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Biostratigraphic and paleoclimatic significance of *Botrychiopsis* fronds in the Gondwana realm

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Abstract

The temporal, geographical and environmental distribution pattern of *Botrychiopsis* in Gondwana Realm is established, considering new data about its distribution which is closely related to the evolution of a Late Paleozoic icehouse stage. The first record of the genus was related to the early interglacial phases within assemblages similar to tundra or taiga, under cold periglacial climate in the Namurian/Westphalian glacial episode. *Botrychiopsis* distribution area in Gondwana became wider in Westphalian/Stephanian, occupying hygro-mesophilous niches, in warming conditions. *Botrychiopsis plantiana* was a typical element in interglacial phases of the glacial episode that peaked in the Asselian/Sakmarian, when *Botrychiopsis weissiana* was extinct. At the end of deglaciation, *Botrychiopsis valida* became a common element in floral assemblages related to coal-forming environments, as well as in mudstones deposited under warm temperate climate. The results confirm the importance of the different species of *Botrychiopsis* as biostratigraphic markers in the Late Paleozoic of Gondwana. The genus had a broader climate tolerance than was initially thought, ranging from cool-temperate to warm-temperate climates in the interglacial periods and also closely related to the final of the deglaciation phase.

Keywords: biostratigraphy, *Botrychiopsis*, Gondwana, paleoclimatology.

Introduction

In Gondwana Paleozoic floras, *Botrychiopsis*, composed of fronds with substantial heteromorphism, presents botanical affinity with either Filicopsida (Schimper & Mougeout, 1844 and Blanckenhorn, 1885), or Cardeopterid (Kurtz, 1895) and Gymnospermopsida/Pteridospermales (Maithy, 1965; Archangelsky & Arrondo, 1971; Artabe et al., 1987). As the natural affinities of the genus have not been established, in the present paper *Botrychiopsis* is considered as a Pteridophyll.

The diagnostic features that are useful to distinguish the three designated species were also determined by Archangelsky & Arrondo (1971): *Botrychiopsis weissiana* (Kurtz) Archangelsky & Arrondo (1971) (Fig. 1a), *Botrychiopsis plantiana* (Carruthers) Archangelsky & Arrondo (1971) (Fig. 1b), *Botrychiopsis valida* (Feistmantel) Archangelsky & Arrondo (1971) (Fig. 1c). According to these authors the definition of different *biochrons* for the distinct species of *Botrychiopsis* attests to its chronostratigraphic relevance. In the first reference to the chronostratigraphic use of *Botrychiopsis*, Archangelsky & Arrondo (1971) indicate a stratigraphic distribution ranging from Late Carboniferous (Westphalian) to Early Permian (Artinskian). Later studies performed in different basins have confirmed the stratigraphic importance of the different species.

The stratigraphic distribution of *Botrychiopsis* has usually been restricted to the beginning of interglacial periods, always related to cold/cool temperate climates (Archangelsky, 1971, 1978, 1984; Rocha-Campos & Archangelsky, 1985; Retallack, 1980, 1999) within assemblages similar to the present-day tundra and taiga.

