (Ricardi-Branco et al., 2011) have been carried out in the past two decades at this locality. The latter finding has been regarded as being of significant importance for the diversity of liverworts (Ricardi-Branco et al., 2011) as Paleozoic records of this group are rather scarce, especially in Gondwana (Pant and Bhowmik, 1998).

However, recent discoveries of larger and more complete specimens from its type locality, partly with casts of tracheid remains in situ at the position of the assumed midrib (sensu Ricardi-Branco et al., 2011), question the taxonomic position of these remains, as well as the interpretations of these findings as remains of liverworts. Here we present an analysis of the new findings, together with a reanalysis of the type material of

Hepaticites iporangae, demonstrating that it is in fact a tracheophyte and that it can best be compared to the genus *Rhodeopteridium* Zimmermann, 1959, of uncertain systematic position, although an unequivocal assignment to this taxon is not possible at the moment.

Geological setting

The Paraná Basin is a 1,400,000 km^2 intracratonic subsidence basin covering part of southern Brazil, Paraguay, Uruguay, and Argentina (Fig. 1). Basin floor subsidence and Paleozoic and Mesozoic sea-level changes, created a six second-order sequence deposited from the Ordovician to Late Cretaceous, divided by regional unconformities (Milani et al., 2007). The coal-bearing Rio Bonito Formation, from which the material studied here originates, integrates part of two third-order depositional sequences of the Carboniferous–Early Triassic second-order sequence, named S2 and S3 (Holz et al., 2010).

The Rio Bonito Formation includes coal deposits adjacent to siliciclastic paralic deposits (i.e., estuarine, deltaic, backshore, foreshore, and shore-face sediments) deposited in back-barrier environments (Holz et al., 2010). Tissue preservation and gelification index of coals indicate deposition in coastal swamp environments (Alves and Ade, 1996). The deposition occurred in a cool temperate climate at a paleolatitude around 50° south (Rees et al., 1999; Scotese, 2000; Torsvik and Cocks, 2011).

The Quitéria outcrop is located in the southeastern part of the Paraná Basin at the Rio Bonito Formation outcropping area, Rio Grande do Sul state, southern Brazil (Fig. 1). It is an isolated and fragmented exposure preserved in a collapsed block following the northwest direction, immediately overlying the granitic basement.

A vertical facies succession (Fig. 2) can be observed throughout the outcrop, representing nine cycles of relative variations of the water level in a lagoon (Jasper et al., 2006). The basal part of the section corresponds to coaly shale interbedded with thin coal layers of hypautochthonous origin. According to Jasper and Guerra-Sommer (1999), it represents a coastal depositional environment associated with a restricted lagoon protected by a barrier island in microtidal conditions. Macroscopic charcoal studies were carried out on this level by Jasper et al. (2008) confirming the occurrence of paleowildfires during the deposition of the Rio Bonito Formation. The upper section is traditionally interpreted as a roof shale with records of a unique megaflora, consisting of the herbaceous lycophyte *Lycopodites riograndensis* (Salvi et al., 2008), in situ stems with leaves of the subarborescent lycophyte *Brasilodendron pedroanum* (Jasper et al., 2003, 2006), the pteridophyll

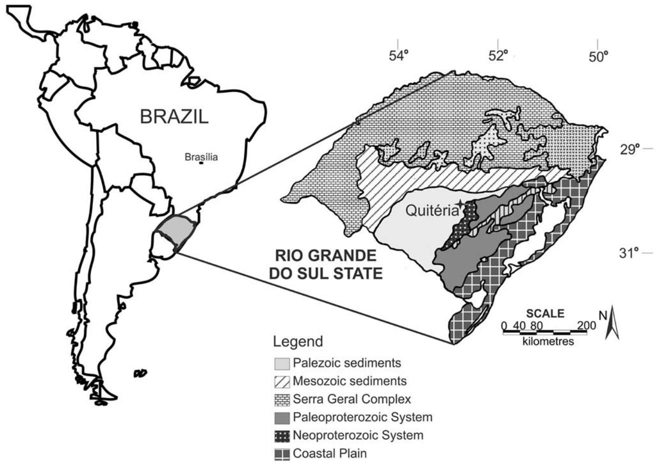


Figure 1. Simplified geological map of the Paraná Basin in Brazil with major tectonic elements and geographic references; location of the Quitéria outcrop is indicated by the star (based on Guerra-Sommer et al., 2008).

