

FIRST RECORD OF VOLTZIALEAN MALE CONE (*LUTANTHUS*) AND PODOCARPACEAN FEMALE CONE (*RISSIKISTROBUS*) FROM THE LATE TRIASSIC OF ARGENTINA, INCLUDING NEW PLANT REMAINS FROM THE PASO FLORES FORMATION

SILVIA C. GNAEDINGER¹
ANA MARIA ZAVATTIERI²

¹Centro de Ecología Aplicada del Litoral, Área de Paleontología, Consejo Nacional de Investigaciones Científicas y Técnicas (CECOAL-CCT CONICET Nordeste-UNNE), Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (FaCENA-UNNE), Casilla de Correo 291, W3410CDB Corrientes, Argentina.

²Laboratorio de Paleopalínología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Centro Científico Tecnológico, Consejo Nacional de Investigaciones Científica y Técnicas (IANIGLA-CCT CONICET Mendoza), Casilla de Correo 330, M5502IRA Mendoza, Argentina.

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SILVIA C. GNAEDINGER¹, AND ANA MARIA ZAVATTIERI²

¹Centro de Ecología Aplicada del Litoral, Área de Paleontología, Consejo Nacional de Investigaciones Científicas y Técnicas (CECOAL-CCT CONICET Nordeste-UNNE), Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (FaCENA-UNNE), Casilla de Correo 291, W3410CDB Corrientes, Argentina. scgnaed@hotmail.com

²Laboratorio de Paleopalínología, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Centro Científico Tecnológico, Consejo Nacional de Investigaciones Científica y Técnicas (IANIGLA-CCT CONICET Mendoza), Casilla de Correo 330, M5502IRA Mendoza, Argentina. amz@mendoza-conicet.gov.ar

Abstract. New plant remains from the upper section of the Paso Flores Formation, at the Cañadón de Pancho locality, western area of the Collón Curá River, Neuquén Province, Argentina, are herein described and illustrated. These are: *Lutanthus ornatus*, *Rissikistrobus plenus*, *Rissikistrobus reductus*, *Rissikia media*, *Umkomasia* sp., *Sphenobaiera argentinae*, *Pseudoctenis spatulata*, *Taeniopteris crassinervis* and *Yabeiella brackebuschiana*. Additionally, *Baiera triassica*, in replacement of the homonymous species previously identified in Argentina as *Baiera taeniata*, *Ginkgo taeniata* and *Sphenobaiera taeniata*, is herein described. Furthermore, species previously described for other localities in the Paso Flores Formation are recorded for the first time for the Quemquemtreu area of the Cañadón Pancho locality. These species are: *Asterotheca rigbyana*, *Marattiopsis muensteri*, *Cladophlebis kurtzii*, *C. indica*, *Dictyophyllum (Dictyophyllum) tenuifolium*, *Goepertella stipanicicii*, *Dicroidium incisum*, *D. odontopteroides*, *D. lancifolium*, *Pachydermophyllum praecordillerae*, *Heidiphyllum elongatum*, *Baiera furcata*, *Sphenobaiera robusta*, *Pseudoctenis carteriana* and *P. falconeriana*. The Voltziales male cone *Lutanthus* herein described from the Paso Flores Formation represents its second record for the Gondwana realm while the Podocarpaceae female cone *Rissikistrobus* is hereby reported for the first time from Triassic strata of Argentina and constitutes its third record for Gondwana. Comparisons with the plant diversity recorded from other localities of the Paso Flores Formation throughout the Neuquén Province are analyzed. The Cañadón de Pancho microflora assemblages suggest a Late Triassic (Latest Norian= Rhaetian) age and therefore the fossil flora is the youngest recorded from Argentinian Triassic basins to date.

Key words. Reproductive structures. Leaves. Paso Flores Formation. Triassic. Argentina.