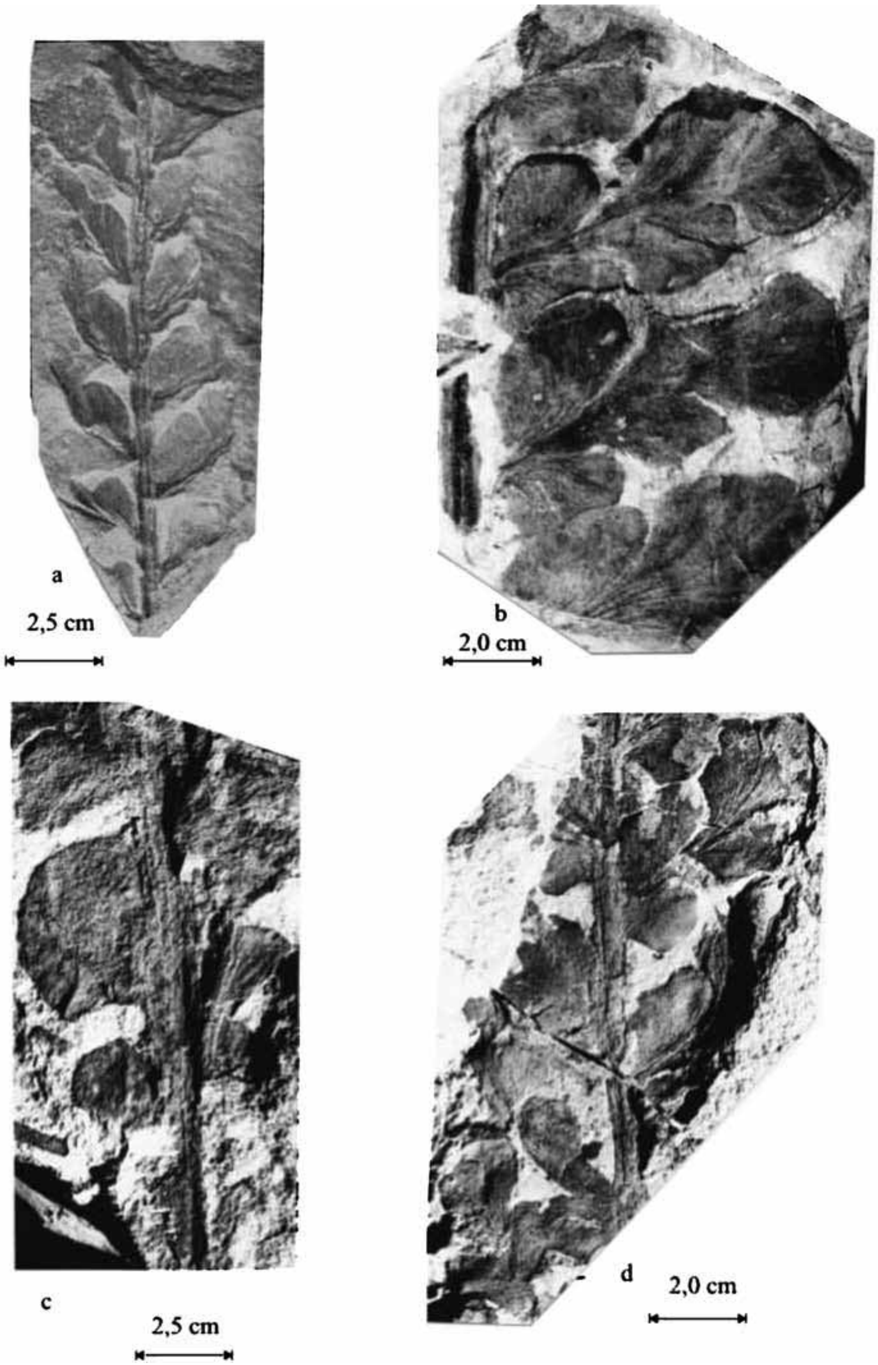

Fig. 1. (a) *Botrychiopsis weissiana* (reproduced from Archangelsky & Arrondo, 1971, Lâm. II, fig. 3 – PB n° 874 – Retamito, Sa. de La Rinconada, San Juan, Argentina); (b) *Botrychiopsis plantiana* (reproduced from Jasper et al., 2003, fig. 3b – PB 2677 – Morro Papaléo Outcrop, Brazil); (c) *Botrychiopsis valida* (reproduced from Jasper et al., 2003, fig. 5c – PbU 0062 – Quitéria Outcrop, Rio Grande do Sul, Brazil); (d) *Botrychiopsis valida* (reproduced from Jasper et al., 2003, fig. 5d – PbU 0061 – Quitéria Outcrop, Rio Grande do Sul, Brazil).

In his attempt to describe phytogeographic patterns and continental configurations during the Permian, Ziegler (1990) included *Botrychiopsis* as a component of both cold temperate (ranging from forest to taiga) and arctic (tundra) biomes. Vijaya et al. (1996) considered *Botrychiopsis* as a characteristic genus of Gondwana, reflecting floral regionalism during the Late Carboniferous (Namurian B and C, Westphalian and Stephanian). Anderson et al. (1999), integrating several previous ideas, characterized the *Nothorhacopteris/Botrychiopsis* Flora as a low-diversity flora that bordered the ice caps in the Late Carboniferous of the Gondwana continent.

However, a review on the distribution of species attributed to *Botrychiopsis* within different Gondwana basins has shown that they are part of stratigraphic successions that represent a broader time interval, encompassing not only glacial but also coal-bearing sedimentary strata. The main goal of this study is to review the stratigraphic range of *Botrychiopsis* within Gond-