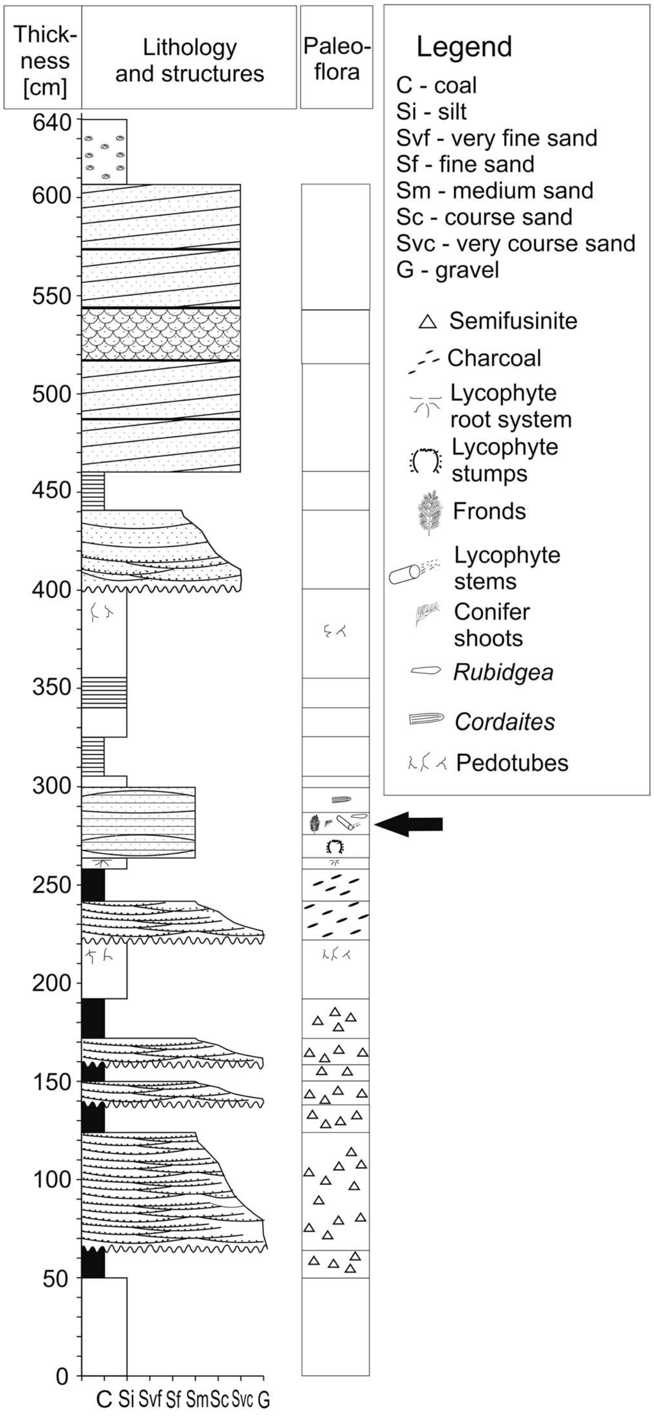


Figure 2. Columnar section of the Quitéria outcrop, from Jasper et al. (2008). The arrow indicates the layer from which the material studied here originates.

Botrychiopsis valida (Jasper et al., 2003), the conifer *Coricladus quiteriensis* (Jasper et al., 2005), and the glossopterid *Glossopteris browniana* (Boardman et al., 2006).

From the analyses of palynoassemblages preserved in the basal level, a correlation with the *Hamiapollenites karrooensis* palynostratigraphic subzone of Souza and Marques-Toigo (2003) has been established (Jasper et al., 2006), corresponding to the Sakmarian according to the criteria defined by Guerra-Sommer et al. (2007).

Materials and methods

This study was based on the original material of *Hepaticites iporangae* by Ricardi-Branco et al. (2011) as well as new material collected from the type horizon and locality, the Quitéria outcrop in Rio Grande do Sul, Brazil.

Structures that seemed to belong to conducting tissues were visible in the supposed midrib portion of one large specimen (MCNPbU 254, part and MCNPbU 255, counterpart; see Fig. 6 in Systematic paleontology). Fragments of those structures were mechanically extracted with the aid of preparation needles and tweezers. Subsequently, they were mounted on standard stubs with adhesive tabs for anatomical analysis under a scanning electron microscope (SEM; Zeiss EVO LS15).

Due to the new anatomical data, which have led to a new interpretation of the systematic affiliation of *Hepaticites iporangae*, the morphology of the plant fragments had to be reinterpreted. To clarify our new morphological interpretation, we provide a schematic sketch of the leaf/frond based on the largest specimen MCNPbU 254 (Fig. 3). In addition, we provided two figures (Figs. 4, 5) already figured in Ricardi-Branco et al. (2011) as visual support for our reinterpretation.

All measurements were taken from calibrated images with the aid of the software package ImageJ (Rasband, 1997–2014).

Repositories and institutional abbreviations.—The material is stored in the Setor de Botânica e Paleobotânica doMuseu de Ciências Naturais da UNIVATES, under the acronym MCNPbU.

Systematic paleontology

Division Tracheophyta Sinnott ex Cavalier-Smith, 1998
Class Incertae sedis
Order Incertae sedis
Family Incertae sedis

Genus *Rhodeopteridium* Zimmermann, 1959

Type species.—*Rhodeopteridium fasciaeformis* (Presl in Sternberg, 1838) Zimmermann 1959, from the upper Carboniferous of Radnice, Bohemia, Czech Republic, by original designation.

