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NEW “FLOWER” AND LEAVES OF BENNETTITALES FROM SOUTHERN BRAZIL AND THEIR IMPLICATION IN THE AGE OF THE LOWER MESOZOIC DEPOSITS

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Abstract. The record of Bennettitales from west-central Argentina and southern Brazil in South America is among the oldest known. In contrast to the better known near-coastal assemblages from the Northern Hemisphere, these Gondwanic elements are restricted to continental areas and isolated rift basins, similar to those in South Africa. *Williamsonia potyporanae* sp. nov. is preserved by impressions that expose distinct longitudinal sections of the ovulate structure, allowing the reconstruction of its tridimensional aspect, and is accompanied by probable *Pterophyllum* leaves. It consists of an ovate-shaped flower covered by two layers of delicate and connected ribbon-shaped and hairy bracts, and an obconic receptacle supporting a great number of megasporophylls, with uniformly aligned and apical fusiform ovules or seeds. The bennettite remains are part of an autochtonous-parautochtonous floral assemblage dominated by conifers and restricted to a thin mudstone interval in a mainly fluvial deposition comprisig the Caturrita Formation. The mud interval suggests a shallow lake supplied by periodic, intense rainfall that affected the vegetation growing along the river banks and/or on a floodplain deposits. An initially proposed Norian age, based on diversified vertebrate remains found in lower levels (Ictidosaur or Mammaliamorpha Cenozone), was recently extended to the Rhaetian. The advanced morphology of ovulate structure described here suggest an even younger Jurassic age, supported by comparisons with other fossil assemblages, mainly those from Argentine basins.

Key words. Bennettitales. *Williamsonia*. *Pterophyllum*. Caturrita Formation. Lower Jurassic. Southern Brazil.

Resumen. NUEVA “FLOR” Y HOJAS DE BENNETTITALES DEL SUR DE BRASIL Y SU IMPLICANCIA EN LA EDAD DE LOS DEPOSITOS DEL MESOZOICO INFERIOR. El registro fósil de Bennettitales en el centro-oeste de Argentina y sur de Brasil, en América del Sur, se encuentra entre los más antiguos conocidos. En contraste con las formas mejor conocidas de los ambientes costeros del Hemisferio Norte, los registros se limitan a las zonas continentales y a pequeñas cuencas de *rift*, semejantes a las de África del Sur. *Williamsonia potyporanae* sp. nov. está preservada como impresiones de distintas secciones longitudinales de la estructura ovular, que permitieron la reconstrucción tridimensional de su aspecto externo e interno, y está acompañada de probables hojas de *Pterophyllum*. Su estructura está compuesta por una flor de forma oval cubierta por dos capas de brácteas delicadas y pilosas, que están conectadas a un receptáculo obcónico que porta numerosos megasporófilos, con óvulos o semillas fusiformes uniformemente alineadas apicalmente. Los fósiles de bennettitales forman parte de una asociación florística de origen autóctono-parautóctono, dominada por coníferas, y que están restringuidos a un delgado estrato de lutitas intercaladas en una sucesión de areniscas fluviales atribuida a la Formación Caturrita. El nivel de lutitas fosilíferas sugiere un ambiente lacustre poco profundo o de llanuras de inundación, propenso a períodos de intensas precipitaciones, que afectaron la vegetación que crecía a lo largo de las regiones ribereñas de ríos y/o depósitos de llanuras de inundación. Inicialmente, fue propuesta una edad noriana para estos niveles basada en los restos de vertebrados hallados en los niveles arenosos inferiores (Cenozona de Ictidosauros o Mammaliamorpha), pero recientemente se ha extendido la edad al Rético. Los caracteres morfológicos avanzados de la estructura ovular aquí descripta sugieren una edad aún más joven, en el Jurásico, apoyada también por las comparaciones con otras asociaciones fósiles, principalmente con las registradas en las cuencas argentinas.

Palabras clave. Bennettitales. *Williamsonia. Pterophyllum*. Formación Caturrita. Jurásico Temprano. Sur de Brasil.

Lower Mesozoic strata in southernmost Brazil are characterized by a red-bed continental succession representing fluvial and alluvial systems that fill apparently independent and short-lived basins formed in the broader context of the southern Paraná Basin. These deposits crop out along the south-central portion of Rio Grande do Sul State (Fig. 1). According to Faccini *et al*. (2007) the facies architecture is a response to climatic and tectonic changes related to the final disconnection from Panthalassa at the end of the Paleozoic and the ensuing breakup of Gondwana. According to Zerfass *et al*. (2004) and Hackspacher *et al*. (2004) the tectonic control is probably the same that conditioned the Triassic rift basins in Western Argentina and southern Africa.

This study documents a new plant fossil assemblage with bennettites, identified in the upper part of the Late Triassic sequence and included in the Caturrita Formation (Rosário do Sul Group) by Andreis *et al*. (1980). In terms of Sequence Stratigraphy, the coarsening-upward succession was considered

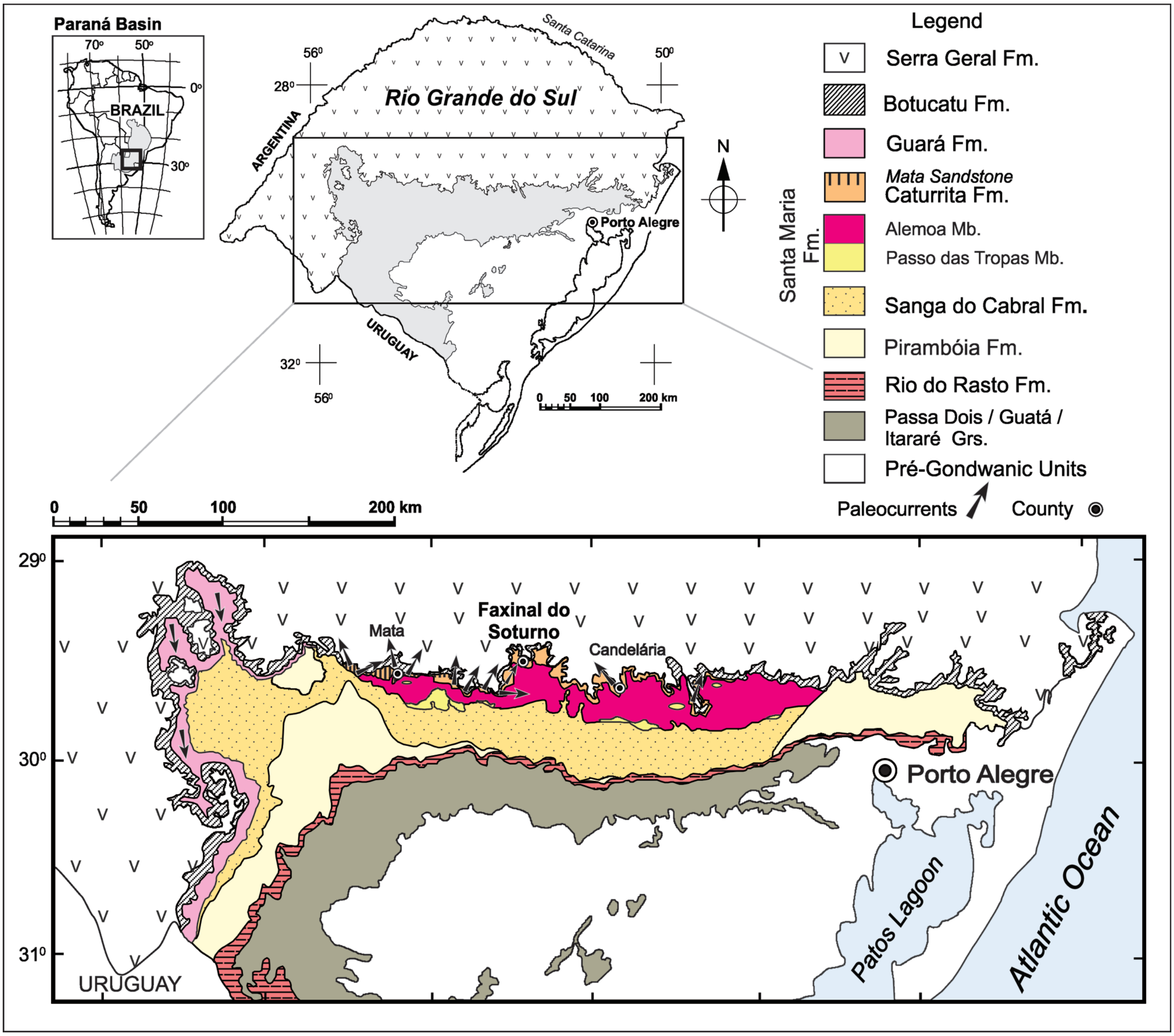

Figure 1. Distribution of the Paleozoic and Mesozoic stratotypes in the central part of the State of Rio Grande do Sul, South Brazil, and the location of the studied area, in Faxinal do Soturno county (modified from Faccini, 2000, 2007; structural data from Da Rosa and Faccini, 2005; Guará Formation as conceived by Scherer *et al.,* 2000). Paleocurrent data from Faccini (2000) and Zerfass (2007).

as part of a third order sequence (Faccini, 2000, 2007) and corresponding to a highstand system tract (Zerfass *et al.*, 2004).