Resumen. PRIMER REGISTRO DE CONO MASCULINO DE VOLTZIALES (*LUTANTHUS*) Y DE CONO FEMENINO DE PODOCARPACEAE (*RISSIKISTROBUS*) DEL TRIÁSICO SUPERIOR DE ARGENTINA, INCLUYENDO NUEVOS RESTOS DE PLANTAS DE LA FORMACIÓN PASO FLORES. Se describen e ilustran nuevos restos de plantas de la sección superior de la Formación Paso Flores, en la localidad Cañadón de Pancho, área occidental del río Collón Curá, Provincia del Neuquén, Argentina. Estos son: *Lutanthus ornatus*, *Rissikistrobus plenus*, *Rissikistrobus*, *Rissikia media*, *Umkomasia* sp., *Sphenobaiera argentinae*, *Pseudoctenis spatulata*, *Taeniopteris crassinervis* y *Yabeiella brackebuschiana*. Además, se describe *Baiera triassica* que reemplaza las especies homónimas previamente identificadas en Argentina como *Baiera taeniata*, *Ginkgo taeniata* y *Sphenobaiera taeniata*. También, se identificaron especies para el área Quemquemtreu, en la localidad de Cañadón de Pancho, que fueron previamente descriptos para otras localidades de la Formación Paso Flores. Las especies identificadas corresponden a *Asterotheca rigbyana*, *Marattiopsis muensteri*, *Cladophlebis kurtzii*, *C. indica*, *Dictyophyllum (Dictyophyllum) tenuifolium*, *Goepertella stipanicicii*, *Dicroidium incisum*, *D. odontopteroides*, *D. lancifolium*, *Pachydermophyllum praecordillerae*, *Heidiphyllum elongatum*, *Baiera furcata*, *Sphenobaiera robusta*, *Pseudoctenis carteriana* y *P. falconeriana*. El cono masculino de Voltziales *Lutanthus* aquí descripto para la Formación Paso Flores, representa el segundo registro para el dominio de Gondwana mientras que el cono femenino de Podocarpaceae *Rissikistrobus* se registra por primera vez para el Triásico de la Argentina, y constituye el tercer registro para Gondwana. Se realizan comparaciones con la diversidad de plantas registradas en otras secciones de la Formación Paso Flores en la provincia del Neuquén. Las asociaciones de microfloras de Cañadón de Pancho sugieren una edad Triásico Tardío (Norian tardío= Retiano), y por lo tanto la flora fósil es la más joven registrada hasta ahora en las cuencas del Triásico de Argentina.

Palabras clave. Estructuras reproductivas. Hojas. Formación Paso Flores. Triásico. Argentina.

The great plant-species diversity loss of the end of the Permian extinction event was followed, in the Triassic, by a new evolutionary radiation from the P/T crisis surviving groups

(Farjon, 2008; Taylor *et al.*, 2009). Amongst the conifers of the end of the Paleozoic (Upper Permian), only the Voltziales group endured the Mesozoic (Triassic–Lower

Jurassic) (Anderson *et al.*, 2007; Farjon, 2008; Taylor *et al.*, 2009) and is therefore considered as the transitional group between Paleozoic and modern conifers, except for the Podocarpaceae and Araucariaceae, for which diversity started in the Triassic (Farjon, 2008; Taylor *et al.*, 2009; Bomfleur *et al.*, 2011). Farjon (2008) and Taylor *et al.* (2009) suggested that much of the evolution of the conifers occurred during the Triassic and that, in order to better understand their evolutionary processes, paleobotanists should focus on the study of fossil conifers from such Period. From studies of dispersed fossil plant remains, some authors suggested different associations (and/or affiliations) of such isolated organs in order to reconstruct the “whole-plant”, and to aid interpreting the evolutionary trends and phylogenetic position of the conifers (Townrow, 1967; Anderson, 1978; Anderson and Anderson, 1989, 2003; Axsmith *et al.*, 1998; Anderson *et al.*, 2007; Escapa *et al.*, 2010; Bomfleur *et al.*, 2011, 2013; Holmes and Anderson, 2013, and others).