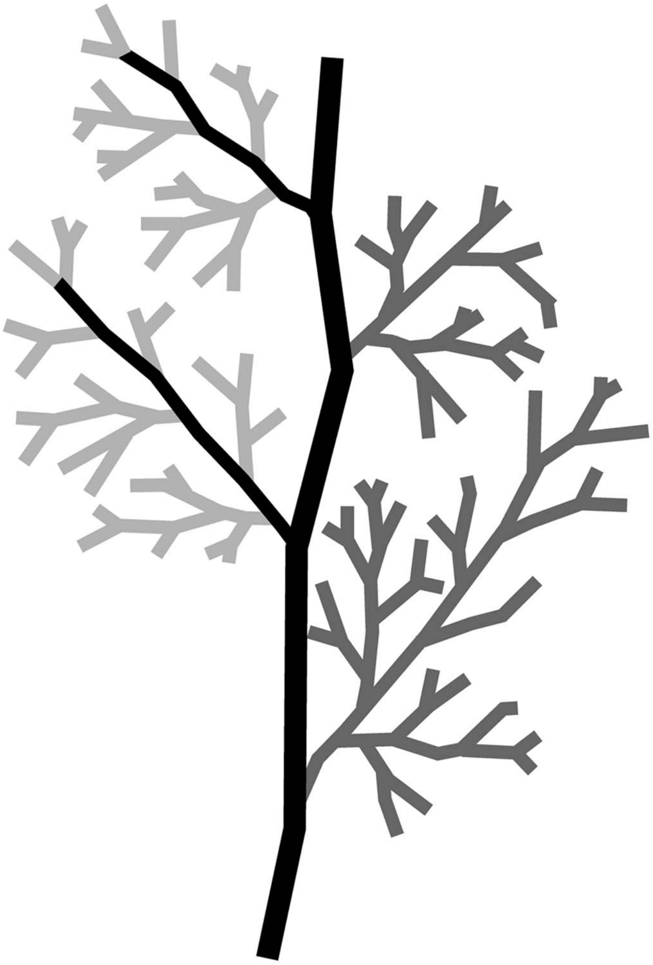


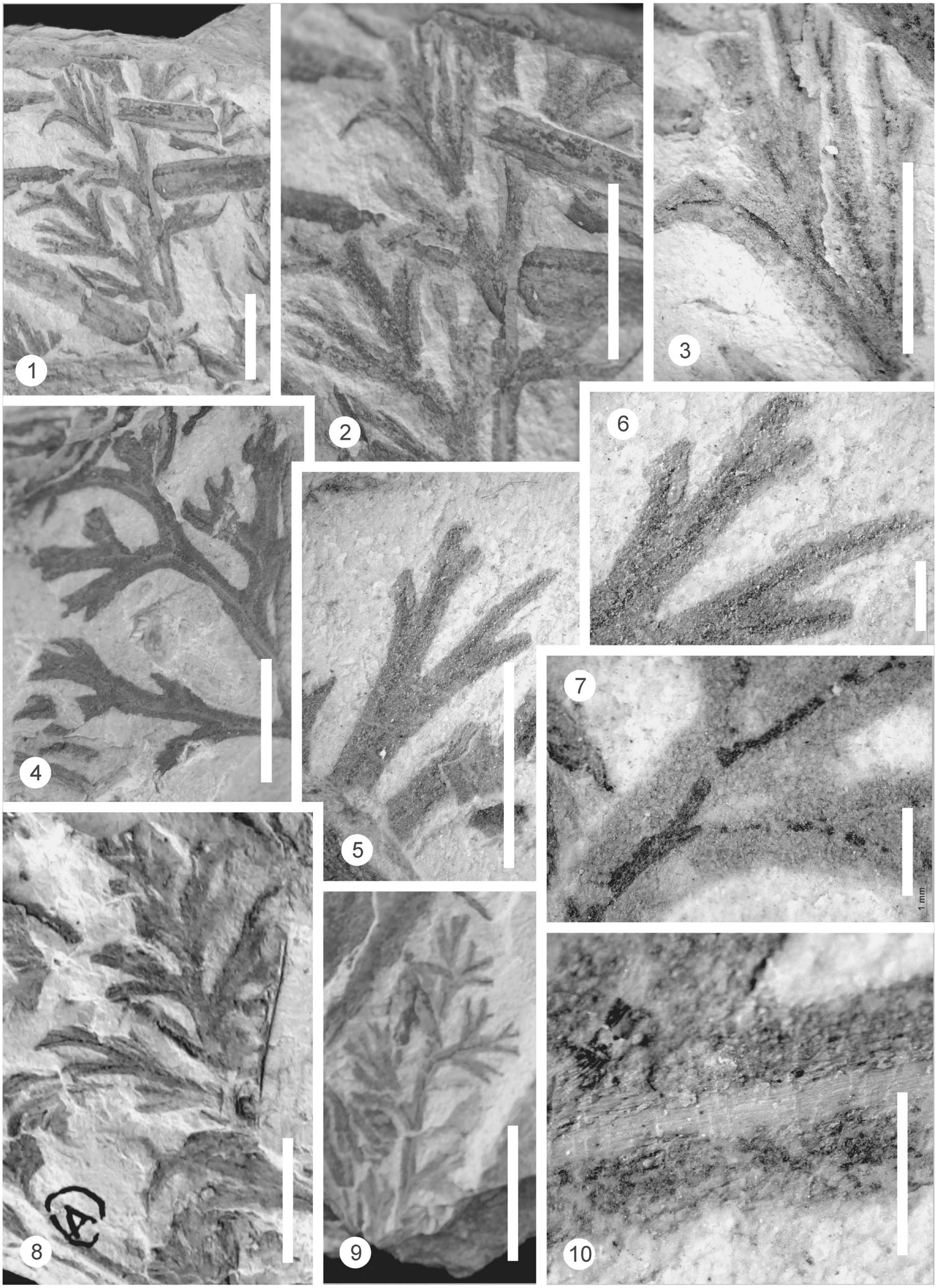
Figure 3. Schematic sketch of a frond fragment of '*Rhodeopteridium*' *iporangae* n. comb. to clarify the descriptive terms used here (based on MCNPbU 254; Fig. 6.1). Pinnae on the right side are colored dark grey; rachis of the frond and pinnae on the left side are colored in black; pinnatifid pinnules on left side are colored in light grey.

Diagnosis.—Pteridophyll with sphenopterid pinnules, in contrast to the genus *Sphenopteris* pinnae dissected into very narrow laminar lobes, with only a single vein (translated from Zimmermann, 1959, p. 727). Originally in Latin: "*Pteridophyllum sphenopterideum*; differt a genere *Sphenopteris segmentis anguste linearibus, uninervibus*" (Zimmermann, 1959, p. 727).

'*Rhodeopteridium*' *iporangae* (Ricardi-Branco, Faria, Jasper, and Guerra-Sommer) new combination
Figures 4–7

2011 *Hepaticites iporangae* Ricardi-Branco et al., p. 363, fig. 2.1.