The Bennettitales or Cycadeoidales are extinct plants with a stratigraphic range spanning the Middle Triassic to the end of the Cretaceous (Anderson *et al.,* 2007; Ryberg *et al.*, 2007; Pott *et al.,* 2010). However, a recent work by McLoughlin *et al.* (2011) attests their survival in high latitudes of southeastern Australia until the beginning of the Oligocene. Its cycad-like foliage and flower-like reproductive organs (Crane, 1988; Taylor *et al.,* 2009), suggest a relationship with the Cycadales, or alternatively with the Gnetales and Erdtmanithecales, as one of the groups involved in the origin of angiosperms (Crane, 1988; Friis *et al.*, 2009). Recent cladistic analyses spurred controversy on this issue. Rothwell *et al.* (2009) do not support the "anthophyte" clade as originally conceived, and Chaw *et al.* (2000) proposed a closer relation between the Gnetales and conifers.

The monosporangiate male fructifications of Bennettitales are generally included in *Weltrichia* Braune, the female ones in *Williamsonia* Harris, and the bisporangiate fructifications are grouped in *Williamsoniella* Thomas (Nathorst, 1909; Delevoryas, 1991; Miller and Hickey, 2010). *Williamsonia* is characterized by a basal peduncle or central axis carrying interseminal scales (sporophylls) with attached ovules/seeds, protected by smooth or hairy bracts, and preserved as impressions or petrifications (Saporta, 1891). Petrified specimens have revealed ultrastructure and tissue disposition (Stockey and Rothwell, 2003; Pott *et al*., 2010).

The leaves of bennettites are generally pinnate (except *Nilssoniopteris* Nathorst) and leathery, with parallel margins, and venation rarely bifurcated or anastomosed (Watson and Sincock 1992; Pott and Krings, 2007; Taylor *et al*., 2009). When present, the epidermal anatomy shows polygonal to rectangular cells, with sinuous and cutinized walls in which stomatal apparatuses are perpendicularly orientated in relation to venation, slightly sunken, and normally restricted to the abaxial side of the leaf (Menéndez, 1966; Archangelsky and Baldoni, 1972; Villar de Seoane, 2001, 2003; Pott and McLoughlin, 2009). Trichomes and papillae are common, the latter normally overarching the brachyparacytic (and syndetocheilic) stomatal complex (Florin, 1933; Harris, 1969; Bose and Banerji, 1984; Pott *et al*., 2010). Salt glands identified on the surface of the epidermis, together with leathery leaves and bracts, suggest a life under xeric conditions. Yet, Pott *et al.* (2008) working with plant material from near-coastal peat swamps of Lunz, Austria, stated that those structures could reflect the influence of saline winds and thus physiological drought. According to Batten (1977) and Wade-Murphy and Van Konijnenburg-van Cittert (2008) the xeromorphic features result from growing in well-drained and unstable soils of the upland drainage areas.

THE FOSSIL RECORD, EVOLUTION AND PALEOGEOGRAPHY OF THE BENNETTITALES

The oldest record of Cycadeoidales are leaves of *Zamites queenslandi* (Walkom) Anderson and Anderson and *Weltrichia*-like reproductive structures, identified in a *Dicroidium* flora from the Anisian (Esk Formation) of Australia (Pattemore and Rigby, 2001; McLoughlin *et al*., 2011). Younger records include *Pterophyllum* Brongniart and *Anomozamites* Schimper from the Ladinian/Carnian of Livingston Island, Antarctic Peninsula, and from the Barreal Formation, Argentina (Lacey and Lucas, 1981; Artabe *et al*., 2007). Since then, *Zamites*, *Pterophyllum* and *Anomozamites* are the nearly exclusive vegetative organs of bennettites in Late Triassic beds around the world.

The earliest evidence of female reproductive structures (*Williamsonia* and allies) comes from Carnian rocks in both hemispheres (online Supplementary File 1). However, most records are from northern Europe and southeastern United States. In this period most forms show an external cover composed by few, leathery and broad bracts, normally preserved open and exposing the inner whorl of fertile seeds (Ash, 1968; Weber, 2008; Wade-Murphy and Van Konijnenburg-van Cittert, 2008; Pott and McLoughlin, 2009). The ovulate structures are represented, for example, by the complex *Bennetticarpus*+*Cycadolepis wettsteinii* of Lunz (Kräusel, 1949; Crane, 1988, Pott *et al*., 2010), *W. newberryi*, from Mexico (Weber and Zamudio-Varela, 1995; Weber, 2008), and *W. nizhonia*, in United States (Ash, 1968). Coeval *Weltrichia* and *Haitingeria* were recorded in Sweden, Switzerland, Mexico, United States, India, and South Africa (online Supplementary File 2.1).

During the Norian/Rhaetian *Williamsonia* representatives reached the highest latitudes. At the same time, the nearly exclusive Carnian ovulate structures from South Africa and Europe diseappeared (Anderson *et al*., 2007; Artabe *et al.,* 2007). At low latitudes, forms growing in interior areas also declined, only recovering their original distribution at the beginning of the Cretaceous (online Supplementary File 2.2–4).

According to McLoughlin and Pott (2009b), the abundant occurrence of Bennettitales in the Jurassic means it is more correct to call it "the age of Bennettitales", instead of the age of cycads. In Gondwanaland, the Early Jurassic was characterized by the replacement of *Pterophyllum* foliage by that of *Otozamites* (Braun) Watson and Sincock, especially in Argentina where an Otozamites Zone was established for this time interval (Stipanicic and Bonnetti, 1970; Quattrochio *et al*., 2007). For Wang *et al.* (2008) *Otozamites* indicates wet and warm climates. Similar conditions may have prevailed in Patagonia, which at the end of the Early Jurassic was under the influence of a transgressive episode (Veiga *et al.,* 2005; Riccardi, 2008) suggesting climate ameriolation and higher humidity.

In the tropical belts an almost exclusively near-coastal distribution similar to that adopted in the Triassic in Europe was maintained by the group until the beginning of the Cretaceous.This distribution persisted for as long as the integrity of Pangea was maintained. The assemblages from Yorkshire and Mexico exemplify this pattern of distribution (Harris, 1969; Wieland, 1914; Delevoryas, 1991).

Perhaps as a response to the more stable climatic conditions, *Williamsonia* "flowers" became more homogenous and acquired a cover of delicate, numerous, linear (*ribbon shaped* from Menéndez, 1966) and hairy bracts. This pattern is apparent in *W. gigas*, first recorded in the Lower Jurassic of Santa Cruz, Argentina (Herbst and Anzótegui, 1968; Archangelsky, 1970), and persisting until the end of the Cretaceous in wet and temperate areas of the Northern Hemisphere (Crane and Herendeen, 2009; Stockey and Rothwell, 2003).The number of ovules/seeds also increased, as shown by *W. netzahualcoyotlii* from Oaxaca —with 25–30 fertile bracts (Weber, 2008)— and

W. gigas —with more than a hundred (Thomas and Batten, 2001). There was also a trend towards more elongated reproductive structures (*e.g.*, *W. harrisiana* and *W. bockii*), with apically disposed seeds like in *W. diquiyui*, *W. bulbiformis*, and *W. bockii* (Delevoryas and Gould, 1973; Delevoryas, 1991; Menéndez, 1966; Stockey and Rothwell, 2003). Internally, the aligned and elongated seeds are very different from those of Triassic representatives showing big and round, dispersed seeds, located in distinct parts of the interseminal scale ring (*e.g.*, *Bennetticarpus wettsteinii* Kraüse *emend*. Pott *et al.*, 2010).

Some of the Jurassic morphologies persisted into the Cretaceous, associated with the reappearing of rigid covers and the return to southernmost areas (online Supplementary File 2.4). A bulbiform general appearance (onion-shaped) became common and the taphonomic constraints indicate the persistence of closed bracts after abcission and seed maturation (*e.g., W. blanfordii, W. kakadbhitensis and W. bulbiformis*). The paradigmatic petrified cone of *W. bockii* shows adjacent interdigitate interseminal scales forming a continuous tissue arround the seeds, with a solid apex in the nucellus, no pollen chamber, and ramified pollen tubes (Stockey and Rothwell, 2003; Rothwell *et al.*, 2009) supporting the siphonogamy proposed by Sharma (1970) and the quiescent nature of the embryos suggested by Delevoryas (1991).

The new oceans resulting from the break'up of Gondwana once again favoured the appearance of marshy environments in tropical areas, and guaranteed the persistence of *Otozamites* foliage in China, India and Argentina (online Supplementary File 2.4). Papilla, tricomes and salt glands over the stomatal complex support the near-coastal habitat and xeromorphy (Villar de Seoane, 2003; Watson and Sincock, 1992). However, between the Albian and Santonian the fossil record shows the restriction of the group to northeastern Australia (Pole and Douglas, 1999) and Japan (Ohana *et al.*, 1998; Saiki and Yoshida, 1999). At the end of the Cretaceous this group became almost extinct, surviving only in poor floras of the high northern latitudes, and represented by the Cycadeoidaceae (Stockey and Rothwell, 2003). According to McLoughlin *et al.* (2011) the recent finding herein commented of *Ptilophyllum* leaves in early Oligocene beds in southeastern Australia could reflect a "Lazarus" behaviour and a ghost lineage surviving nearly 65 million years.