Even though Voltzialean foliage and seed cones are ubiquitous in Gondwanan Triassic floras, the inferred organ affiliations remain under dispute (leaves, male and female cones and wood). The affiliation of the leaves (*Heidiphyllum*) and the ovulate cone (*Telemachus*) with the Order Voltziales is widely accepted given their morphological (cuticular) correspondence and the co-occurrence of data in numerous records in Gondwana (Anderson, 1978; Retallack, 1981; Anderson and Anderson, 1989, 2003; Spalletti *et al.*, 1990; Axsmith *et al.*, 1998; Nielsen, 2005; Anderson *et al.*, 2007; Gnaedinger and Herbst, 2008; Arce and Lutz, 2010; Gnaedinger, 2010; Escapa *et al.*, 2010; Morel *et al.*, 2011; Bomfleur *et al.*, 2013, and others). However, there are discrepancies regarding the attribution of the male cone. While three different genera of Voltzialean pollen cones have been described from the Molteno Formation (Anderson and Anderson, 2003), two taxa are known from the Triassic of Antarctica (Cantrill *et al.*, 1995; Hermsen *et al.*, 2007). Anderson and Anderson (2003) established the affiliation with *Odyssianthus* but identified two additional Voltzialean male cones in the Molteno Formation: *Lutanthus* and *Fredianthus*. These three genera are represented by a total of nine specimens (see comparisons in Anderson and Anderson, 2003: tab. 32, p. 58). According to these authors, *Odyssianthus* and *Lutanthus* could also be included within a single genus due to their similarities. Conversely, Bomfleur

et al. (2011, 2013) presented affiliations of genera including trunks, branches and roots (*Notophytum*), leaves (*Heidiphyllum* and *Notophytum*), seed cones (*Telemachus* and *Parasciadopitys*), pollen cones (*Switzianthus* and *Leastrobus*) and bisaccate pollen (*Alisporites*-type) based on their similarities in terms of cuticle and pollen morphology as well as on their co-occurrence. However, *Switzianthus*, which was recorded from Southern Africa by Anderson and Anderson (2003), from Australia by Holmes and Anderson (2013) and from Argentina by Gnaedinger and Herbst (2007) and Gnaedinger (2010), was affiliated with *Dejerseya* leaves based on closely similar cuticles and their mutual occurrence (related with an enigmatic group of pteridosperms) (Anderson and Anderson, 2003). During the Triassic, the cosmopolitan and ubiquitous dispersed-pollen genus *Alisporites* is known to have been produced by voltzialean conifers as well as by corystospermalean and peltaspermalean seed ferns (Osborn and Taylor, 1993; Anderson and Anderson, 2003; Hermsen *et al.*, 2007; Bomfleur *et al.*, 2011, 2013). In the Paso Flores microfloral assemblages, the genus *Alisporites* (and its counterpart *Falcisporites*) is a frequent to dominant component of the palynoflora (Zavattieri and Volkheimer, 2002; Zavattieri and Mego, 2008).

Podocarpaceae (Triassic to Recent), together with Araucariaceae, represent the oldest conifer families and molecular studies have suggested a sister group relationship (Chaw *et al.*, 1997; Farjon, 2008; Rai *et al.*, 2008). Within Podocarpaceae, the affiliation of *Rissikia* foliage shoots, *Rissikistrobus* female cones and *Rissikianthus* male cones is determined by morphological correspondence and by their mutual occurrence in the Molteno Formation, South Africa, as well as in the Basin Creek Formation, Australia (Townrow, 1967; Anderson and Anderson, 2003; Holmes and Anderson, 2013). Gnaedinger and Herbst (2008) and Gnaedinger (2010) also mentioned such mutual occurrence in the Triassic of Argentina (Cañadón Largo Formation, El Tranquilo Group, Santa Cruz Province). Although the insertion of the three above mentioned genera within the Podocarpaceae remains debatable (Townrow, 1967; Retallack *et al.*, 1977; Anderson and Anderson, 2003, p. 105; Anderson *et al.*, 2007, p. 137), all the mentioned authors finally concluded on their inclusion within the Family. In the palynofloristic assemblages of the Paso Flores Formation

at the Cañadón de Pancho locality, several species of pollen-grain genera *Podocarpidites*, *Alisporites (pars)* and *Inpertur-pollenites (pars)* are of podocarpacean affinity (Zavattieri and Volkheimer, 2002).

The main aim of this contribution is to provide a systematic description of the Voltzian male cone *Lutanthus* as well as the podocarpacean female cone *Rissikistrobus*, which are hereby recorded from the Upper Triassic of Argentina for the first time.