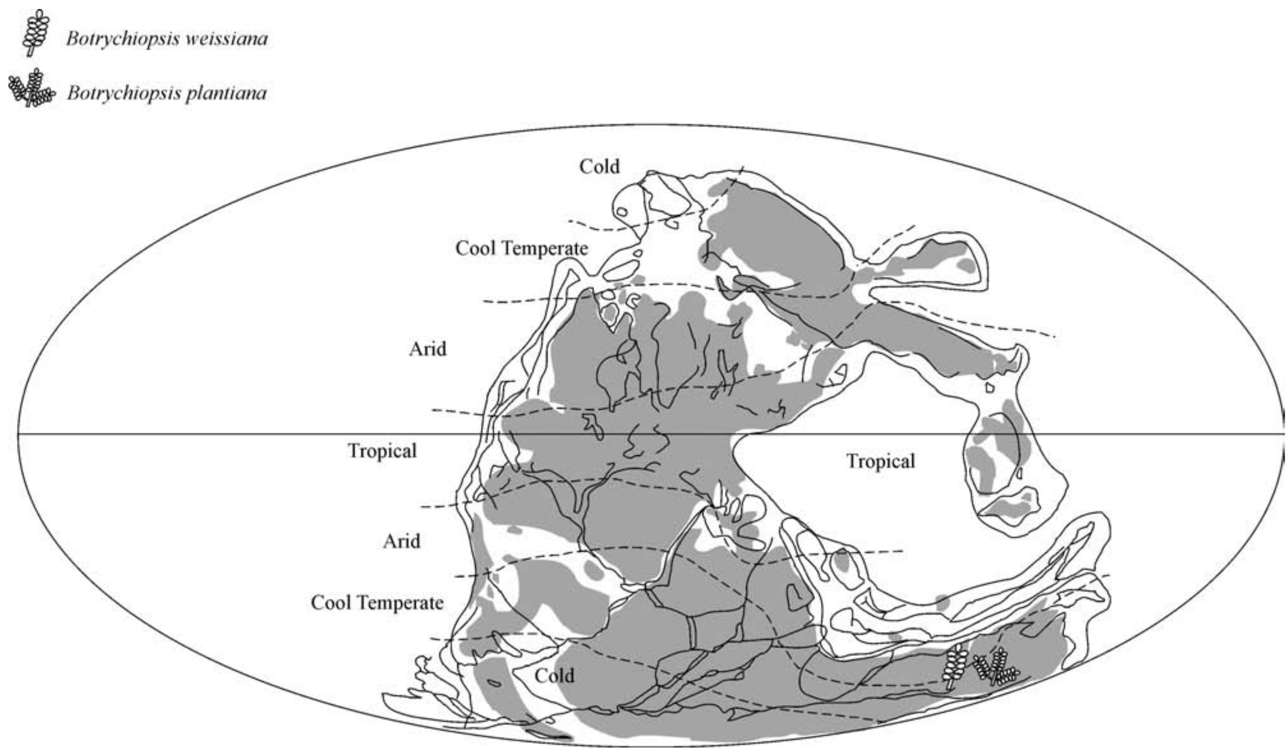

Fig. 2. Global distribution of *Botrychiopsis* during the Westphalian – Upper Carboniferous (paleomap adapted from Scotese, 2000).

wana and to tie its record to specific paleoclimatic and paleoenvironmental conditions.

The paleofloristic data presented here have been plotted on to the paleogeographic reconstructions of Scotese & McKerrow (1990).

The chronostratigraphic relevance of *Botrychiopsis* in Gondwanaland

The history of the genus began in the Westphalian with the record of *Botrychiopsis weissiana* and *Botrychiopsis plantiana* in Australia (Fig. 2). Forms described as *Adiantites robusta* by Walkom (1934) in paleofloras of Late Paleozoic successions of Australia (New South Wales), were re-described as *Botrychiopsis weissiana* by Archangelsky & Arrondo (1971).

Rigby (1973) established a revision of pteridospermic fronds from Eastern Australia, Argentina and Kashmir, characterizing a Westphalian/Stephanian *Gondwanidium* Flora, which followed the Namurian/Stephanian *Pseudorhacopteris* Flora, near the local Westphalian/Stephanian boundary in New South Wales. Nowadays the base of the *Botrychiopsis* Flora, is defined by the first appearance of *Botrychiopsis plantianum*, associated with glaciogenic sediments and probably related to climate changes (Anderson et al., 1999).

Retallack (1980), through the study of fossil plants and palynology, established distinct floral assemblages from Carboniferous to Middle Triassic rocks of the Sydney Basin. The presence of *Botrychiopsis weissiana* is recorded in the *Sphenopteridium* Flora, which is considered pre-glacial (Mount Johnstone Formation – Visean/Namurian). According to Jones et al. (1974) this paleoflora is coeval to the *Levispustula levis* brachiopod assemblage. However, radiometric dating of these rocks yielded ages between 323 and 302 m.y. corresponding to the Namurian/Moscovian interval (Roberts et al., 1996). Analysis of specimens precedent of pre-glacial successions of the Mount Johnstone Formation, stored at the National Australian Museum (PB 77976) and ascribed to *Botrychiopsis weissiana*, indicates that these forms don't present the diagnostic characteristics of *Botrychiopsis* (Roberto Iannuzzi, personal communication). The features observed in the specimens are identifiable to either *Triphyllopteris austrina* or *Bergiopteris*, as Rigby (1993) and McLoughlin (1995) previously noticed. Therefore, the inferences of Retallack (1980) about forms hypothetically related to *Botrychiopsis* and their relation to climate should not be taken into account.

Stratigraphic studies performed in Argentinean basins by Archangelsky et al. (1987) deemed the record of *Botrychiopsis weissiana* to be restricted to the *Nothorhacopteris argentinica*, *Botrychiopsis weissiana*–*Ginkgophyllum diazii* (NBG) zone. Later, Archangelsky & Cúneo (1981, 1991) suggested the existence of an interval zone between the NBG and *Gangamopteris* zones of those basins, in which *Botrychiopsis weissiana* and *Botrychiopsis plantiana* were coexistent.