GEOLOGICAL SETTING AND AGE OF THE STUDIED AREA

Initialy considered as a basal member of the Early Cretaceous Botucatu Formation (Bortoluzzi, 1974), the Caturrita Formation was formally established by Andreis *et al.* (1980) as an independent unit linked to the Triassic deposits in the Paraná Basin. According to Faccini (2007) it is characterized by the deposition of crevasse splays, crevasse channels and lacustrine delta fronts, in a sequence composed by two parts, each one containing distinct fossil assemblages and probably representing distinct ages (Fig. 2). The basal section was considered as early Norian due to it vertebrate fauna (Barberena, 1977; Schultz *et al.*, 2000). A Rhaetian age was proposed for the upper section ("Mata Sandstones"); yet its fossil content was restricted to mostly allochtonous wood logs of *Araucarioxylon* (Guerra Sommer and Cazzulo Klepzig, 2000) and Ginkgophyta (Bardola *et al.,* 2009). According to Zerfass *et al.* (2003) the Caturrita Formation represents the younger of the second order sequences that characterize the Triassic deposits in Rio Grande do Sul State (Santa Maria Supersequence).

The detected tectonism (Andreis *et al.*, 1980; Zerfass *et al.,* 2004; Da-Rosa and Faccini, 2005) —rendering the deposits involved a Tectonostratigraphic Sequences (TS) *sensu* Olsen *et al.* (2003)— implies changes in base-levels and supports the intracontinental and extentional character of this southern sector of Paraná basin, similar to that generating the Late Triassic and Early Jurassic rift basins in South Africa (Bordy *et al.,* 2004) and Argentina (Cuyo and Ischigualasto basins; Barredo *et al.*, 2012). The dominantly sandy character of the deposits and the presence of longitudinal and transversal faults with block dislodgement, difficults the correlations and renders fossil assemblages of different ages being found in similar topographic levels.

In this context, the paleontological content is critical in the age determination of those deposits. Four distinct faunal biozones or assemblages (AZ) of vertebrates were described to the Santa Maria Supersequence, and considered intercalated between two floristic levels (*i.e.*, the *Dicroidium* and "*Araucarioxylon*" dominated floras). The first three tetrapod Assemblage Zones were assigned to the red mudstones of the basal Alemoa Member of the Santa Maria Formation (Santa Maria 2 Sequence—SMS 2), considered Ladinian–Carnian in age. The fourth one (Mammaliamorpha AZ) was included in the Caturrita Formation (corresponding to SMS 3) and is characterized mainly by little "ictidosaurian" cynodonts (Bonaparte *et al.*, 2003; Martinelli *et al.*, 2005; Bonaparte and Sues, 2006; Bonaparte *et al.*, 2010; Soares *et al.*, 2011). The age of Mammaliamorph AZ is more controversial —it has been considered as early Norian (Schultz *et al.*, 2000; Rubert and Schultz, 2004; Schultz and Langer, 2007) or late Norian–Rhaetian (Langer *et al.*, 2007; Abdala and Ribeiro, 2010) and correlated with the assemblages in the Los Colorados (Argentina) and

Elliot (South Africa) formations. Among its fossil representatives, some are exclusive to the São Luis outcrop discussed herein. Figure 2 summarizes the state of the art of the stratigraphical and architectural elements and the associated faunal and paleofloristic events proposed.

The São Luis outcrop, that contains the plant fossils here discussed, is located 1.5 km north of the Faxinal Soturno County (29°33′45″S–53°26′48″W), in the state of Rio Grande do Sul, southern Brazil (Fig. 1). The 20 m high sedimentary section is composed mainly of fluvial sandstones with a restricted interval of mudstones-siltstone (Fig. 3.1). Its basal levels consist of low angle cross-bedded and well sorted fine- to medium-grained sandstones, containing abundant axial and thick roots (Fig. 4.1–2). This gives way upwards to small scale trough cross-bedded sandstones (ribbon channels), followed by massive and/ or sigmoidal trough cross-laminated fine sands, that according to Faccini (2007) represent crevasse splay deposits. This sand interval —which yielded the bones

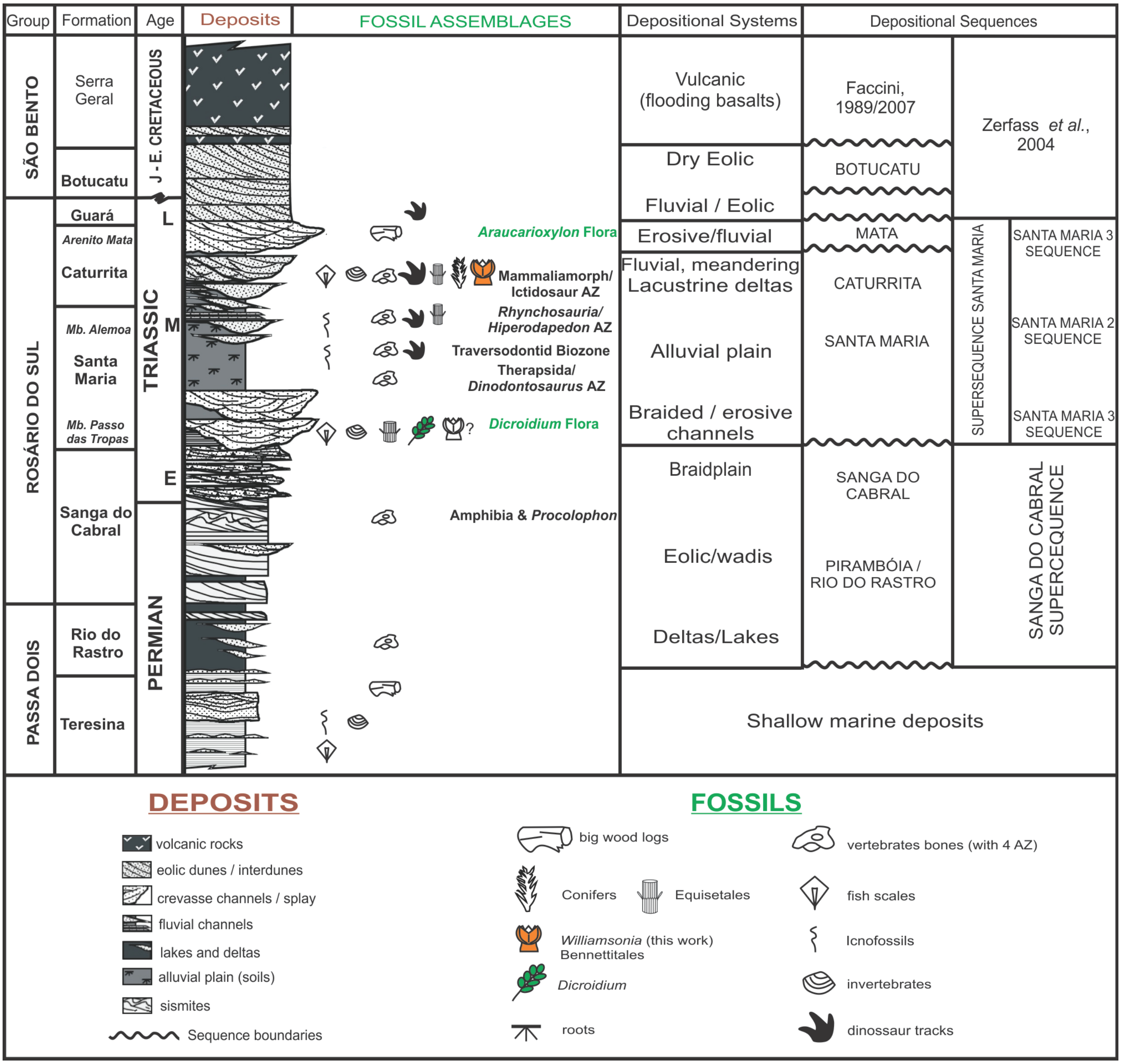

Figure 2.Lithologies and sequences proposed for the Late Permian and Mesozoic strata of Parana Basin in central Rio Grande do Sul, the associated fossil assemblages and levels of Caturrita Formation containing the herein described new species of *Williamsonia*. Preservational styles and lithofacies modified from Faccini (2000). Guará Alloformation follows Scherer and Lavina (2005). Vertebrate zones or assemblages (AZ) from Barberena (1977), Schultz and Langer (2007), and Langer *et al*. (2007). Fossil floras from Guerra-Sommer and Cazzulo-Klepzig (2000).

of a sphenodontida, a procolophinida, four little "ictidosaurian" cynodonts and two archosauria— also preserved at least three distinct phases of soil formation. Two of these record fibrous and thick roots and one is characterized by thin and intensely ramified roots (Fig. 4.3).

