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First record of *Ginkgo*-related fertile organs (*Hamshawvia*, *Stachyopitys*) and leaves (*Baiera*, *Sphenobaiera*) in the Triassic of Brazil, Santa Maria formation

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A B S T R A C T

This paper describes new ginkgophytes recently discovered in a new exposure of the original type section of the Passo das Tropas Member, Santa Maria Formation, linked to Paraná Basin succession. The well-preserved fossils come from a very fine red laminated mudstone representing a lacustrine interval, within a broader low-sinuosity fluvial succession. The material occurs in a *Dicroidium*-dominated assemblage and is represented by the leaves *Baiera* and *Sphenobaiera*, accompanied by the fertile structures *Hamshawvia* and *Stachyopytis*. Cuticle fragments preserved on leaf impressions of *Sphenobaiera schenkii* show xeromorphic features. The geology, paleogeography and paleoclimate of the Passo das Tropas Member (PTM), Santa Maria Formation, is discussed. By comparing these ginkgophytes with those from other Gondwanan assemblages, the Brazilian deposits earlier assigned to Anisian–Ladinian age can now be extended to the Carnian age.

1. Introduction

Since the end of the Paleozoic and through the Mesozoic, the Ginkgoales have been an important component in the floras reaching a great diversity in the end of Triassic and onwards (Anderson and Anderson, 1989; Zhou and Wu, 2006; Bauer et al., 2013a). Some taxonomic uncertainties remain due to morphological characters shared with the Peltaspermales, Dicranophyllales and Coniferales (Stewart and Rothwell, 1993; De Franceschi and Vozenin-Serra, 2000; Taylor et al., 2009). This is the case with the Permian genera *Trichopitys*, *Polyspermophyllum* and *Dicranophyllum* (Meyen, 1987; Archangelsky and Cúneo, 1990; DiMichele et al., 2013). The fossil record of ginkgophytes extends over Laurasia (Seward, 1919; Meyen, 1987; Kerp, 1996; Zhou, 2009) and Gondwana (Archangelsky, 1996; Silva and Iannuzzi, 2000), dating from the Pennsylvanian to recent times. Bauer et al. (2013a) provided a thorough synthesis of the history of ginkgophytes.

The establishment of relations between Ginkgoales in the fossil record and their younger representatives are complex. More recently, reproductive structures and leaf anatomy have shown some features that allow researchers to correlate the Paleozoic ginkgophytes and those from the Mesozoic, and with some aberrant leaves produced by modern *Ginkgo* (Stewart and Rothwell, 1993; Fischer et al., 2010). Anomalous inflorescences, with multiple ovules, were detected in *Trichopitys* Saporta from the French Permian, and in *Karkenia* Archangelsky from the Lower Cretaceous of Santa Cruz in Argentina (Archangelsky, 1970). A revaluation of the ginkgophytes from the Kupferschiefer in Germany revealed that truly petiolate leaves were present by the end of Permian, suggesting the establishment and diversification of the ginkgophytes by that time (Bajpai, 1991; Bauer et al., 2013a).

A major innovation is record in the Late Triassic with the first appearance of dwarf shoots, the differentiation of leaves into lamina and petiole, and a reduction in the number and increase in

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size of the ovules (Zhou and Wu, 2006). Between the end of the Triassic and Early Cretaceous the group reached its acme in abundance and a global distribution, showing distinct leaf morphologies, most of which broadly resemble modern *Ginkgo* and are assigned to the fossil taxon *Ginkgoites* (Zhou and Wu, 2006; Anderson et al., 2007). Others, with more dissected leaves, were included in *Baiera* and *Sphenobaiera* genera (Florin, 1936; Zhou, 1997; Watson et al., 1999). Fossil seedlings and twigs found in the Middle Triassic of France show some analogy with those of modern *Ginkgo biloba* and attest to the development and evolution of the group in the early Mesozoic (Bauer et al., 2013b).

Ginkgoales were an important group (second only to corystosperms) in the Middle Late Triassic *Dicroidium* floras of Gondwana (Du Toit, 1927; Artabe, 1985; Anderson and Anderson, 1989; Gnaedinger and Herbst, 1999; Troncoso and Herbst, 1999; Artabe et al., 2007; Moisan et al., 2010; Lutz et al., 2011; and Supplementary online data). In the Nymboida Flora from Australia, leaves with intergradational morphologies found in unique assemblages, were included in morphospecies complexes. This prevented taxonomic multiplication of names (species) which would probably reflect only subtle morphological variations, due to adaptations in the local environment (Holmes and Anderson, 2007).

Microsporangiate and ovuliferous structures, although rarer, was globally found after the end of the Permian (Shirley, 1898; Walkon, 1917; Frenguelli, 1942; Jain and Delevoryas, 1967; Krassilov, 1982; Zhou et al., 2002; Holmes and Anderson, 2007; Naugolnykh, 2007; Yang et al., 2008; Zhou et al., 2012).

In the Upper Triassic Molteno Formation, in South Africa, ginkgoalean foliages were included in *Sphenobaiera*, *Ginkgoites* and *Paraginkgo*. The ovuliferous structures were assigned to the new genus *Hamshawvia*, and to a new order, the Hamshawviales and an immature form of *Hamshawvia*, attached to leaves of *Sphenobaiera "schenckii"*, was described (Anderson and Anderson, 2003). Anderson and Anderson (2003) transferred to this new genus, *Umkomasia cacheutensis* originally described from Argentina by Frenguelli (1942). In the Nymboida Flora, Australia, *Hamshawvia*, *Stachyopitys* and *Sphenobaiera schenkii* was founded associate, albeit without organic connections (Holmes and Anderson, 2007, 2013).