The paleobotanical content of the Paso Flores Formation has been studied by several authors (Frenguelli, 1937; Bonetti and Herbst, 1964; Spalletti *et al.*, 1988; Arrondo *et al.* 1991; Ganuza *et al.*, 1992, 1995; Morel *et al.*, 1992, 1999, 2011; Herbst, 1993; Artabe *et al.*, 1994; Zamuner and Artabe,

1994; among others) and abundant and diverse megafloora assemblages have been recorded. Morel *et al.* (1999: tab. 2, p. 402) revised the previous fossil flora records and provided an updated list of 41 fossil taxa recovered from different outcrop localities throughout the Formation. This contribution aims to offer further descriptions of the new fossil flora specimens collected in 1996 (by AMZ) from the upper section of the Paso Flores Formation, Cañadón de Pancho locality, western area of the Collón Curá River, Neuquén Province (Fig. 1), of which eleven species had been previously described from other outcropping localities. Finally, an updated and complete list of the taxa identified from the Paso Flores Formation at the Cañadón de Pancho locality is herein included.



Figure 1. Aerial view of the southern region of Neuquén Province and north-western region of Río Negro Province showing the main outcropping sections of the Paso Flores Formation (based on Spalletti *et al.*, 1988 and González Díaz, 1982). "A" indicates the location of the studied fossil flora described herein. Image taken from Google Earth-Internet (2016).

GEOLOGICAL SETTING

In the southern border of the Neuquén Basin (Legarreta and Gulisano, 1989), the Upper Triassic continental Paso Flores Formation is exposed in isolated outcrops along a latitude of approximately 40° S (Piedra del Aguila) to the north and located a few kilometers NE of the Alicurá Dam and on both margins of the Limay River to the south. The north western exposures of the Formation outcrop in the western region of the Collón Curá River and, its tributary, the Quemquemtreu River, in the south of Neuquén Province, northern Patagonia (Fig. 1). The type section of the Paso Flores Formation is exposed in the area surrounding Estancia Manantiales de Paso Flores and Cerro Mariana, on the south-eastern margin of the Limay River along the boundary between the Río Negro and Neuquén provinces (Fig. 1) (Nullo, 1979). The Paso Flores strata have been studied by many authors, including Frenguelli (1948), Galli (1969), Nullo (1979), González Díaz (1982), Lapido *et al.* (1984), Morel and Ganuza (2002), among others, since Fossa Mancini (1937) named them "Serie de Paso Flores". Spalletti *et al.* (1988, 1990), Arrondo *et al.* (1991), Ganuza *et al.* (1995) and Morel *et al.* (1999) identified five sedimentary facies representing an alluvial fan, braided and meandering fluvial systems and lacustrine deposits in the Paso Flores strata. These sequences are exposed in Estancia Corral de Piedra, the Paso Flores type area (on both margins of the Limay River), Lomas and Cañadón Ranquel Huao as well as in the Cañadón de Pancho localities (Fig. 1). Spalletti *et al.* (1988) provided a detailed description of the lithology, the sedimentology and the environmental interpretations of the sedimentary facies. Morel *et al.* (1999) made a paleofloristic revision of the Paso Flores strata in those sequences and a biostratigraphical analysis of the paleobotanical assemblages that indicated a late Late Triassic age.

As described by Spalletti *et al.* (1988, 1990) from the Corral de Piedra area in Neuquén Province (Fig. 1), the thicker sections of the Paso Flores strata represent alluvial fan deposits and gravelly braided complex systems. The outcrops of the Paso Flores Formation on both sides of the Limay River (near the Paso Flores area, more than 3 km east of the Alicurá Dam), together with those of Lomas and Cañadón de Ranquel Huao, have been interpreted as braided river deposits (Spalletti *et al.*, 1988, 1990; Jenchen, 2001). All of

the above-mentioned outcrops along the Limay River and its surrounding areas represent the lower to middle outcropping parts of the Paso Flores Formation (Fig. 1). The thinnest section of the formation is indicative of a braided-plain and meandering river that developed on a flood plain and lacustrine deposition and is exposed at the Cañadón de Pancho locality, near the Quemquemtreu River (González Díaz, 1982; Ganuza *et al.*, 1995). This section has been considered to constitute the upper part of the formation (Zavattieri and Mego, 2008).