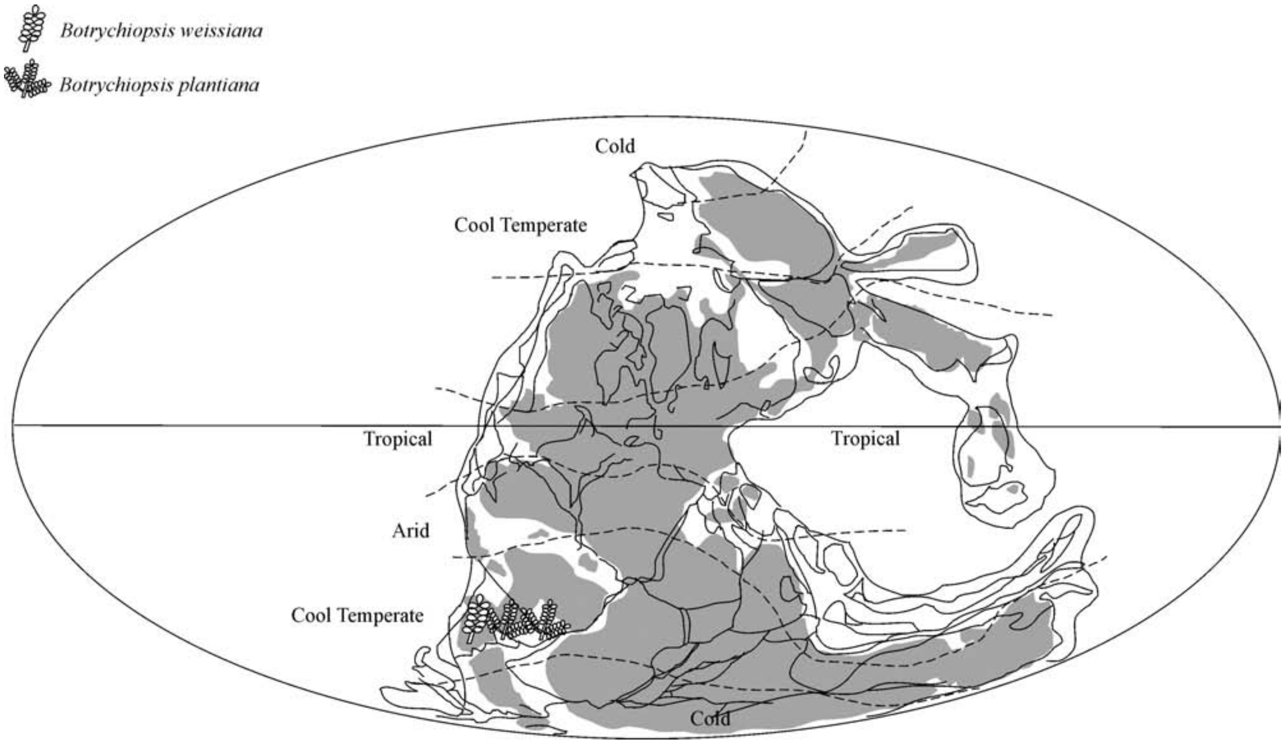

Fig. 3. Global distribution of *Botrychiopsis* during the Westphalian/Stephanian interval – Upper Carboniferous (paleomap adapted from Scotese, 2000).

Andreis & Archangelsky (1996) outlined a phytostratigraphic donation for the Upper Paleozoic, in which *Botrychiopsis* is considered as a valuable stratigraphic marker. In their framework (pag. 392, table I.2), the *Nothorhacopteris argentinica*, *Botrychiopsis weissiana – Ginkgophyllum diazii* (NBG) zone (Westphalian/Stephanian) was recognized in the Argentinean Paganzo, Rio Blanco, Calingasta-Uspallata and St. Raphael basin, according Sessarego & Césari (1986).

In slightly younger (Westphalian/Stephanian) deposits of Argentina (Paganzo, Rio Blanco, Calingasta-Uspallata, San Rafael basins), *Botrychiopsis plantiana* still appears associated with the ancestral species *Botrychiopsis weissiana* (Fig. 3).

An informal phytozonation for the Paraná Basin of Brazil was proposed by Rösler (1978), using previous data of Carruthers (1869), White (1908), Dolianiti (1948), Lundqvist (1919) and Millan (1975), documenting *Botrychiopsis plantiana* in Fossil Flora A. This taphoflora was included in a succession that was spread over the entire Paraná Basin during the early phases of the Late Carboniferous deglaciation. Andreis & Archangelsky (1996), in a review of the Late Paleozoic basins of Southern South America, attributed a Stephanian age to this fossil flora.

While defining floral levels for the coal seams, occurring interlay with glaciogenic sequences of Paraná Basin (Itararé Group) Milan (1987) characterized the Monte Mór Fossil Flora (Montemorense Level) which was ascribed to the Westphalian/Stephanian and correlated to the *Potonieisporites/Lundbladispora* Zone of Archangelsky & Césari (1986). *Botrychiopsis plantiana* constitutes the most important element within Montemorense Level.

Zampirolli (2001) revised the type locality of the Montemorense Level (Santa Marta Flora). Some important diagnostic elements, such as *Eusphenopteris* sp. and *Nothorhacopteris* cf. *argentinica*, were included along with *Botrychiopsis*. Fossil plants and microflora data suggest a Westphalian/Stephanian age for the Santa Marta Flora.

Botrychiopsis is not registered in paleofloras from the Upper Carboniferous of Southern Africa and India. It must be highlighted that the absence of this genus may be the result of a lack of significant deposits of this age and/or the absence of sediments suitable for preservation of plant fossils.

