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Rare Carboniferous and Permian glacial and non-glacial bryophytes and associated lycophyte megaspores of the Paraná Basin, Brazil: A new occurrence and paleoenvironmental considerations

Fresia Ricardi-Branco [a, *], Rosemarie Rohn [b], Marcia Emilia Longhim [c], Juliana Sampaio Costa [d], Ariel Milani Martine [d], Isabel Cortez Christiano-de-Souza [d]

[a] Instituto de Geociências, Universidade Estadual de Campinas, Campinas, SP, Postal Zone 13083-970, P. Box 6152, Brazil
[b] Instituto de Geociências e Ciências Exatas, Departamento de Geologia Aplicada, Universidade Estadual Paulista, Campus de Rio Claro, Rio Claro, SP, Postal Zone 13506-900, P. Box 178, Brazil
[c] Gerencia de Bioestratigrafia e Paleoecologia Aplicada, PDGEO, CENPES, PETROBRAS, Rio de Janeiro, RJ, Av. Horacio Macedo, 950- prédio, 20 sala, 1112 Ilha do Fundão, Postal Zone 21941-915, Brazil
[d] Programa de Pós-graduação em Geociências, Instituto de Geociências, Universidade Estadual de Campinas, Campinas, SP, Postal Zone 13083-970, P. Box 6152, Brazil

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ABSTRACT

Fossil bryophytes are rare because their preservation is compromised by the presence of a thin cuticle (if any) and a lack of lignin. Except for the occurrence of one bryophyte in the glacial Dwyka Group of the Karoo Basin, the other rare Late Paleozoic records in Gondwana are notably from the Paraná Basin in Southeast/South Brazil. Four bryophyte sites (including a newly discovered one) were found in the lower part of the thick Permo-Carboniferous glacial succession of the Itararé Group, and one was found in the Guadalupian Teresina Formation, which was roughly assigned to an epeiric sea (or "lake") dominated by a warm, semi-arid climate. This study describes the fossils from the new occurrence from the Itararé Group and discusses the context in which the bryophyte beds originated in the basin. The new samples confirm that all of the bryophytes of the Itararé Group can be classified as *Dwykea araroii* Ricardi-Branco et al. (a possible pleurocarp) and are associated with the lycophyte megaspore *Sublagenicula brasiliensis* (Dijkstra) Dybová-Jachowicz. In the much younger Teresina Formation, the bryophytes are *Yguajemanus yucapirus* Cristiano-de-Souza et al. and *Capimirinus riopretensis* Cristiano-de-Souza et al., and abundant charophytes and rare dwarf lycophyte stems and bracts are present in the same layers. Although the two stratigraphic units represent distinct paleoenvironments and climates, they seem to share some characteristics: a) the bryophyte assemblages were transported very little; b) they were deposited in very calm environments; c) they were the main components (along with some lycophytes) of local or poorly diversified regional vegetation. The low number of species, which is characteristic of opportunistic communities, can be explained by local or regional conditions that would have been stressful for the vascular plants in other areas. During the deposition of the Itararé Group, the main control was probably the cold climate in addition to a relative (liquid) water deficit because the bryophyte vegetation may have belonged to a tundra biome in areas of retreating glaciers. For the Teresina Formation, it is possible that the control was scarce freshwater, an unstable environment and water-saturated soil in a scenario of bryophyte vegetation living around temporary ponds in a wide marginal area of the epeiric sea.

1. Introduction

Mosses (Class Bryophyta), in contrast to tracheophytes, are small, fragile "non-vascular" plants, which are generally without conducting tissues and lack lignin (Taylor et al., 2009). A particularly distinctive characteristic of bryophytes is the dominance of the

* Corresponding author.
E-mail addresses: fresia@ige.unicamp.br (F. Ricardi-Branco), rohn@rc.unesp.br (R. Rohn), melonghim@petrobras.com.br (M.E. Longhim), sampaiojcosta@gmail.com (J.S. Costa), ariel_bia@yahoo.com.br (A.M. Martine), isabel.cortez@ige.unicamp.br (I.C. Christiano-de-Souza).

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haploid (gametophyte) generation in their life cycle, including the possibility of an occasional sporophyte phase (Frey, 2009; Taylor et al., 2009). Acrocarpic specimens found in the Mississippian of Germany, which are related to ancestral forms, are traditionally believed to be the oldest fossil mosses (http://www.amjbot.org/content/102/11/1883.fullHübers and Kerp, 2012), and the earliest pleurocarpic mosses are evidenced in the Permian of Gondwana (Cristiano-de-Souza et al., 2012; Johnson et al., 2016). However, the Mesozoic moss record is more diverse than that of the Late Paleozoic (Shelton et al., 2015).

Some Devonian fossils are similar to bryophytes, but their affinities are uncertain, or they probably belong to other plant groups. One example is the Upper Devonian fossil that was first designated as *Hepaticites devonicus* Hueber (1961) and later moved to *Pallavicinites* (Goffinet et al., 2009). According to biophysical and morphological criteria as the size, Boyce (2008) suggested that Silurian-Early Devonian cooksonioid specimens may correspond to moss sporophytes, which may have been too small for sufficient aerated photosynthetic tissue. Gerrienne et al. (2006) proposed that the supposedly Eutracheophyta *Cooksonia paranaensis* from the Paraná Basin had a liverwort-like habit.

Bryophytes have been regarded as pioneer plants of deglaciated areas, but the preservation potential of these delicate plants in such sedimentary environments is very low. Therefore, the rare proglacial bryophyte fossils, such as those related to the Carboniferous-Permian Gondwanic glaciation, are very intriguing (Barclay et al., 2013).