Cañadón de Pancho locality

In the western area of the Collón Curá River, southern Neuquén Province, the Paso Flores Formation is exposed along an extensive area between the Quemquemtreu and the Caleufú rivers (Fig. 1). This formation lies unconformably on the upper Paleozoic basement of the Neuquén Basin and is constituted by an igneous and metamorphic complex and in turn covered discordantly by the typical light-grey tuffitic continental sedimentary strata of the Collón Curá Formation (middle Miocene). The Paso Flores Formation at the Cañadón de Pancho section is composed of four successive sedimentary facies associations (Ganuza *et al.*, 1995). In this locality, the Paso Flores successions consist of: a) clast-supported conglomerates and sandstones deposited in a braided fluvial system; b) laminated and rippled light mudstones and siltstones (lacustrine facies); c) interbedded tabular mudstones and lenticular sandstones belonging to a low-sinuosity meandering fluvial system; and d) coarse-grained sandstones and conglomerates that formed in a braided fluvial system. The majority of the studied microfloral assemblages and the well-preserved megafloreal remains of a *Dicroidium* Flora were recovered from such low-sinuosity meandering fluvial system and the aforementioned lacustrine deposits (González Díaz, 1982; Spalletti *et al.*, 1988, 1990; Arrondo *et al.*, 1991; Ganuza *et al.*, 1992, 1995; Artabe *et al.*, 1994).

Age of the Paso Flores Formation

So far, the only data available for the determination of the age of the Paso Flores Formation is that provided by its stratigraphic relationships and its floristic content (megaflorea and microflora) (Zavattieri and Volkheimer, 2002; Zavattieri *et al.*, 2008). The palynological studies of

the lowermost part of the Formation at its type section were published by Zavattieri and Mego (2008) while those palynological assemblages from the uppermost part recorded from the Cañadón de Pancho locality were outlined in Zavattieri (2002) and Zavattieri and Volkheimer (2002). The paleofloristic assemblages of the Paso Flores Formation suggest a late Late Triassic age (Morel *et al.*, 1999). However, the palynological data constrains the age of the unit between the Late Triassic (late Carnian–early Norian), for the lower section of the Paso Flores Formation (Zavattieri and Mego, 2008) and the uppermost Norian (=Rhaetian), for the uppermost levels at the Cañadón de Pancho section, Quemquemtrey area (Zavattieri, 1997, 2002). Therefore, the palynoflora evidence suggests that the paleobotanical content of the Paso Flores Formation represents the youngest Triassic flora known from Argentina.

MATERIAL AND METHODS

The specimens recovered are well-preserved impressions and were studied using a Leica M50 stereoscopic microscope with an attached EC3 camera with Leica Application Suite EZ. 3.2.1 software and a Nikon Coolpix P100 camera. Measurements of venation density were taken on the leaves close to their margins. CorelDRAW X7 software was used for the line drawing of the main features of the fossil plants. For higher taxonomic categories, the proposal of Stewart and Rothwell (1993) was used.

Institutional abbreviations. MCF-PBPH, Museo Carmen Funes, Paleobotánica de Plaza Huinca, Neuquén, Argentina; CTES-PB, Colecciones Paleontológicas de la UNNE “Dr. Rafael Herbst”, Sección Paleobotánica, Corrientes, Argentina.

SYSTEMATIC PALEONTOLOGY

Order VOLTZIALES Andreanszky, 1954

Family *Incertae sedis*

Genus *Lutanthus* Anderson and Anderson, 2003

Type species. *Lutanthus hemidiscus* Anderson and Anderson, 2003.

Lutanthus ornatus Anderson and Anderson, 2003

Figures 2.1–3, 3.1

2003. *Lutanthus ornatus* Anderson and Anderson, p. 76, pl. 9 (1–6).

Description. Male cone of small size, ca. 15 mm long, preserved, 12 mm wide, with straight to moderately upcurving axis (1.5 mm); apex and base not preserved (Figs. 2.1, 3.1). Axis 6 mm long preserved, with eight microsporophylls, helically attached. Stalk of the microsporophylls is linear and of 0.9 mm, with a laminar wing of 0.4 mm and broad distal lamina, slightly lobed or longitudinally striate in the incomplete distal lamina, ca. 3–4 mm (Figs. 2.1–2, 3.1). Microsporophylls bear 2 lateral rows, each with 3–4 microsporangia possibly abaxially attached (Figs. 2.1–2, 3.1). Microsporangia of 0.95–1.45 mm is oval to circular in shape, with linear ornamentation (Figs. 2.3, 3.1).