The following single laminated mudstone-siltstone intercalation (2.20 meters high, contains the bennettites remains discussed herein) (Fig. 3.2) and according to Zerfass *et al.* (2004) represents a lacustrine to delta lake deposit. In the lower part they are associated with authigenically preserved conifer shoots (mainly *Pagiophyllum* sp.; Wilberger, 2009) and autochnous and alochtonous wood logs (Fig. 4.4), some maintaining the medulate characters (Pires and Guerra Sommer, 2004; Crisafulli and Dutra, 2009). In the middle-upper levels the bennettites are more common and occur with a poorer but still diverse flora represented by leaf impressions of a probably cycadeoid-related leaf (here described) and other kind of gymnosperms, invertebrate remains (insect wings and conchostraceans) and isolated fish scales (Fig. 3.2). The mudstones give way upwards to heterolithic sandstone-mudstone deposits, with evidence of episodic subaerial exposure with rare undescribed vertebrate bone fragments and the impression of two large tracks (50 cm long) of a theropod dinosaur (Silva et al., 2012). The lateral restriction, depositional features and taphonomy of the floristic assemblage from the Caturrita Formation at São Luis outcrop are comparable with those from the older lacustrine deposit represented by the basal Passo das Tropas Member of the Santa Maria Formation, which carries a *Dicroidium* flora (Fig. 2) suggesting a similar depositional context. Yet, in the Caturrita Formation the Corystospermales are still absent, and conifer remains represent nearly 90% of the assemblage (Dutra and Faccini, 2002; Pires and Guerra Sommer, 2004; Wilberger, 2009; Crisafulli and Dutra, 2009).

According to Faccini (2000) the complete section at São Luis implies a reduction in accommodation space, shallowing of the water bodies and a change in fluvial styles to mostly tabular, multi-storey sheet sandstones.

MATERIAL AND METHODS

The bennetitte-related remains at the São Luis outcrop show a unique preservation including diverse impressions of different parts of the ovulate structure, allowing reconstruction of the tridimensional aspect of the original flower. They are homogenously distributed throughout the mudstone succession (Fig. 3.2) but are more common in the middle and upper beds. Twenty-four samples of parts and counterparts of the reproductive structures and impressions of leaves were analyzed. Two samples, including the holotype, are housed in the Natural Sciences Museum from the Zoobotanical Foundation of Rio Grande do Sul (**FZBRS**), under the code MCN–PB. The others pertain to the paleontological collection (LaViGæa) in the Museum of Geological History of Rio Grande do Sul (**MHGEO**) at Vale do Rio dos Sinos University (UNISINOS), under the code **ULVG**.

Due to the friable character of the muds —that dry and crack easily when exposed— the technique proposed by Barboni *et al.* (2008) was applied. This involves wraping the samples in a PVC film coating for two weeks after their previous fixation in the field with common glues (cianoacrilate) when necessary. Also, the traditional quadrats procedure used in taphomic and paleoecological field-studies (*e.g.*, Pfefferkorn *et al.*, 1975) was modified and the fossil material was collected at 15 cm intervals in 45x45 cm areas.

Analysis of reproductive structures and their graphic representation were carried out using a Zeiss Discovery 8 stereomicroscope coupled with a *camera lucida*. Photos were taken with a Canon EOS (Rebel XT) digital camera, with reading macro. Nomenclature used to describe the reproductive and vegetative structures follows that proposed by Watson and Sincock (1992), Stockey and Rothwell (2003), Pott and McLoughlin (2009), and Miller and Hickey (2010).

Pott *et al.* (2010) pointed out the different methods used to describe reproductive organs of bennettites, including those that use terminologies normally applied to angiosperms, such as "flower" and "perianth". Here we follow their informal nomenclature for the female structures, *i.e.*, "seed cone", "outer surface", and "ovulate organ".

Fossil occurrences of Bennettitales in Triassic–Cretaceous basins from other parts of the world were reviewed (Barboni, 2010). Data were plotted on paleogeographic maps, in order to disclose dispersal routes and to reveal the distinct responses of the group to environmental and climatic changes (online Supplementary File 2.1–4).

The proposed reconstruction of ovulate structure was performed using the BLENDER©3D Program (www.blender.org).

SYSTEMATIC PALAEONTOLOGY

Order BENNETTITALES Engler, 1892

Family WILLIAMSONIACAEA (Carruthers) Nathorst, 1913

Genus *Williamsonia* (Carruthers) Harris, 1969

Type species. *Williamsonia gigas* (Lindley and Hutton) Carruthers, 1870

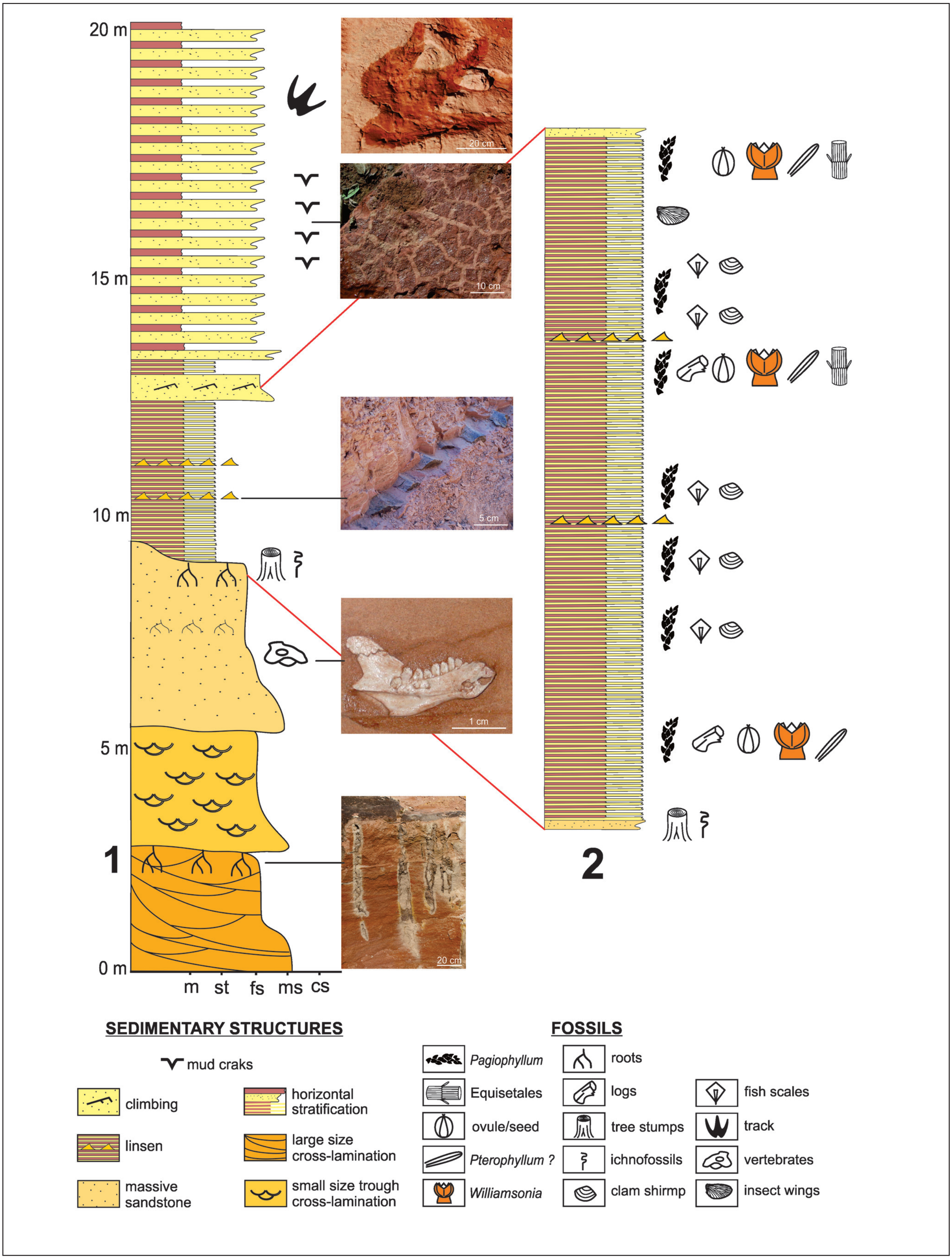

Figure 3.1. Stratigraphic section, sedimentary features and the fossil content of Linha São Luis outcrop; **2**, Detail of the laminated mudstone-siltstone interval that concentrates the plant fossil remains.