Botrychiopsis plantiana was geographically and temporally more confined to the basal Early Permian. The species is recorded in the Asselian/Sakmarian of Australia (Joe Joe Formation, Sydney Basin), Argentina (Arroyo Totoral Formation, Paganzo Basin, and Bajo de los Vélez Formation, Paganzo Basin) and Brazil (Itararé Group, Southernmost Paraná Basin).

In Australia, *Botrychiopsis ovata* (synonymized to *Botrychiopsis valida* by Archangelsky & Arrondo, 1971) persisted throughout the initial phases of climate amelioration, after the glaciation (Retallack, 1980). It was then associated with *Gangamopteris* and *Noeg-*

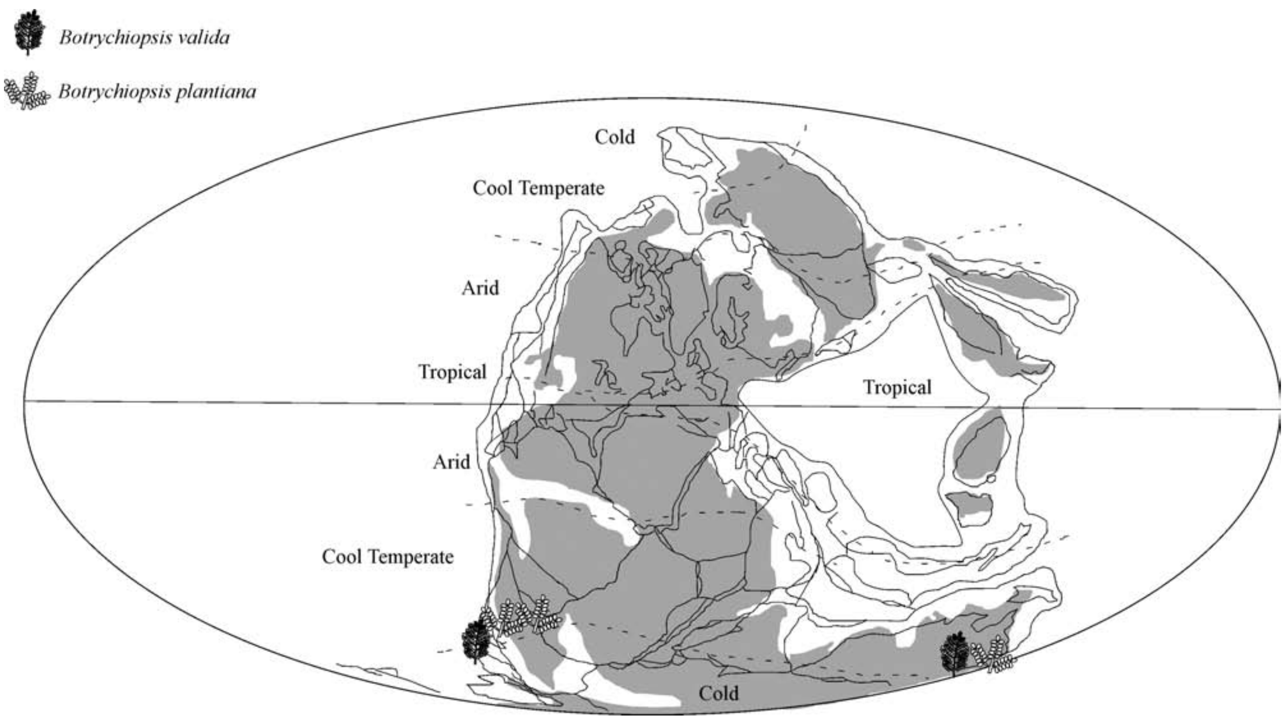

Fig. 4. Global distribution of *Botrychiopsis* during the Asselian/Sakmarian interval – Lower Permian (paleomap adapted from Scotese, 2000).

gerathiopsis in Early Permian coastal peatlands (Joe Joe Formation of the Markwell Coal Measures – Central Queensland). These assemblages corresponded to the Taiga *Gangamopteris* (Retallack, 1980), correlated to the *Protohaploxipinus* Zone or Stage 2 of Kemp et al. (1977). Rigby (1983) established a range of megafloras after Retallack (1980), characterizing a *Botrychiopsis* Flora interval (Stephanian/Permian), with *Botrychiopsis ovata* (Mc'Coy) Rigby (synonymized to *Botrychiopsis valida* by Archangelsky & Arrondo, 1971) as *index taxon* for the zone.

In a biozonation of Southern Paraná Basin proposed by Guerra-Sommer & Cazzulo-Klepzig (1993), the most striking feature of the basal Sakmarian/Artinskian *Botrychiopsis plantiana* Zone is the dominance of *Botrychiopsis plantiana* in association with protoglossopterids (*Rubidgea)* and glossopterids, mostly represented by *Gangamopteris*. The association is preserved in sandstone packages corresponding to lowland glacio-continental sediments (Itararé Group). Guerra-Sommer et al. (2001) assumed a gradual change in the flora during the initial phases of deglaciation of the icehouse stage at the Asselian/Sakmarian boundary (Fig. 4). The onset of a cold/cool temperate climate occurred together with the reorganization of the hygro-mesophilous elements.