Studied material. MCF-PBPH 102a (impression and counterpart).

Comments. Anderson and Anderson (2003, p. 58) identified three genera of Voltzilean male cones. The Paso Flores specimen closely resembles the genera *Lutanthus* Anderson and Anderson, 2003 and *Odyssianthus* Anderson and Anderson, 2003. However, the Argentinian specimen differs from the genus *Odyssianthus* by its amount of microsporangia in the microsporophylls.

Anderson and Anderson (2003) identified three species for the genus *Lutanthus* from the Molteno Formation (Southern Africa): *Lutanthus hemidiscus* Anderson and Anderson, 2003, *Lutanthus ornatus* Anderson and Anderson, 2003 and *Lutanthus robustus* Anderson and Anderson, 2003. The microsporophylls of *L. ornatus* present a distinctively multilobed and fairly large distal lamina as well as clearly ornamented oval-circular microsporangia while *L. hemidiscus* is characterized by a microsporophyll with a large hemispherical distal lamina, its entire margin and microsporangia with a dehiscence line, and *L. robustus*, by a robust axis, a microsporophyll with a relatively small distal kidney-shaped lamina and its dentate-crenate margin as well as irregularly rhomboidal microsporangia. According to the diagnostic characters of each species and the features previously described for the Paso Flores specimen, such specimen can be clearly identified as *Lutanthus ornatus*. Thus this species is described for the first time from Argentina and represents the third specimen recorded from Gondwana (the other two were recorded from the Molteno Flora of South Africa).