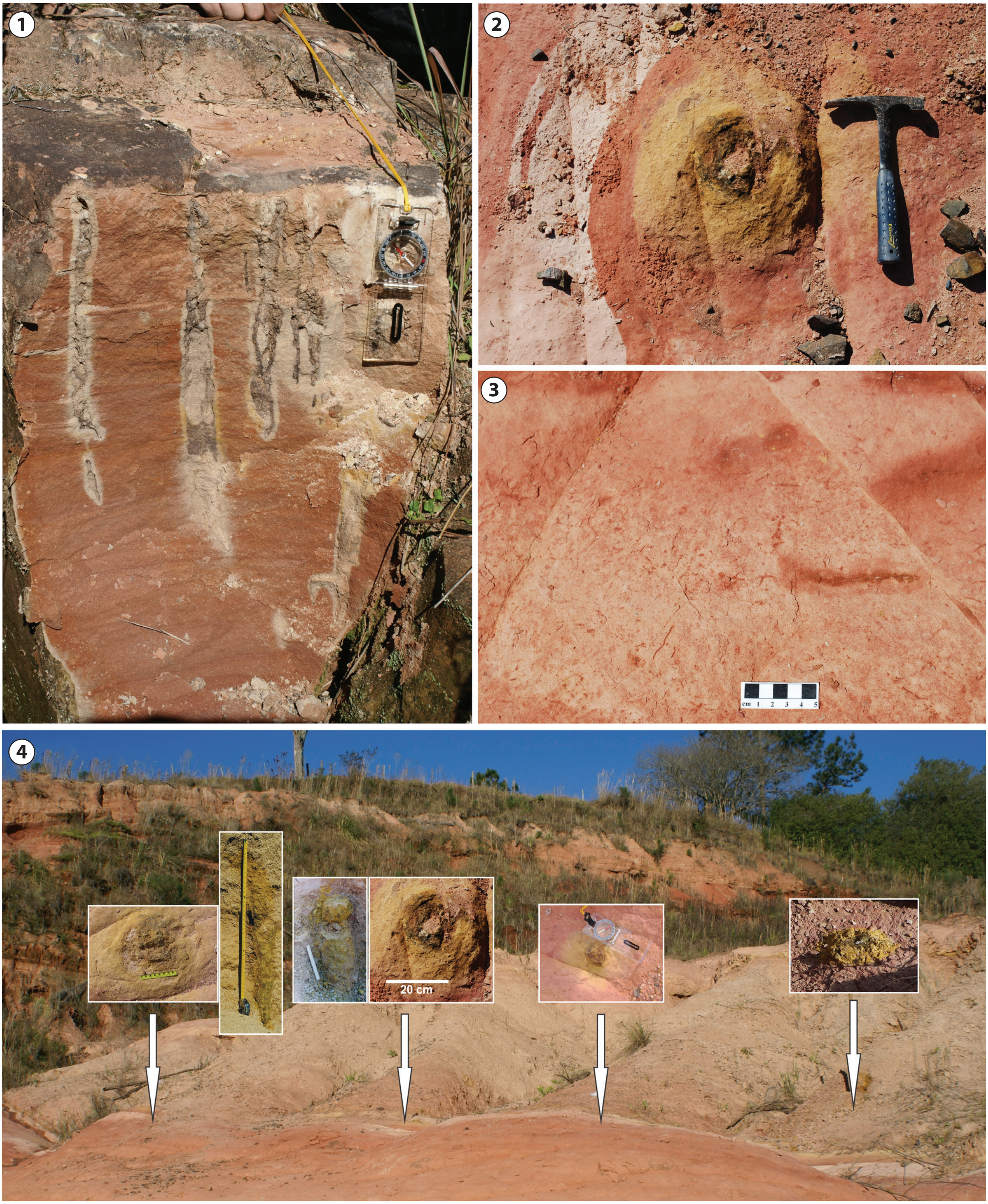

Figure 4. Paleosols and root pavements in the São Luis succession; **1**, Fibrous and large root impressions, homogeneous in size and arrangement, from the basal sheet flow and overbanking deposits, suggestive of an arbustive vegetation linked to non-confined river channels; **2**, Detail from the upper level of a crevasse splay deposit showing thin and densely bifurcate root impressions indicating a herbaceous kind of soil covering; **3**, Root halos on the surface of crevasse splay, coincident with the autochtonous stumps that penetrate in the base of superior lacustrine deposit; **4**, Panoramic view of the location of root halos in the upper part of sandy deposits and its coincidence with that of authoctonous stumps in basal mudstone succession, suggesting sparse open arbustive vegetation growing in overbanking deposits.

Williamsonia potyporanae sp. nov.

Figures 5.1–8 and 6.1–4

Holotype. MCN–PB 311A and B (Fig. 5.1,5.2)

Paratypes. MCN–PB 307A, ULVG 7201A-B, ULVG 7202a, ULVG 7186Aa-B, ULVG 7196A-B, ULVG 7202A-B, ULVG 7131A-B, ULVG 7232A-B, ULVG 7437A-B, ULVG 7429, ULVG 7197, ULVG 7430, ULVG 7433, ULVG 7435, ULVG 7436, ULVG 7438, ULVG 7439, ULVG 7440, ULVG 7441.

Derivation of name. Specific name derived from the Guaraní language (*poty*=flower, *porá*=beautiful), spoken by the indigenous people inhabiting southern Brazil. Refers to the delicate and beautiful ovulate organ.

Stratigraphic horizon. Laminated mudstones-siltstones from the Caturrita Formation, Rosário do Sul Group (Andreis *et al.,* 1980).

Locality. Linha São Luis, Faxinal do Soturno, Rio Grande do Sul, Brazil.

Specific diagnosis. Ovulate structure, obovate, 3.8–4.3 cm long and 3.0 cm broad, apex rounded; base cuneate on small striated peduncle, outer surface composed of two layers of persistent elongated and delicate bracts; outer bracts striated and covered by long prominent hairs, inner bracts with entire margin and parallel sides, 30 mm long and 1.42 mm wide at broadest region, obconic receptacle, 1.4 cm in diameter, carrying many interseminal scales measuring 2–2,5 cm long, with apically disposed fusiform orthotropous ovules or seeds, 8 mm long and 1,5 mm wide, radially arranged and aligned, occupying equatorial zone of female structure, leading to a sterile disc in the basal part; twenty-three seeds visible, each one covered by a cutinised coat, independently attached in long stalks, and separated by few interseminal scales; their point of attachment is visible in some parts of the receptacle surface.

Description. Isolated and pedunculate ovulate structures, some probably in the stage of seed maturity (seed cone), 4.3 cm long and 3.0 cm wide, and covered by two layers of elongated, striate, hairyand membranaceous bracts, parallel orientated (nearly 30 mm long and 1.4 mm wide, Figs. 5.1–2, 5.8, 6.1–2). The peduncle extends in an obconic receptacle, with average diameter of 1.4 cm (Figs. 5.3, 6.3–4), that preserves polygonal scars corresponding to the insertion of the distal end of the interseminal scale (Fig. 5.4). The numerous sporophylls are disposed at a 60º angle around the receptacle formed —in the preserved views— by a basal sterile ring (6 mm high) exmedially bearing 23 fusiform apically aligned ortotropous ovules or seeds, separated by few interseminal scales and wrapped by cutinized tegument (Figs. 5.5–7, 6.3).

Comparisons. The fertile organ described shows morphological similarities with other ovulate structures of *Williamsonia* in the fossil record. It includes the architecture of its external bracts and the presence of a receptacle bearing fertile sporophylls, intercalated with sterile interseminal scales. In addition, several morphological features allow establishing affinities with previously described species of the genus.

The apical placement of the seeds/ovules on the sporophylls and few interseminal scales between them (Figs. 5.5–7) are common to the permineralized *W. diquiyui* from the Middle Jurassic in Oaxaca (Delevoryas and Gould, 1973), and to W. *bockii* from the Late Cretaceous of Canada (Haslam Formation), analyzed by Stockey and Rothwell (2003). Yet, the São Luis outcrop material differs by its preservation as impressions and by the obconical character of the receptacle.

The apical seed arrangement is not common in other members of *Williamsonia*, in which the seeds are normally disposed in distinct sectors of the interseminal scales ring, probably reflecting different ontogenetic stages (Bose, 1968). However, seed/ovules aligned at the apex of the sporophylls are common in the Cycadeoidaceae (*e.g.*, *Cycadeoidea wielandi* Ward and *C. dakotensis* Wieland), and this was considered a strategy to expose the micropiles to pollination. Also referring to seeds/ovules, attention is drawn in to the two different sizes and morphologies found in the different sections of the ovulate structure here preserved. Some present a delicate structure, smaller sizes and aparently non-cutinized teguments, probably reflecting imature seeds or ovules (Fig. 5.5). Others are larger, connected, and with an apparently hard cover, seemingly fertilized ovules (Figs. 5.6–7, 6.3). The reduction of the space between sporophylls and the integument cutinisation is common in post-fertilized *Williamsonia* (Sharma, 1976; Delevoryas and Gould, 1973). Stockey and Rothwell (2003) also pointed out this character in *W. bockii*.

The elongated and membranaceous texture of the external bracts approximates *W. potyporanae* to *Williamsonia* sp. from