Figure 4. Photographs of '*Rhodeopteridium*' *iporangae* n. comb. (from Ricardi-Branco et al., 2011, fig. 2). (**1**) Holotype MCNPbU 259, showing 2 (4) deeply dissected pinnatifid pinnules. (**2**) Detail of holotype MCNPbU 259 showing details of forking. (**3**) Detail of apical portion of holotype MCNPbU 259 showing lamina margins. (**4**) MCNPbU 246, lamina margins and central vein of the apical segments. (**5**) MCNPbU 244, showing portion of lobes with rounded tips and evident central veins. (**6**) Detail of MCNPbU 244 showing central veins with several rows of cells. (**7**) MCNPbU 259a, showing central vein with several parallel rows of cells, with thick cell walls at the point of branching. (**8**) MCNPbU 86, showing pinnatifid pinnule with five branchings with conspicuous central vein. (**9**) MCNPbU 269, showing pinnatifid pinnule with seven branchings. (**10**) MCNPbU 259, showing central vein cells of the lamina. (**1, 2, 8, 9**) Scale bars = 10 mm; (**3–5**) scale bars = 5 mm; (**6, 7**) scale bars = 1 mm; (**10**) scale bar = 0.5 mm.


1
2
3
4
5
6
7
1 mm
8
9
10

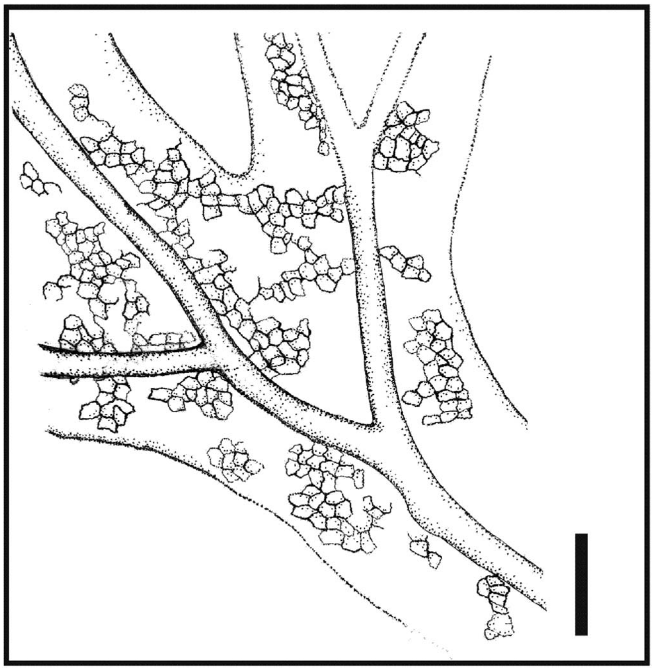


Figure 5. Line drawings of epidermal cell pattern of '*Rhodeopteridium*' *iporangae* n. comb. (from Ricardi-Branco et al., 2011, fig. 4.4), holotype MCNPbU 259: detail of lamina showing polymorphic epidermal cells. Scale bar = 0.25 mm.

Holotype.—Fragment of frond (MCNPbU 259, Fig. 4.1) from the Rio Bonito Formation, early Permian, Quitéria outcrop (30°17'S, 52°11'W), municipality of Encruzilhada do Sul, state of Rio Grande do Sul, Brazil (Ricardi-Branco et al., 2011).

Diagnosis.—Frond with pinnae, consisting of deeply dissected pinnatifid pinnules with narrow ± laminar lobes. Pinnules branching repeatedly and dichotomously in laminar lobes up to 1.6 mm in width. Lobes with entire margins, epidermal cells polymorphic (?), varying from 50 to 110 μm in diameter. Lobes of pinnules rather short with rounded tips. Central portion of rachis, pinnae, pinnules, and lobes with a single, rather thick vein at least vein of rachis composed of tracheids with helical thickenings on cell walls. Individual laminar lobes are shorter than in all other species of the genus.

Occurrence.—Quitéria outcrop (30°17'S, 52°11'W) Rio Bonito Formation, early Permian; municipality of Encruzilhada do Sul, state of Rio Grande do Sul, Brazil.

Description.—Fourteen specimens were studied. Pinnatifid pinnules deeply dissected into very narrow laminar lobes, alternating with angles between 25° and 90° (Figs. 4.1–4.4, 4.8, 4.9, 6.1). The pinnae are differentiated in up to nine pinnatifid pinnules with one to five narrow ± laminar lobes (Fig. 6.1). Pinnules are 13 to 23 mm long and around 10 to 17 mm wide (Figs. 4.1–4.10, 6.1, 6.2). Lobes repeatedly bifurcated, up to 5 mm long, with 0.5 to 1.59 mm very narrow lamina (Figs. 4.1, 4.8, 4.9, 6.1, 6.2). Epidermal cells polymorphic (?), varying from 50 to 110 μm in diameter (Figs. 4.10, 5). The midvein is up to 0.5 mm wide, running up to the tips (Figs. 4.1–4.9, 6.1). Tips rounded (Fig. 4.5, 4.6). Conducting tissue of rachis composed of tracheids with helical thickenings on cell walls (Fig. 7.1–7.4), 9–12 tracheids wide in proximal portions of pinnae (Fig. 4.6, 4.7, 4.9) and 6–8 tracheids in more distal portions (Fig. 4.10). Lumina of tracheids 9–11 μm wide (Fig. 7.1–7.4).

Materials.—MCNPbU 086a, 086b, 086c, 130, 244a, 244b, 246a, 246b, 246c, 246d, 254, 255, 259, 269b, and 269c.