The earliest record of *Botrychiopsis valida* associated with swamps related with coal forming floras is made by Cúneo (1987), in the Arroyo Totoral Formation (Paganzo). According to Andreis & Archangelsky (1996), the coal seams were formed by assemblages dominated by arborescent lycophytes associated with swamps developed on alluvial fans or deltas.

Botrychiopsis valida occurs exclusively in the *Ferugliocladus* Superzone, *Gingkoites* Zone (Asselian/Sakmarian) of Archangelsky & Cúneo (1984), which is typified, besides *Botrychiopsis valida*, by some exclusive *taxa* as *Barakaria dichotoma*, *Genoites patagonica* and *Cordaites casildensis*.

The presence of *Botrychiopsis valida* in these lycopod-dominant swamp floras indicates a significant climatic warming, reached only in Artinskian/Kungurian in other gondwanic regions. Their evidences could be explained by the alternative view of Cúneo (1989), in relation of the concepts of Archangelsky (1990) about the Western Upper Paleozoic Gondwana floras. According to his hypothesis, three floristic regions, the Patagonian, the Paganzo/Precordillera and the Chacoparana had developed in South America. The Patagonian Region's sub-tropical climate and highly diversified flora persisted, according to Cúneo (1989), throughout the Permian.

The presence of *Botrychiopsis valida* in South Africa, in the Karoo Basin floras is well-documented by Plumstead (1952, 1956), Rayner (1985, 1986), Rayner & Coventry (1985), Anderson & Anderson (1985) and Kóvack-Endrödy (1991), all of them related to the Vereeniging Flora. This fossil flora occurs in contemporaneous outcrops associated with refractory clays interlay within coal seams (Leukuil Quarries) comprising the Upper Ecca Group paleofloras (*sensu* SACS, 1980), assigned to Early Permian (Anderson & Anderson, 1985) or Late Permian (Rayner & Coventry, 1985; Kóvack-Endrödy, 1991). Anderson & Anderson (1985) and Anderson et al. (1999) included the paleobotanical content present in the different localities within a single megafloral assemblage related to the Vryheid Formation. This unit represents a well-defined regressive cycle encompassing coal-forming environments such as delta front and delta plain. According to those authors, two plant-communities can be defined: one of them, dominated by glossopterids, with the occurrence of *Glossopteris*, *Azaniodendron*, *Cyclodendron*, *Sphenophyllum*, *Annularia* and *Phyllotheca*, as components of forests with medium diversity, along river banks, and a second one, primarily composed of monospecific arborescent lycophytes, to which *Botrychiopsis* – type creeping vegetation is associated with, developed in interdistributary fans and swamps. Rayner (1995) inferred a seasonal, warm temperate climate for the Vereeniging assemblages. In these assemblages, *Botrychiopsis valida* is also considered as an element of the creeping vegetation.

In India, *Botrychiopsis valida* is cited as a common element in coeval floras of the Giridish, Damuda of Deogarh, Karanpura, Auranga, Hutar, Daltonganj, Umaria (Rewah), Pali (Johilla), Mohpani (Narbada Valley) and Shahpur (Betul) coal measures, frequently preserved in siltstone beds interlay with coal seams, in Kaharbary stage Early Artinskian (Maithy, 1965; Surange, 1975; Shah et al., 1971; Chandra & Tewari, 1991; Maheshawari, 1992; Maithy, 1965; Pant & Gupta, 1968).

Venkatachala (1992) associated the presence of *Botrychiopsis valida* in the Kaharbari Stage as well as *Euryphyllum*, *Rubidgea* and *Buriadia*, with a climate improvement. Forms such as *Euryphyllum*, *Gangamopteris* and *Glossopteris* are more conspicuous in the Kaharbari Stage than in the underlying Talchir Stage, which is characterized by low species diversity. Srivastava (1997) assumed that the Kaharbari flora is clearly distinct from the underlying, Talchir Flora that is strongly influenced by glaciation and also from the overlying Barakar Flora, the latter being related to the main coal-bearing strata that were deposited in India under a warm temperate climate.

The record of *Botrychiopsis valida* in megafloras from Kungurian roof-shale of Southern Paraná Basin (Quitéria outcrop in the Rio Grande do Sul State), in association with glossopterids (*Glossopteris*, *Gangamopteris*, *Rubidgea*), Filicophyta (*Rhodeopteridium*?), conifers (*Coricladus quiteriensis*), arborescent Lycophyta (*Brasilodendron pedroanum*) and herbaceous Lycophyta (*Lycopodites*) demonstrates a broader distribution of the genus in the Gondwana (Jasper et al., 2003). Zircon radiometric dating of volcanic rocks interbedded in coal seams of the Rio Bonito Formation in Southernmost Paraná Basin, made by Cazzulo-Klepzig (2001) yielded an age of 267.1 ± 3.4 My wish corresponds to the Kungurian-Roadian. Based on these evidences Jasper et al. (2003) proposed a new phytostratigraphic framework in which a *Botrychiopsis* Zone (Asselian/Kungurian) is delimited. It comprises two sub-zones, the Sakmarian/Artinskian *Botrychiopsis plantiana* and the Early Artinskian to Late Kungurian *Botrychiopsis valida* sub-zones (Fig. 5).