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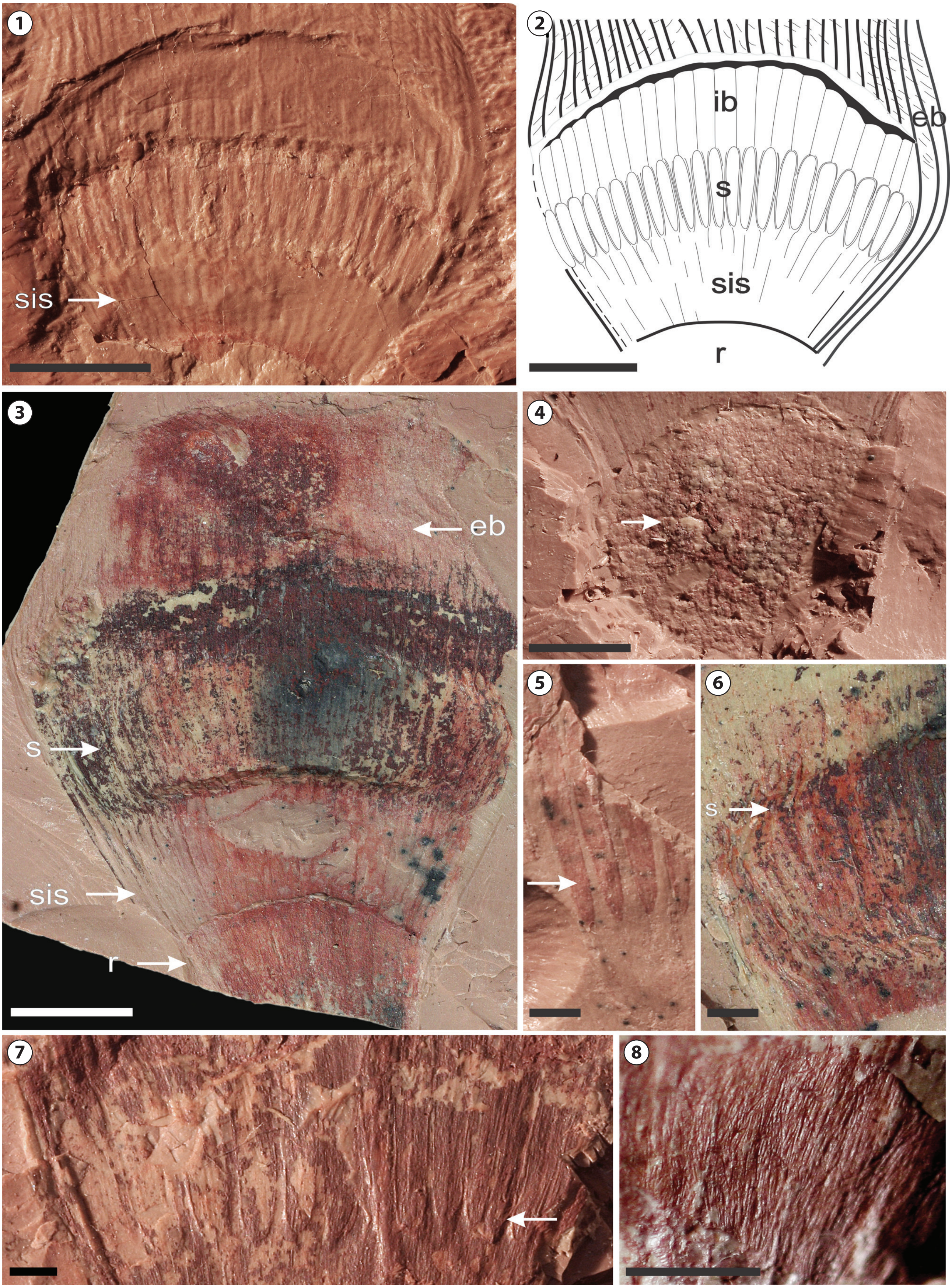
Figure 5. Morphological aspects of *Williamsonia potyporanae* sp. nov.**1-2**, external bracts covered by hairs (eb), smooth internal bracts (ib), fusiform and stalked seeds/ovules (s), ring of sterile interseminal scales (sis) and obconic receptacle (r), MCN–PB 311B, scale bar: 10 mm; **3**, section of a complete cone showing fertile and sterile rings of interseminal scales and the receptacle. Abreviations are the same that in figures 1-2, ULVG 7186Aa, scale bar: 5 mm; **4**, a detail of the receptacle with some dispersed polygonal scars (arrow) left by the distal end of interseminal scales, ULVG 7131, scale bar: 5 mm; **5**, impressions of ovules or immature seeds (arrow) between interseminal scales, ULVG 7186B, scale bar: 2 mm; **6**, apical part of a probable mature seeds, covered by cutinized tissues, ULVG 7201B, scale bar= 2 mm; **7**, a detail of the seed insertions (arrow), ULVG 7202a, scale bar: 2mm; **8**, the hairy cover on external bracts, ULVG 7440. Scale bar= 1 mm.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the El Freno Formation, Lower Jurassic of Mendoza, Argentina (Artabe *et al.*, 2005, fig. 5B), *W. bella* (Wu, 1999) and *W. gigas* (Harris, 1969); the latter is also comparable by having densely hairy external bracts.

The clove form of the whole structure in *W. potyporanae* sp. nov. is comparable with that in *W. bulbiformis* from the Lower Cretaceous of Argentina (Menéndez, 1966). However, and despite the common character alleged, *W. potyporanae* sp. nov. differs from the Argentine species because the latter carries broad and less numerous external bracts (10 to 14 bracts are proposed), small-sized ovulate structures, and a pyriform receptacle with a palissade ring lining it. Also, in *W. bulbiformis* interseminal scales occur in large numbers and occupy nearly 300º of the receptacle surface (Menéndez, 1966, figures 45–47). These distinct and important characters preclude the nclusion of the form studied herein in the Argentine species *W. bulbiformis*. There are also some similarities —more difficult to establish due the fragmentary nature of the Indian material— with *W. kakadbhitensis* Pandya and Sukh-Dev, that also have in common the persistent post-dehiscent closed cones (Pandya and Sukh-Dev, 1990). According to Pott *et al.* (2010), dehiscent cones and flower maturation, even after abscission, are typical of Jurassic and Cretaceous elements, with the sole exceptions of *W. netzahualcoyotlii* (Delevoryas and Gould, 1973) and *W. bockii* (Stockey and Rothwell, 2003).

The distinct characters mentioned herein support the proposition of this new species from the Caturrita Formation. A reconstruction based in the different sections of ovulate structure is presented in Figure 7.

***Pterophyllum*? Brongniart, 1825**

Figure 8

Material. ULVG 7332, ULVG 7326, ULVG 7330.

Stratigraphic horizon and locality. The same as that where the cone was collected.

Description. Impressions of the basal and middle parts of an isolated coriaceous leaf segment, elongate and ensiform in shape, slightly curved upright, seven times longer than broad (45x6.5 mm), margins entire and parallel. Base truncate and straight, slightly decurrent and constricted (4 mm wide). Five to six veins rarely bifurcate in the admedial part, with parallel and equidistant courses, giving place to nearly ten in the mid portion of the segment, which thus contains two to three veins per millimeter.

Comparisons. The set of characters, including linear outline of the segments, their length, smooth margins and parallel veins with few ramifications suggest affinities —although with some uncertainty due to the incomplete preservation— with some pinnules of the fossil-genus *Pterophyllum*. The affinity is also supported by the constricted and decurrent base on both sides of the segment, which distinguishes it from *Ptiophyllum*, another bennetites-related foliage in which only the basiscopic side of the segment is decurrent (Watson and Sincock, 1992).

Wade-Murphy and Van-Konijnenburg-van Cittert (2008), when working with *Pterophyllum* leaves identified in the Rhaetian of Bintan, Indonesia, pointed out that the presence —like in our specimens— of two veins per milimeter is a criterion to recognize the genus in fossil assemblages. However, the incompleteness (lack of apices and anatomical features), the rarity in the assemblage, and short length, prevent a more precise association with *Pterophyllum* until new material is recovered. According to Pott and McLoughlin (2009) knowledge of cuticle anatomy and apex morphology is critical in the establishment of the affinities of detached segments and leaves of bennettites, because of the similarity of the leaves to those of Ginkgoales (*e.g.*, *Phoenicopsis* Heer) and isolated leaves of conifers (*e.g.*, *Desmiophyllum* (Lesquereux) Miller and Hickey, *Podozamites* Braun, and *Heidiphyllum* (Retallack). The constricted base found here, for instance, is more common in *Heidiphyllum* than in *Pterophyllum* (Watson and Sincock, 1992; Pott *et al.* 2008). On the other hand, the striations between veins and the number of veins that characterize *Heidiphyllum* are absent in our specimens.

All things considered, a preferred affinity with *Pterophyllum* is adopted, taking in account the joint occurrence of ovulate structures of bennettites. In previously described materials, the general outline and admedial bifurcation of main veins in the leaf segments described herein also reveal a close affinity with *P. acutifolium* Morris, another species occurring in the El Freno Formation (Artabe *et al.*, 2005). In the Rhaetian–Hettangian floras of Greenland, Sweden and Poland, *P. subaequale* Hart, discussed by Pott and McLoughlin (2009), also presents comparable characters in venation and form.

When the complete distribution of *Pterophyllum* is analyzed, it shows four species exclusive to the Anisian-Ladinian (one extending into the Carnian), 38 from the Carnian to Rhaetian levels, 31 restricted to the Norian-Hettangian, and 22 that appear in the Middle Jurassic and become extinct in the Early Cretaceous (Barboni, 2010). Thus, 72% of the species of this genus characterizes the Triassic/Jurassic boundary.