Occurrence.—Quitéria outcrop (30°17'S, 52°11'W) Rio Bonito Formation, early Permian; municipality of Encruzilhada do Sul, state of Rio Grande do Sul, Brazil.

Remarks.—The presence of tracheid casts with helical thickenings has to be seen as undisputable evidence that *Hepaticites iporangae* is in fact not a liverwort as previously assumed by Ricardi-Branco et al. (2011) but a tracheophyte. Following the recognition that the material does not represent a liverwort, we assigned the material provisionally to the genus *Rhodeopteridium*, following the views concerning the validity of this genus presented by Pšenička and Schultka (2009). Due to this reinterpretation, we provided an emended diagnosis for the species based on a reinterpretation of the description by Ricardi-Branco et al. (2011) and data from new specimens. Unfortunately, it is not possible to compare the epidermal structures seen in the material from the Quitéria outcrop with information from other *Rhodeopteridium* species (e.g., Pšenička and Schultka, 2009). This is because neither SEM images (cf. Ricardi-Branco et al., 2011, fig. 3.1, 3.4) nor camera lucida drawings (cf. Ricardi-Branco et al., 2011, fig. 4.1–4.4; partly refigured here as Fig. 5) of the epidermal impressions on the rock surface allowed detailed insights into epidermal anatomy of the specimens investigated.

Although it has repeatedly been argued that Zimmermann (1959) used *Rhodeopteridium* as an illegitimate substitute for the genus *Rhodea* (e.g., Stepanek, 1987; Ameron and Kabon, 1999), this view is not generally accepted (e.g., Josten and Ameron, 2003; Pšenička and Schultka, 2009). A resolution of this nomenclatural problem is beyond the scope of the present contribution.

Most species assigned so far to the genus *Rhodeopteridium* are known from the Mississippian, but some occur in Pennsylvanian strata (e.g., Presl in Sternberg, 1838; Pšenička and Schultka, 2009; Hübers et al., 2014). Because many remains that may be assigned to this morphologically 'simple' taxon are rather fragmentary, many authors avoid assigning such material formally to the genus *Rhodeopteridium* (or *Rhodea*; Hübers et al., 2014) by using informal expressions like 'cf. *Rhodea* sp. foliage type' (e.g., Meyer-Berthaud and Rowe, 1997) or rhodeopterid frond (e.g., Boardman et al., 2012). For comparable material from the Rio Bonito Formation of the Paraná Basin, the generic assignment to *Rhodeopteridium* has repeatedly been used (e.g., Guerra-Sommer and Cazzulo-Klepzig, 1993; Jasper et al., 2003, 2005; Ianuzzi, 2010; Boardman et al., 2012), unfortunately without any in-depth morphological analysis and discussion of the respective specimens as well as their taxonomic treatment.

We also decided to place the species from Quitéria provisionally into the genus *Rhodeopteridium*, although there are other late Palaeozoic genera that include species with a comparable frond morphology, i.e., *Zeilleria* Kidston and