In Brazil, the previous fossil record of Ginkgoales was scarce and restrict to the southern Paraná Basin (Fig. 1A). The oldest examples, from the Lower Permian Itararé Group and Rio Bonito Formation, include incomplete leaves of *Ginkgoites eximia* Seward, *Ginkgophytopsis* Høeg, *Dicranophyllum* and *Cheirophyllum speculare* Césari and Cúneo, the latter exhibiting dubious affinities to the Ginkgoales (Silva and Iannuzzi, 2000). They were associated with assemblages composed mostly by pteridosperms (*Glossopteris* and *Gangamopteris*), accompanied by sphenopsids and primitive conifers (Guerra-Sommer et al., 1999; Guerra-Sommer and Klepzig, 2000).

In the Triassic, the ginkgophytes were record in levels correlated to those herein studied (Santa Maria Formation, Passo das Tropas Member, PTM), represented by *ex situ* fossil woods (Bardola et al., 2009), sparse seeds, reproductive structures (*Stenorrachis*) and incomplete leaves of *Sphenobaiera* and *Ginkgoites antarctica* (Pinto, 1956; Bortoluzzi et al., 1983).

Besides the dominant corystosperms component (70% of estimated relative frequency), the Ginkgoales were the second most abundant group in the PTM, which includes *Neocalamites*, conifers, *Taeniopteris* and rare *Cladophlebis* (Gordon and Brown, 1952; Pinto, 1956; Bortoluzzi et al., 1983; Guerra-Sommer and Klepzig, 2000). The poorly preserved *Sphenobaiera* leaves was compare with *S. ugotheriensis* and *S. argentinae*, respectively from Australia and Argentina (Bortoluzzi et al., 1983). In the Anisian–Ladinian age proposed for the Passo das Tropas Member (PTM) was taking into account the range of *Dicroidium* species (Mastroberti, 1995; Guerra-Sommer et al., 1999).

In this study new ginkgoalean fossils are described from an outcrop near Santa Maria city, central Rio Grande do Sul (Fig. 1B), not far from the original type-section of the PTM (Bortoluzzi, 1974). Along with the other Triassic deposits in Brazil, PTM beds are exclusive to the southern areas of the Paraná Basin.

1.1. Geological background

According to Zerfass et al. (2004), the facies and geometry of the Brazilian Triassic deposits are related to an extensional phase of an intraplate rifting associate with the Gondwanides orogeny, that also originate the back-arc rift basins from Argentina and South Africa (Central West Gondwana basin complex from Linol et al., 2014). The Early Triassic initial compressional phase was follow by successive extensive events spanning the Middle to Late Triassic transition and which anticipated the initial stages of Gondwanan break-up. The Sierra de La Ventana and Cape Fold Belt orogenic belts (Uliana et al., 1989; Kokogián et al., 2001; Zerfass et al., 2004; Faccini, 2007; Barredo et al., 2011) also controlled those efforts.

In this scenario the Karoo Basin and probably the Santa Cruz basin in Southern Argentina, were located at 30°S of paleolatitude, influenced by extratropical warm and wet temperate climates. The Ischigualasto, Paganzo and the southern Paraná basins, located in between 30°–15°S, varied from a transitional condition or the influence of drier subtropics (Spalletti et al., 2003; Holz, 2015). Only the La Ternera Basin in Chile may have been located at <10°S (Zerfass et al., 2004).

According to Milani et al. (1998), six stratigraphic megasequences bounded by interregional unconformities characterize the Paraná Basin. The three upper (Middle–Late Triassic to Late Cretaceous) attest a gradual continentalization, expressed by fluvial, lacustrine and wind generated red bed deposits, covered by the Jurassic – Cretaceous volcanic rocks (Bortoluzzi, 1974; Andreis et al., 1980; Milani et al., 1998). In the State of Rio Grande do Sul these sedimentary sequences are exposed along an east–west central belt (Fig. 1B–C).

Faccini and Paim (2001) and Zerfass et al. (2003), applying the Sequence Stratigraphy principles to the Triassic deposits from southern Brazil consider that the basal Sanga do Cabral (Early Triassic) and upper Santa Maria (Middle–Late Triassic) supersequences represent 2 s-order cycles. To the Santa Maria supersequence they proposed three sequences (Santa Maria 1, 2 and 3), with a southward located source area and depositional architectures, comparable to those from other Western Gondwana rift basins.

In this approach, the ginkgophyte and the *Dicroidium* flora from the Passo das Tropas Member (PTM) were assign to the basal part of Santa Maria 2 Sequence (SM2), were the tetrapod fauna indicates a Carnian age (Schultz et al., 2000; Langer et al., 2007). In the sequential framework proposed by Zerfass et al. (2004), the mud facies of the PTM deposits containing the fossil flora represent phases of base level changes that led to the massive lacustrine beds containing the tetrapod fossils. The Carnian age proposed to the PTM deposits is in agreement with the associated coleopteran faunas (Pinto and Ornellas, 1974), comparable to that identified in Los Rastros, Cacheuta, Ischichuca and Santa Joana formations, in Argentina (Mancuso et al., 2007; Martins-Neto et al., 2011).

The lenticular geometry of the plane-bedded mudstones from the PTM (Fig. 2A) suggest flood plains/lacustrine deposits formed in abandoned low areas (or channels) protected from erosion, of a broad and dominant fluvial system of low sinuosity rivers (Zerfass et al., 2003; Faccini, 2007).

In the outcrop herein studied, located at geographical coordinates 29°44′37, 85″S and 53°47′ 31, 12″W (Fig. 1C, Fig. 2A–D),