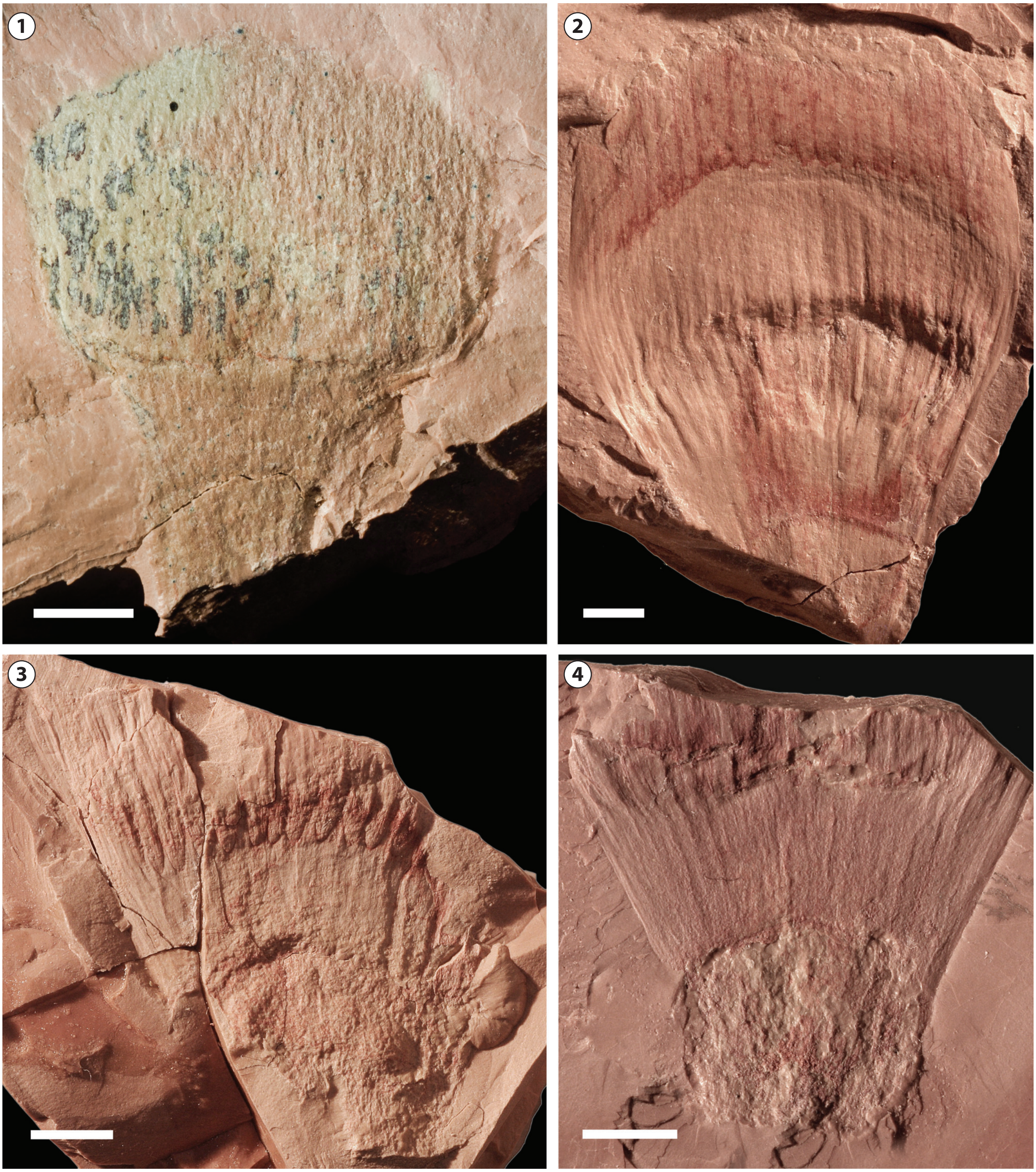

Figure 6. Distinct sections of *Williamsonia potyporanae* sp. nov. ovulate structure; **1**, external view from the basal part of the cone showing its covering by bracts, ULVG 201B; **2**, counterpart from the inner surface, exposing the internal layer of bracts with its fertile and sterile rings and part of the receptacle, ULVG 7433; **3**, detail of seed bases, ULVG 7437B; **4**, inner section showing the receptacle and the sterile ring of interseminal scales, ULVG 7196. Scale bars= 5mm

DISCUSSION

Paleoecology and taphonomy of bennettite assemblage from southern Brazil

The elongate and membranaceous bracts of the new species of *Williamsonia* herein described and the geological context in which they were found suggest a life under warm and wet climate, but with seasonal or irregularly distributed humidity, marked by short and intense rain episodes. This is attested by the successive paleosols and root impressions preserved and the associated depositional features, that indicate a vegetation growing over unstable soils of the alluvial plains and/or crevasse splay deposits. According to Stiles and Gierlowski-Kordesch (2006), in isolated rift basins the favorable conditions for plant development coincide with dryer periods favoring soil stability and colonization by sparse shrubs and low trees.

The isolated *W. potyporanae* structures with rare related leaf segments in a lake deposit confirm previous transport to the depositional site and the dehiscent character attributed to Bennettitales. Their good preservation suggest that the bearing tree or shrub grew nearby in the better drained areas, and that their roots were drowned during flooding episodes or else by lateral migration of river channels. A similar ecological behavior was recently proposed for the bennettites by Steinthorsdottir *et al.* (2011) and analogue deposits were identified in Late Triassic assemblages of the Transantarctic Mountains (Cúneo *et al.*, 2003), and Ischigualasto Formation in Argentina (Colombi and Parrish, 2008), both containing bennettite remains.

Monsoonal climates were inferred by many authors for the continental areas of Pangea during the Mesozoic, especially in the subtropical latitudes (Parrish, 1993; Rees *et al.*, 2000; Royer *et al.*, 2004). Such climates entail favourable conditions for cyclic vegetation renewal and postmortem transport to depressed areas. In the São Luis section this kind of climate regime is also supported by the false growth rings of conifer woods (Pires *et al.*, 2005) and signs of vegetation recovery.

The global fossil record of bennettites and the paleogeographic pattern proposed for southern Brazil during the Early Mesozoic (online Supplementary File 2) suggest it is unlikely that bennettites in Southwestern Gondwana had the same ecological requirements as those growing in swamps or peat bogs in the Northern Hemisphere; the latter environments are favourable to permineralizations and yield greater amounts of plant material (Pott *et al.*, 2008; Stockey and Rothwell, 2003). In South Hemisphere this kind of taphonomic pattern is only recorded in rocks from the Early Jurassic of India and Patagonia, where paleoenvironmental data indicate high sea level intervals (Artabe *et al.*, 2005; Cúneo *et al.*, 2010). Thus, the few sclerophyllic structures detected in *W. potyporanae* —such as the hairy (but delicate) bracts— seem to reflect a real but not drastic hydric depletion.

The first appearance and diversification of the group in Gondwana coincides with the establishment of isolated basins

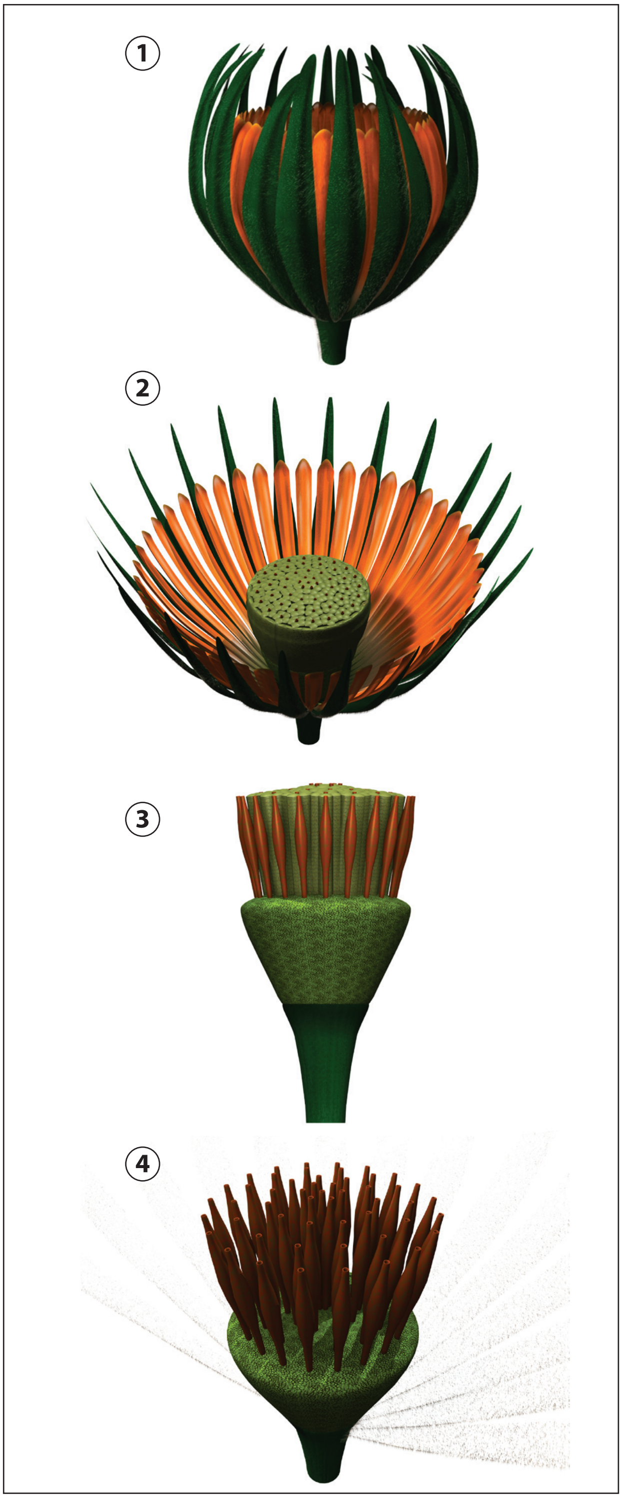

Figure 7. A reconstruction proposed to the*Williamsoniapotyporanae* sp. nov. ovulate structure; **1**, partially open bracts allows seeing the two layers of ribbon-shaped bracts, with acute apices, the external one covered by hairs; **2**, the same general view with artificially open bracts to show the internal disposition of floral parts, stand out the probable aspect of the interseminal scales ring surface and micropiles; **3**, the receptacle reconstrution (in green) and the sustaining seeds and interseminal scales; **4**, detail of the stalked seeds, incumbent over the receptacle surface. Interseminal scales supressed.

in southern Africa and South America, with a rapid dispersion and conquest of marginal marine enviroments (online Supplementary File 2.1). It supports that the more dry conditions in continental areas probably helped stimulate the xeric adaptations needed for life in the near-coastal saline areas (online Supplementary File 2.2), and was favoured by the high levels of atmospheric CO_2 (and methane) —and consequent hot climates— that characterized the end of theTriassic onwards (McElwain *et al.,* 1999; Ruhl *et al.,* 2010; Steinthorsdottir *et al.*, 2011).