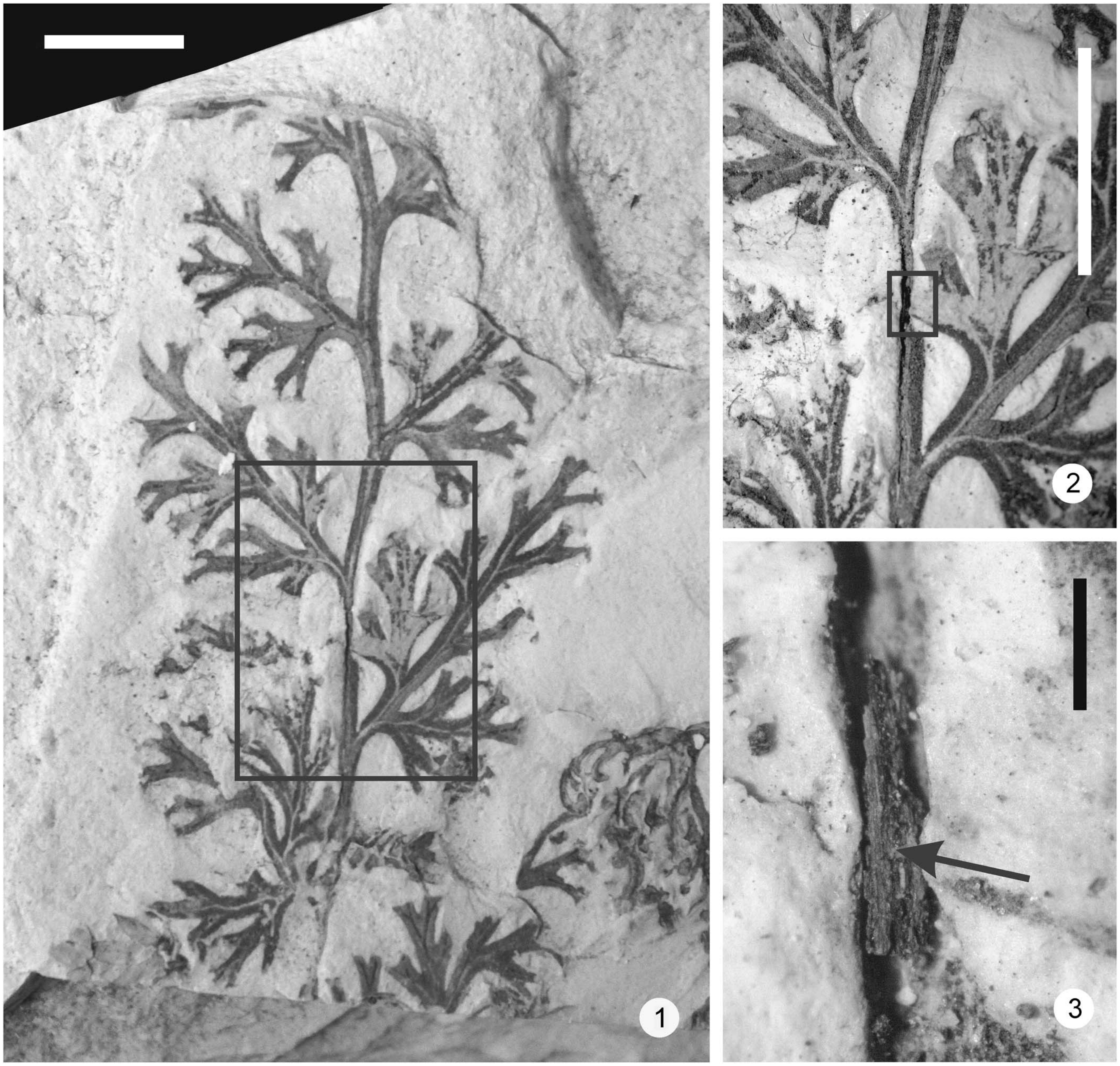


Figure 6. Photographs of '*Rhodeopteridium*' *iporangae* n. comb. (**1**) MCNPbU 254, largest specimen with 7 (9) deeply dissected narrow laminar lobed pinnatifid pinnules; box indicates position of (**2**). (**2**) MCNPbU 254, box indicates position of (**3**). (**3**) MCNPbU 254, enlargement of central area from which casts of tracheids were extracted (arrow). (**1, 2**) Scale bars = 10 mm; (**3**) scale bar = 0.5.

Palmatopteris Potonié. However, *Zeilleria* is mostly classified as a true fern (e.g., Pšenička, 2005), but there is no evidence that the specimens from the Quitéria outcrop represent remains of a fern; thus, we decided against such an affiliation. The genus *Palmatopteris* also includes fern-like species with sphenopterid pinnules, which are differentiated into very narrow laminar lobes. However, this genus is characterized by a double dichotomy of the main rachis (Potonié, 1892). As the specimens from the Quitéria outcrop are rather small and show no signs of such a double dichotomy, we decided against such an affiliation. As it is, the material from the Quitéria outcrop fits well within the generic diagnosis provided by Zimmermann (1959), although some doubts remain due to the relatively small size of all fragments.

The provisional reassignment of *Hepaticites iporangae* to '*Rhodeopteridium*' reduces the overall diversity of plants known from the Quitéria outcrop but increases the taxonomic robustness of the generic placement of this material with *Rhodeopteridium*. At the moment such a generic affiliation seems at least provisionally justified as the material fits well within the generic diagnosis presented by Zimmermann (1959) and used by previous authors (e.g., Pšenička and Schultka, 2009). However, compared to other species in this genus, the individual laminar segments are rather short