The establishment of abundant lycophyte trees was the major floral change in wet coastal plant communities at the Kungurian, which were before dominated by glossopterid communities; ferns became important components of the understory communities in these biomes. This rapid transition was related to the final period of the glaciation of an ice age, when physical stress was expressed (Guerra-Sommer et al., 2001).

Therefore, the data presented herein broaden *Botrychiopsis* biochron and characterize a stratigraphic hierarchy regarding *Botrychiopsis plantiana* and *Botrychiopsis valida*. In Southern Paraná Basin, *Botrychiopsis plantiana* occurs in Asselian/Artinskian strata whereas *Botrychiopsis valida* is restricted to the Kungurian.

Conclusions

The temporal, geographical and environmental distribution pattern of the *Botrychiopsis* genus is closely related to the evolution of a Late Paleozoic icehouse stage. Figure 6 summarizes the time and geographical distribution of the different *Botrychiopsis* species within the Gondwana continent, and its relationships with the Glacial and IRD Frequencies (Frakes et al., 1992). The appearance of *Botrychiopsis* is associated with the early interglacial phases in the Namurian/Westphalian glacial episode, within assemblages similar to tundra or taiga, under cold, periglacial climate (Retallack, 1980, 1999). Throughout deglaciation, *Botrychiopsis* distribution area in Gondwana became wider by means of adapting itself to warming conditions, which took place during the Westphalian/Stephanian, and occupying hygromesophilous niches (Guerra-Sommer, 1989).

The floras connected to the early interglacial phases, following the glacial episode that peaked in the Asselian/Sakmarian, are differentiated by the presence of *Botrychiopsis plantiana* and the absence of *Botrychiopsis weissiana*, the latter being extinct at the Carboniferous/Permian boundary. At the end of deglaciation, *Botrychiopsis* (with the species *Botrychiopsis valida*) became a very common element in floral assemblages related to coal-forming environments, under cool/warm

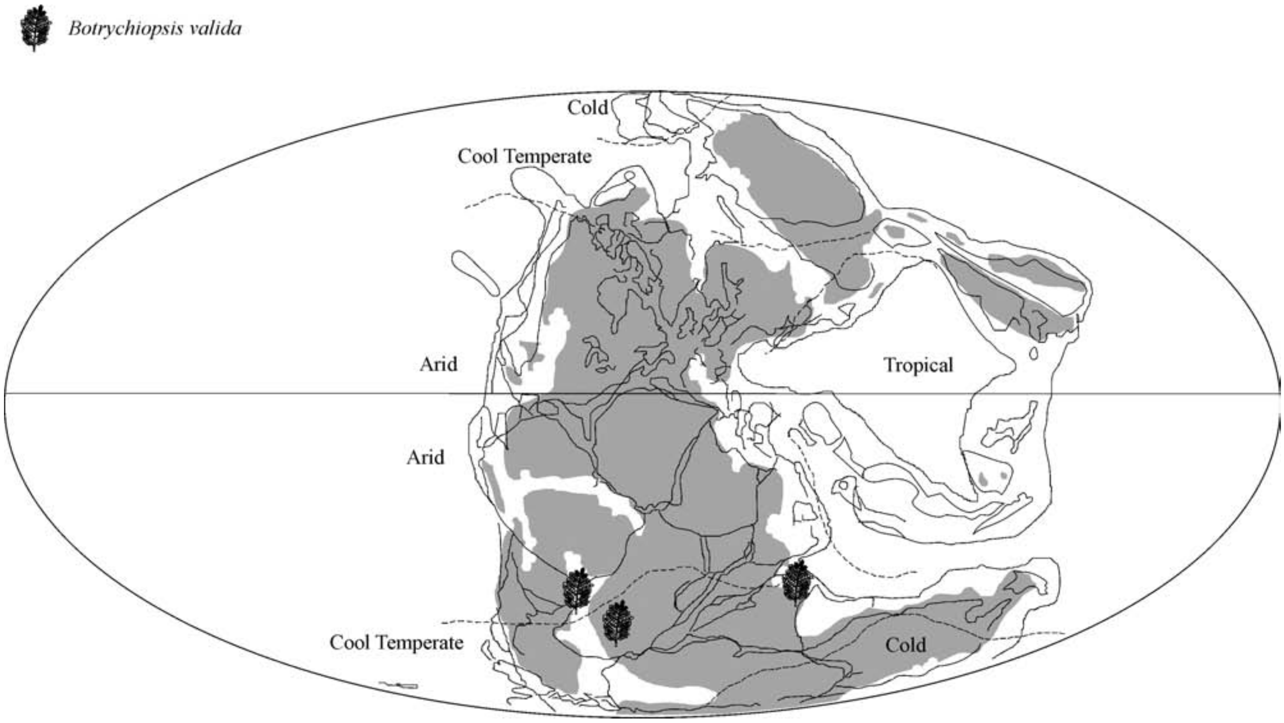

Fig. 5. Global distribution of *Botrychiopsis* during the Artinskian/Kungurian interval – Lower Permian (paleomap adapted from Scotese, 2000).