The bryophytes described herein record, in part, a vegetation of a cold climatic context during the Late Paleozoic Ice Age (LPIA, Parrish et al., 1986; Fielding et al., 2008).

They were found in three previously known outcrops (Ricardi-Branco et al., 2013) and a new one of the Itararé Group in the northern portion of the Paraná Basin (State of São Paulo, southeastern Brazil, Western Gondwana). These elements were preserved in association with megaspores.

The only non-glacial bryophytes of the Paraná Basin are recorded in a single outcrop of the Guadalupian Teresina Formation (Cristiano-de-Souza et al., 2012).

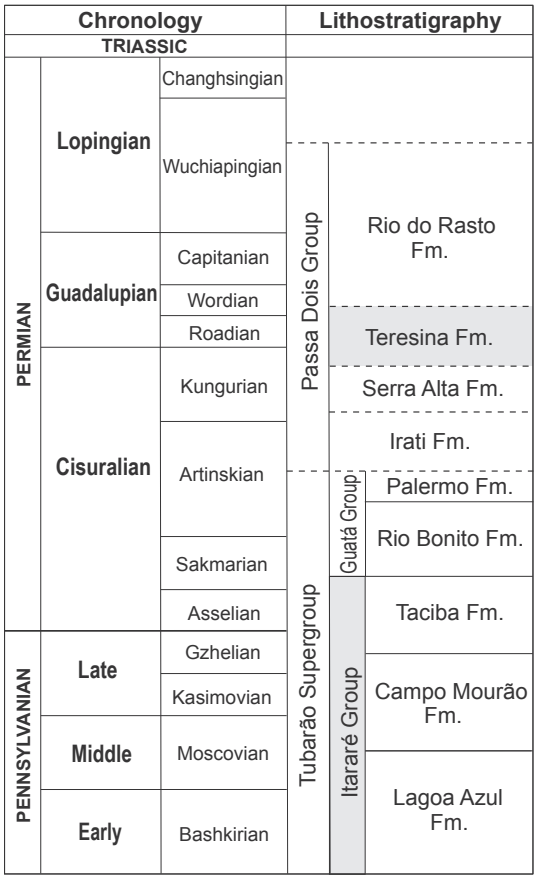

Fig. 1. Cronostratigraphy of the Paraná Basin during Gondwana 1 Supersequence (Milani et al., 1998). Ages of the Tubarão Supergroup according to Holz et al. (2010) and Passa Dois Group by Ferreira-Oliveira and Rohn (2010). Gray-coloured lothostratigraphic units contein bryophyte records.

2. Regional Geology and Paleontology

The Paraná Basin (*s.l.*) encloses a large intracratonic syneclise in central-southern South America that was directly connected to the Chaco Basin (Argentina and Paraguay) and linked by seaways and/or continental environments to the Cape-Karoo Basin (South Africa) and the Huab Basin (Namibia) (Milani and DeWitt, 2008). The Ordovician to Cretaceous sedimentary fill is divided into six depositional sequences (Milani et al., 2007), of which the Carboniferous-Permian interval (Supersequence Gondwana I), 1.5–2.4 km thick, comprises the Itararé, Guatá and Passa Dois groups (Fig. 1) (Milani et al., 2007; Bocardi et al., 2009). During this time, a probable clockwise rotation and northward movement of the Gondwana plate, as well as other global changes, caused a shift from a cold to a warm semi-arid climate in the Paraná Basin (Milani and DeWitt, 2008).

The Itararé Group encompasses one of the most expressive records of the Late Paleozoic Ice Age – LPIA in Southwestern Gondwana (Castro, 2004). According to palynological data (Souza, 2006; Souza et al., 2010) and the radiometric ages of overlying post-glacial strata (Rio Bonito Formation) (Souza, 2006; Holz et al., 2010), the deposition of the Itararé Group began in the Moscovian (Pennsylvanian) and ended in the Sakmarian (Cisuralian).

This unit is characterized by a great variety of lithofacies: claystones, sandstones, conglomerates, diamictites, varvites, turbidites, and thin coal seams, which formed in marine, coastal and continental environments under glacial, proglacial, and interglacial conditions (Rocha-Campos et al., 2008). A different interpretation is that almost all of the deposits represent deglaciation sequences (ice-retreat depositional tracts in stratigraphic sequences), and only small intercalated intervals may correspond to ice-advances (Vesely and Assine, 2006). Several fossils, such as brachiopods, mollusks, foraminifers, insects, fishes, and plants, are recorded in the Itararé Group. The marine fossils indicate that the paleoenvironments were mostly marine (Vesely and Assine, 2006; Rocha-Campos et al., 2008), but the origin of some rocks remains controversial (Rocha Campos et al., 2008). The most important vascular plant occurrences are associated with coally beds in the states of Rio Grande do Sul and São Paulo, which are likely related to interglacial intervals (Bernardes-de-Oliveira et al., 2005). The youngest interglacial interval has the first elements of the *Glossopteris* Flora (Rösler, 1978; Rohn et al., 2000).

In the northeastern portion of the Paraná Basin (State of São Paulo), where the studied fossils were collected, the Itararé Group is exposed in a narrow NE-SW strip, although it reaches its greatest thicknesses in this region (approximately 1300 m; Vesely and Assine, 2006). The studied fossiliferous beds occur in the lower part of the group, only a few meters above the Precambrian basement, but the lower boundary of the unit is irregular because of glacial erosion. The depositional basin was a semi-isolated glacial inlet or estuary with salinity controlled by sea-level change (Rocha-