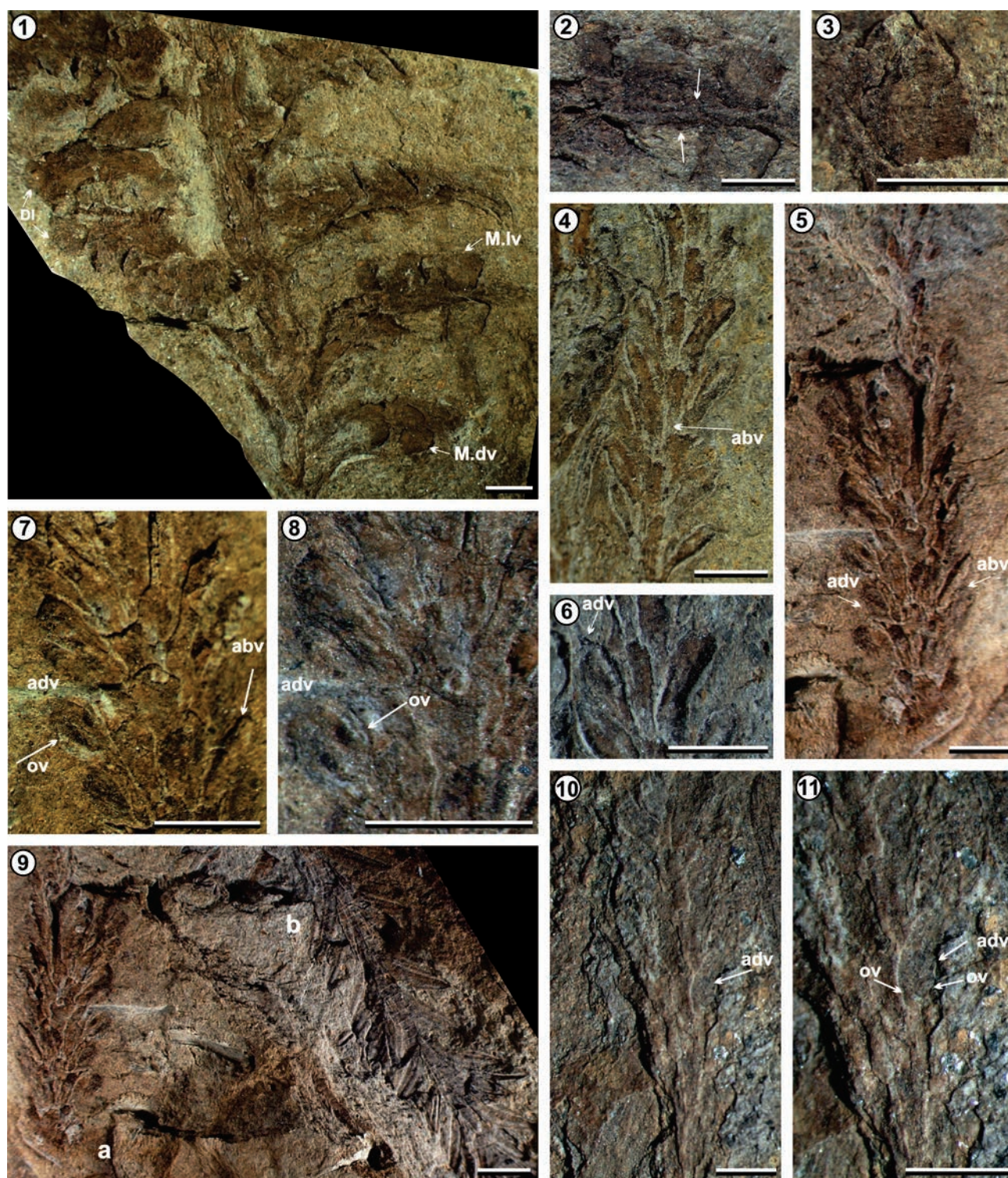


Figure 2. 1–3, *Lutanthus ornatus*, MCF-PBPH 102a. 1, Male cone; 2, microsporophylls with microsporangia and stalk with a wing (arrows); 3, microsporangia with linear ornamentation. 4–9, *Rissikistrobus plenus*; 4, 6, young female cone, MCF-PBPH 102c, bract/scale complexes of the megasporophylls: bracts; ovuliferous 3-lobed scale; 5, 7–8, mature female cone, MCF-PBPH 089b, bract/scale complexes of the megasporophylls: bracts (abv= abaxial view); ovuliferous 3-lobed scale, and ovule; 9a, *Rissikistrobus plenus*, MCF-PBPH 089b, 9b, *Rissikia media*, MCF-PBPH 089a. 10–11, *Rissikistrobus reductus*, MCF-PBPH 089f, female cone with ovuliferous scale single, and ovule. Abbreviations: abv, abaxial view; adv, adaxial view; DI, distal lamina of the microsporophylls; M.lv, microsporangia lateral view; M.dv, microsporangia distal view; ov, ovule; S.dv, scale of the microsporophylls, dorsal view. Scale bars= 1.5 mm (1–9), 2.5 mm (10–11).

Order CONIFERALES Engler, 1897
 Family PODOCARPACEAE Endlicher, 1847

Genus *Rissikistrobus* Anderson and Anderson, 2003

Type species. *Rissikistrobus plenus* Anderson and Anderson, 2003.

Rissikistrobus plenus Anderson and Anderson, 2003

Figures 2.4–9a, 3.2–3, Table 1

1967. Seed scale *Rissikia media* Townrow, p. 111, 113, pl. 1 (A–B),
 tf.8 (B, C, E–J).

2003. *Rissikistrobus plenus* Anderson and Anderson, p. 106, pl. 19
 (1–7), 20 (1–8).

Description. Female cone linear, more than 14 mm long, 3–4 mm wide, with megasporophylls spirally arranged (Figs. 2.4–5, 9a; 3.2–3). Megasporophylls consist of bract/scale complexes. Bracts (to 1.8–2.5 mm) lanceolate, cuspidate, erect, distinctly longer than ovuliferous scale (Figs. 2.4–9a, 3.2–3). Ovuliferous scale consists of three lobes of similar size each of which bears a pair of adaxial ovules (Figs. 2.7–

8, 3.3). Lobes obtusely pointed, sometimes dentate? (Fig. 3.3). Ovuliferous scale of ca. 1.3–1.5 mm of length and, in wider portion, of 0.9 mm. Ovule egg-shaped (ca. 0.8 x 0.3 mm) (Figs. 2.7–8, 3.3).

Studied material. MCF-PBPH 089b-c-d, 102c, 418 (six specimens).