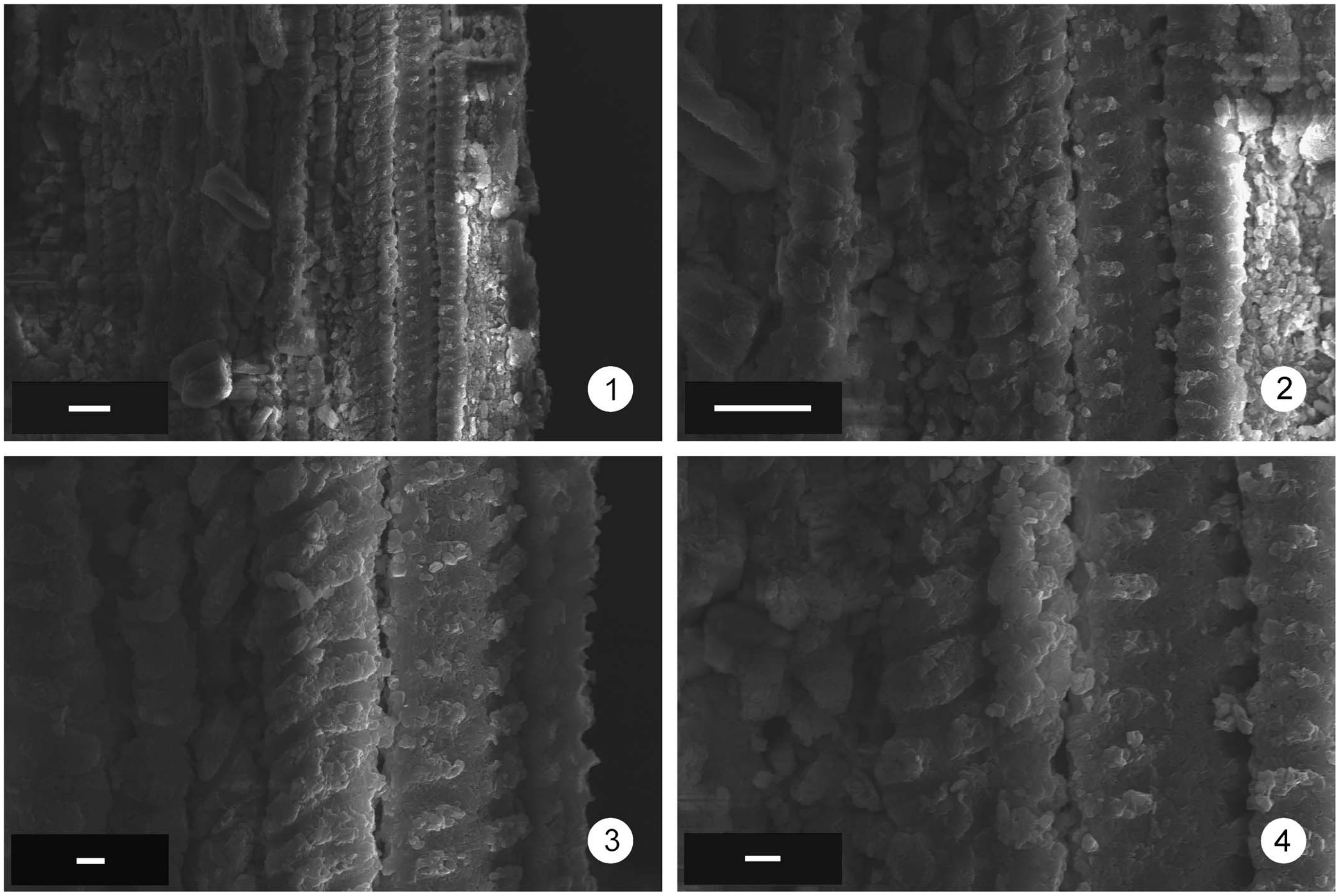


Figure 7. SEM photographs of casts of tracheids extracted from specimen MCNPbU 254. (**1, 2**) Scale bars = 10 µm; (**3, 4**) scale bars = 2 µm.

(a diagnostic character that distinguishes this species from all other species in the genus). At the moment, this difference does not justify erecting a new genus for the material from the Paraná Basin, considering the stratigraphic distribution of most taxa so far assigned to *Rhodeopteridium* and the fragmentary nature of the material from the Quitéria outcrop, which lacks meaningful information about epidermal (cuticular) anatomy. It is, however, possible that in the future new and more complete material will be recovered, which may fully justify assignment into *Rhodeopteridium* or may lead to changing the generic position of this material again.

Acknowledgments

The authors thank M. B. Horn (UNIVATES) for help with SEM facilities, as well as FAPERGS (Brazil), CAPES (Brazil), CNPq (Brazil), and Alexander von Humboldt Foundation (Germany) for funding.

References

Alves, R.G., and Ade, V.B., 1996, Sequence stratigraphy and coal petrography applied to the Candiota Coal Field, Rio Grande do Sul, Brazil: A depositional model: International Journal of Coal Geology, v. 30, p. 231–248. doi:10.1016/0166-5162(95)00041-0.

Amerom, H.W.J., and Kabon, H., 1999, Neue fossile Floren aus dem Nötscher Karbon (1. Teil): Carinthia, v. 2, p. 637–672.

Boardman, D.R., Tybusch, G.P., Iannuzzi, R., Dutra, T.L., and De Lima, L., 2006, Presença de *Glossopteris browniana* no topo do afloramento Quitéria, no Rio Grande do Sul (Permiano Inferior, Formação Rio Bonito, Bacia do Paraná): Gaea, v. 2, p. 9–17.

Boardman, D.R., Souza, P.A., Iannuzzi, R., and Mori, A.L.O., 2012, Paleobotany and palynology of the Rio Bonito Formation (Lower Permian, Paraná Basin, Brazil) at the Quitéria Outcrop: Ameghiniana, v. 49, p. 451–472. doi:10.5710/AMGH.5.7.2011.424.

Cavalier-Smith, T., 1998, A revised six-kingdom system of life: Biological Reviews of the Cambridge Philosophical Society, v. 73, p. 203–266.

Christiano-de-Souza, I.C., and Ricardi-Branco, F.S., 2015, Study of the West Gondwana Floras during the late Paleozoic: A paleogeographic approach in the Paraná Basin—Brazil: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 426, p. 159–169.

Gastaldo, R.A., DiMichele, W.A., and Pfefferkorn, H.W., 1996, Out of the icehouse into the greenhouse: A late Paleozoic analog for modern global vegetation change: GSA Today, v. 6, p. 1–7.

Guerra-Sommer, M., and Cazzulo-Klepzig, M., 1993, Biostratigraphy of the southern Brazilian Neopaleozoic Gondwana sequence: A preliminary paleobotanical approach: XII Internacional Congress of Carboniferous and Permian Geology, Buenos Aires, v. 2, p. 61–72.

Guerra-Sommer, M., Cazzulo-Klepzig, M., Santos, J.O.S., Hartmann, L.A., Ketzer, J.M., and Formoso, M.L.L., 2007, Radiometric age determination of tonsteins and stratigraphic constraints for the lower Permian coal succession in southern Paraná Basin, Brazil: International Journal of Coal Geology, v. 74, p. 13–27. doi:10.1016/j.coal.2007.09.005.

Guerra-Sommer, M., Cazzulo-Klepzig, M., Jasper, A., Kalkreuth, W., Menegat, R., and Barboza, E.G., 2008, Palaeoecological patterns at the coal roof-shale transition in an outcrop of the Permian Brazilian Gondwana: Revista Brasileira de Paleontologia, v. 11, p. 11–26.

Holz, M., França, A.B., Souza, P.A., Iannuzzi, R., and Rohn, R., 2010, A stratigraphic chart of the late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America: Journal of South American Earth Sciences, v. 29, p. 382–399. doi:10.1016/j.jsames.2009.04.004.

Hübers, M., Bomfleur, B., Krings, M., Pott, C., and Kerp, H., 2014, A reappraisal of Mississippian (Tournaisian and Visean) adpression floras from central and northwestern Europe: Zitteliana, v. 54, p. 39–52.

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

Iannuzzi, R., 2013, The Carboniferous–Permian floral transition in the Paraná Basin: New Mexico Museum of Natural History and Science Bulletin, v. 60, p. 132–136.