The open areas with vegetated uplands subject to high-humidity periods in a broader arid context, also agree with the design of *W. potyporanae* and other *Williamsonia* "flowers". Cupullate reproductive organs protected by delicate and sometimes pillose envoltories are found nowadays in plants growing in modern analogue environments, *i.e.*, some Ranunculaceae (*e.g.*, *Adonis amurensis* Regel. and Radde from Asia), Cactaceae (*Parodia* spp. from Brazil), and Proteaceae (*Protea* spp. from Africa).

Morphology of the ovulate cone, associated paleoflora and age implication

The main evolutionary stages of the fossil record of *Williamsonia* and related forms herein analyzed support the evolved character of the new species described and its singular morphology when compared with other early Mesozoic forms. The known Late Triassic record shows elements with distinct and exclusive morphologies (*e.g.*, *Sturianthus langeri* Kräusel, *Pramelreuthia haberfelneri* Krasser, *Westersheimia pramelreuthensis* Krasser*, Williamsonianthus keuperianus* Kraüsel and Schaarschmidt, *Williamsonia alpina* Krasser, *Bennetticarpus wettsteinii* Kraüse *emend.* Pott, Krings,Kerp and Friis, and *Fredlindia fontifructus* Anderson and Anderson). Yet, according to Pott *et al.* (2010) the few (25–30), large and round seeds of *B. wettsteinii* could represent a plesiomorphic character, suggesting that the nearly 50 sporophylls inferred for *W. potyporanae* place it in an intermediate condition between those typically Triassic and the more evolved foms, in which hundreds are counted (Thomas and Batten, 2001).

On the other hand, when an affinity is better established with some Triassic remains (*e.g.*, *W. nizhonia*, *W. newberry*, and *Vardekloeftia* of Harris, 1932), they present cones normally covered by broad, leathery and, in general, free bracts, with the pronounced "sun" or "star" designs. Spindle seeds, for exemple, are not common in Triassic forms, only being record from the Cretaceous onwards (*e.g. W. leckenbyi, W. diquiyui*, *W. oligosperma, W. harrisiana, W. bockii* and *W. bulbiformis*). Finally, the seed-length in *W. potyporanae* (8 mm) can only be compared to that of the Late Cretaceous representatives (Stockey and Rothwell, 2003), being even longer than those of *W. diquiyui* from the Middle Jurassic .

Another evolved aspect of *W. potyporanae* is the hairy covering of the external bracts, exclusive to Jurassic and Cretaceous fossils, such as *W. gigas* (Lignier, 1903; Archangelsky, 1970; Thomas and Batten, 2001) and the Indian species (Bose and Banerji, 1984). And the obconic receptacle and "floral" arrangement —sporophylls with a sterile basal sector and a fertile apical one— is only comparable to that of the Albian *W. aculeata* and *W. winthorpensis* (Miller and Hickey, 2010).

Other floristic elements in the fossil assemblage that contribute to age discussions are the absence of Corystospermales and the conifer dominance. This fits well with the latest Late Triassic–Early Jurassic assemblages from Argentina (Stipanicic and Bonetti, 1970; Spalletti *et al.,* 1999; Artabe *et al.*, 2007; Escapa *et al.*, 2008a,b; Gnaedinger and Cúneo, 2009), where the first known record of *Williamsonia* is Early Jurassic. When

Figure 8. A *Pterophyllum?* related leaf segment showing well developed and parallel veins, with few admedial ramifications (arrow), ULVG 7326. Scale bar= 1 cm.

we compare the São Luis paleoflora with other Lower Mesozoic ones from the middle and high latitudes of the Southern Hemisphere (Barboni, 2010), the greatest affinity also lies with those from the Lower Jurassic of Argentine, *e.g.*, El Freno (Herbst, 1964a,b; Artabe *et al.*, 2005), Roca Blanca (Herbst, 1966; Gnaedinger and Herbst, 2007; Gnaedinger *et al.*, 2009) and Nestares formations (Spalletti *et al.*, 2007), mainly by their content of primitive conifers. El Freno Formation also shares a similar paleolatitudinal location and environmental setting (Giambiagi *et al.*, 2005). In the Roca Blanca Formation, *W. gigas* is the most important element and —as in southern Brazil— it is associated with *Brachyphyllum, Pagiophyllum* and conifer wood including the Taxaceae (Gnaedinger and Herbst, 2007).

Williamsonia-related remains are presently unknow from the Upper Triassic of Chile; yet *Pterophyllum* sp. is present (Leppe and Moisan, 2003; Troncoso and Herbst, 2007). Fossil wood of Coniferales and Ginkgoales becomes common in the Lower Jurassic, where it is represented by *Agathoxylon* and *Baieroxylon* (Torres and Philippe, 2002). The bennettites is also very rare in the Jurassic of Australia and New Zealand and mainly represented by leaves (Gould, 1975; White, 1981; Pole and Raine, 1994).

The only other area in Gondwana where male and female (*Fredlindia fontifructus*) bennettite remains occur later than the Carnian is South Africa (Molteno Formation), where they appear associated to leaves of *Nilssoniopteris* (Anderson *et al.*, 2007). Unfortunatelly, younger assemblages are either rare or restricted to Equisetales, conifers and other wood logs (Bamford, 2004). Poorly diverse plant assemblages were identified in the Elliot and Clarens formations (Late Triassic–Early Jurassic "Stormberg Group"), the former unit being similar to Caturrita Formation by its depositional features (Bordy *et al.*, 2004).

Finally, in Antarctica the Triassic floras contain *Dicroidium, Heidiphyllum* and *Linguifolium*, giving way to those characterized by *Otozamites,* Dipteridaceae, Marattiales and conifers only at the beginning of Jurassic (Rees and Cleal, 2004; Bomfleur *et al.*, 2007; Birkenmajer and Ociepa, 2008).

Supported by the data discussed above, an age younger than the Norian (Rubert and Schultz, 2004; Bonaparte and Sues, 2006) and Rhaetian (Langer et *al.*, 2007; Abdalla and Ribeiro, 2010) —both based on tetrapods faunas— is suggested for the Caturrita Formation, particularly for the beds at the the São Luis section. Its exclusive flora provides further support towards the proposition of Abdalla and Ribeiro (2010). These authors stated that each vertebrate assemblage in the Caturrita Formation could represents a single faunal association, and that from the São Luis outcrop representing a younger age than those assigned to the Ischigualastian faunas. The large theropod footprints recently discovered in the upper beds of the São Luis outcrop, twice as large as those previously known from the Caturrita Formation (Silva *et al.*, 2009) also support a probable Early Jurassic age for this deposit.

More recent contributions also have implications for the discussions about the age of Mesozoic faunal and floral assemblages from southern Brazil. Soares *et al* (2008) points towards a Late Triassic–Jurassic age for the Caturrita Formation based in field relationships, facies and the tectonism affecting the Parana Basin sector in Rio Grande do Sul. The other is the proposal of Barredo *et al.* (2012) suggesting the absence of a Late Triassic (Norian and Rhaetian) deposition in Cuyo Basin, Argentina.

CONCLUSIONS

The *Williamsonia* and *Pterophyllum* remains identified in southern Brazil represent the oldest unequivocal record of Bennettitales from this area of Gondwana. Their association in the same outcrop with an important vertebrate fauna —including taxa consider restricted to the Late Triassic and others that foreshadow Early Jurassic forms— renews discussions about the age and genesis of these and other mid-latitude deposits in South America and Africa. The difficulty for establishing the age is magnified by its deposition in isolated rift basins, which encouraged faunal and floral endemisms. The environmental context and taphonomic constrictions, so distinct from the other supposed coeval worldwide record of bennettites, also hamper comparisons. Nonethless, *W. potyporanae* sp. nov. is quite distinct from others taxa known from Triassic deposits, by its delicate and connected pilose bracts and the seed/ovule arrangement in the sporophylls. Presently, and until more results are obtained, it seems reasonable to confirm an age younger than the Norian proposed for the nearby vertebrate faunas.

The paleoassemblage with the new form of *Williamsonia* herein described —containing autochtonous to parautochtonous primitive conifers and paleosols preserved in a restricted lacustrine/deltaic context from a broader river system— supports a deposition under warm and seasonal climate, characterized by periods of intense rainfall. The periodic high water-supply guarantees its preservation and the seasonal renewal of woody and herbaceous vegetation, physiognomicaly similar to that which presently covers modern rainshadow and continental areas, at the boundary between tropical and subtropical climate belts.

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