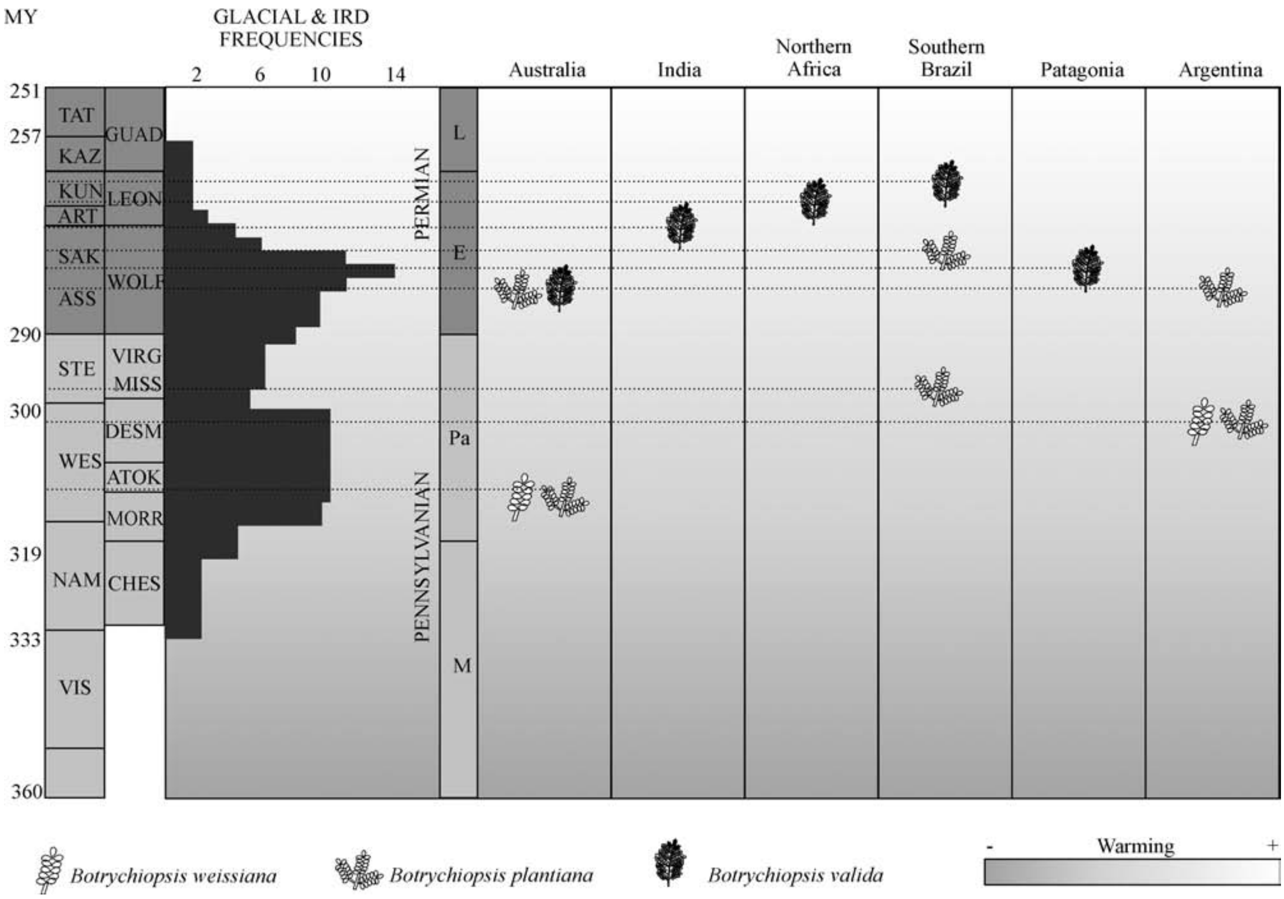

Fig. 6. Relation between global glaciation and the paleogeographic distribution of the *Botrychiopsis* genus in the Gondwana Realm (glacial and IRD Frequencies based on Frakes et al., 1992, *in* Gastaldo et al., 1996, fig. 2).

temperate climate. This certifies that the distribution of *Botrychiopsis* is directly related to the icehouse stage that took place in the Late Paleozoic. It was extinct when the environmental conditions typical of a greenhouse stage were created by the end of the Early Permian. During the final phases of deglaciation, under warm temperate conditions, the fossil flora changed with the introduction of new elements, such as arborescent lycophytes, sphenopterids and pecopterids (Fig. 6).

The results here presented confirm the importance of *Botrychiopsis* as a biostratigraphic marker in the Late Paleozoic of Gondwana, corresponding to a *taxon* typical of an icehouse interval. It is also clear that the genus had a broader climate tolerance than was initially thought, ranging from cool-temperate to warm-temperate climates closely related to the entire deglaciation phase.

The present knowledge of the stratigraphic record of *Botrychiopsis*, agrees with the conclusions of López-Gamundi (1997) that indicates a temporal and spatial evolution of the Gondwana glaciation. The present data are also in accordance with those of Diekmann (2001), who concluded that while the onset of major glaciation might have been a diachronic event due to plate-tectonic motions, major deglaciation was a synchronous climatic-induced feature (Wopfner, 1994; Ziegler et al., 1997).

Acknowledgements

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