Jasper, A., and Guerra-Sommer, M., 1999, Licófitas arborecentes in situ como elementos importantes na definição de modelos deposicionais (Formação Rio Bonito – Bacia do Paraná – Brasil): Pesquisas, v. 26, p. 49–58.

Jasper, A., Guerra-Sommer, M., Cazzulo-Klepzig, M., and Menegat., R., 2003, The *Botrychiopsis* genus and its chronostratigraphic implication in Southern Paraná Basin: Anais da Academia Brasileira de Ciências, v. 75, p. 513–535. doi:10.15590/S0001-47652003000400009.

Jasper, A., Ricardi-Branco., F., and Guerra-Sommer, M., 2005, *Coricladus quiteriensis* gen. & sp. nov. a new conifer in Southern-Brazil Gondwana (lower Permian, Parana Basin): Anais da Academia Brasileira de Ciências, v. 77, p. 157–168. doi:10.1590/s0001-37652005000100012.

Jasper, A., Menegat, R., Guerra-Sommer, M., Cazzulo-Klepzig, M., and Souza, P.A., 2006, Depositional cyclicity and paleoecological variability in Quitéria Outcrop—Rio Bonito Formation, Paraná Basin, Brazil: Journal of South American Earth Sciences, v. 21, p. 276–293. doi:10.1016/j.jsames.2006.05.002.

Jasper, A., Uhl, D., Guerra-Sommer, M., and Mosbrugger, V., 2008, Palaeobotanical evidence of wildfires in the Late Paleozoic of South America—early Permian, Rio Bonito Formation, Paraná Basin, Rio Grande do Sul State, Brazil: Journal of South American Earth Sciences, v. 26, p. 435–444. doi:10.1016/j.jsames.2008.08.002.

Josten, K.H., and Amerom, H.W.J., 2003, Die Flora des Namur B aus Hagen-Vorhalle: Geologie und Paläontologie in Westfalen, v. 61, p. 1–303.

Meyer-Berthaud, B., and Rowe, N.P., 1997, A lower Carboniferous plant assemblage from Thuringia (Germany): Review of Paleobotany and Palynology, v. 97, p. 361–379.

Milani, E.J., Melo, J.H.G., Souza, P.A., Fernandes, L.A., and França, A.B., 2007, Bacia do Paraná: Boletim de Geociências da Petrobrás, v. 15, p. 265–346.

Montañez, I.S., Tabor, J.N., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, L.P., and Rygel, M.C., 2007, CO_2-forced climate and vegetation instability during late Paleozoic deglaciation: Science, v. 315, p. 87–91.

Pant, D.D., and Bhowmik, N., 1998, Fossil Bryophytes with special references to Gondwanaland forms, *in* Chopra, R.N., ed., Topics in Bryology. New Delhi, Allied Publishers, p. 1–52.

Potonié, H., 1892, Über einige Carbonfarne: Jahrbuch der Koeniglich Preussischen geologischen Landesanstalt und Bergakademie zu Berlin für das Jahr 1889, v. 10, p. 26–27.

Pšenička, J., 2005, Taxonomy of Pennsylvanian–Permian ferns from coal Basins in the Czech Republic and Canada [Ph.D. thesis]:, Faculty of Science, Charles University, Prague, Czech Republic, 185 p.

Pšenička, J., and Schultka, S., 2009, Revision of the Carboniferous genus *Rhodeites* Nemejc from European and American localities: Bulletin of Geosciences, v. 84, p. 241–256. doi:10.3140/bull.geosci.1105.

Rasband, W.S., 1997–2014. Image J, U.S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/.

Rees, P.M., Gibbs, M.T., Ziegler, A.M., Kutzbach, J.E., and Behling, P.J., 1999, Permian climates: Evaluating model predictions using global palaeobotanical data: Geology, v. 27, p. 891–894.

Ricardi-Branco, F., Faria, R.S., Jasper, A., and Guerra-Sommer, M., 2011, *Hepaticites iporangae* n. sp., Rio Bonito Formation, early Permian (Sakmarian), Paraná Basin, Brazil, Western Gondwana: Journal of Paleontology, v. 85, p. 360–368. doi:10.2307/23020051.

Salvi, J., Jasper, A., Ricardo-Branco, F., Bernades-De-Oliveira, M.E.C., and Guerra-Sommer, M., 2008, Record of the genus *Lycopodites* in the lower Permian of Paraná Basin, Brazil: Anais da Academia Brasileira de Ciências, v. 80, p. 553–563. doi:10.1590/S0001-37652008000300015.

Scotese, C.R., 2000, Paleomap project: http://www.scotese.com (accessed December 8, 2015).

Souza, P.A., and Marques-Toigo, M., 2003, An overview on the Palynostratigraphy of the upper Paleozoic strata of the Brazilian Paraná Basin: Revista del Museo Argentino de Ciencias Naturales, v. 5, p. 205–214. doi:10.2113/27.1.39.

Stepanek, I., 1987, Die Flora des unteren Oberkarbons von Diersburg-Berghaupten bei Offenburg (Mittlerer Schwarzwald) III: Pteridophylle (Filicatae und Lyginopteridae): Jahreshefte des geologischen Landesamtes Baden-Württemberg, v. 29, p. 169–208.

Sternberg, K.M., 1838, Versuch einer geognostischen botanischen Darstellung der Flora der Vorwelt: Gotlieb Hässe Söhne, Prague, v. 2, p. 81–220.

Torsvik, T.H., and Cocks, L.R.M., 2011, The Palaeozoic palaeogeography of central Gondwana, *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, v. 357, p. 137–166.

Zimmermann, W., 1959, Die Phylogenie der Pflanzen: Stuttgart, Gustav Fischer, 777 p.

Accepted 23 March 2016