Comments. Female cone with ovuliferous scale consisting of three lobes bearing two ovules each lobe, bract longer than ovuliferous scale and associated with the foliage shoots *Rissikia media* described by Townrow (1967) and Retallack *et al.* (1977). Anderson and Anderson (2003) identified the species *Rissikistrobus plenus* Anderson and Anderson, 2003 and *Rissikistrobus semireductus* Anderson and Anderson, 2003 on the basis of the above-mentioned features. The latter species presents lateral lobes of the ovuliferous scale in a more reduced form than those of *R. plenus* (Tab. 1).

Anderson and Anderson (2003, p. 104) confirmed the affiliation between *Rissikia* and *Rissikistrobus* (female cone) initially put proposed by Townrow (1967) based on their co-

TABLE 1– Comparison between species of *Rissikistrobus* and associated seed scale of *Rissikia*.

SPECIES	<i>R. plenus</i>	<i>R. semireductus</i>	<i>R. reductus</i>	Seed scale <i>Rissikia media</i>	Seed scale <i>Rissikia apiculata</i>	<i>Rissikistrobus sp. A</i>	<i>R. plenus (this work)</i>	<i>R. reductus (this work)</i>
CONE	Length, ca. 80 mm	Length, ca. 85 mm	Relatively short, ca. 60 mm	25–60 mm long	About 3 mm long preserved	Longer than 50 mm	Longer than 15 mm	12 mm long, without base and apex
MEGASPOROPHYLLS	Bracts	Distinctly longer than scale, ca. 3–4 mm	Distinctly longer than scale, ca. 5 mm	Reduced, shorter than scale, 1 mm	ca. 3 mm long	ca. 1.5 mm long	Lanceolate, longer than scale, ca. 1.8–2.5 mm	Reduced, shorter than scale, ca. 1 mm
	Ovuliferous scales	3-lobed, with outer lobes slightly reduced bearing a pair of adaxial ovules on each lobes (ca. 2.4 mm x 1.5 mm)	3-lobed, with outer lobes strongly reduced bearing a pair of adaxial ovules on each lobes (ca. 3 mm x 1.3 mm)	Single lobe bearing a pair of adaxial ovules on lobes (ca. 4.5 x 1.4 mm)	Lobes obtusely pointed, sometimes dentate, with two ovules per lobes. All lobes about same size (ca. 6 mm)	Lobes sharply pointed, not dentate; one seed only per lobe the central lobe probably longer than the laterals (ca. 2.5 mm)	Bract/scale, 4 mm long and 2 mm wide, ovate with acute apex. Pair of ovules on bract/scale	3 nearly similar-sized lobe, obtusely pointed dentate? Pair of adaxial ovules on each lobe (ca. 1.3–1.5 x 0.9 mm)
OVULE /SEED	Tear-shaped (ca. 1 x 0.5 mm)	Linear-elliptical (ca. 2 x 0.5 mm)	Linear-elliptical (ca. 0.8 x 0.35 mm)	Egg-shaped, narrow (0.3-1 x 0.2-0.75 mm)	More or less oval (ca. 0.5 x 0.25 mm)	?	Egg-shaped (ca. 0.8 x 0.3 mm)	Linear-elliptical (ca. 0.7 x 0.25 mm)

Data taken from Townrow (1967); Anderson and Anderson (2003); Holmes and Anderson (2013).

occurrence in seven localities. The Paso Flores specimens also suggest an affinity between *R. media* foliage shoots and *Rissikistrobus plenus* and *R. semireductus* cones, therefore implying that, as pointed out by Anderson and Anderson (2003, p. 106), both species (*R. plenus* and *R. semireductus*) may represent parts of a morphological continuum or ontogenetic series and may actually belong to one species.

Rissikistrobus reductus Anderson and Anderson, 2003

Figures 2.10–11, 3.4, Table 1

1967. Seed scale *Rissikia apiculata* Townrow, p. 113, pl. 1(C–D), tf. 8 (D).

2003. *Rissikistrobus reductus* Anderson and Anderson, p. 107, pl. 21 (1–5).

2013. *Rissikistrobus* sp. A, Holmes and Anderson, p. 58–59, figs. 9A–C, 10A–G, 11A.

Description. Linear female cone compact, 12 mm long? preserved, without the base and the apex conserved. Megasporophyll spirally arranged, consisting of bract/scale complexes (Figs. 2.10, 3.4). Bracts reduced, far shorter than scale, 1 mm long. Ovuliferous scale consisting of a single

lobe (or un-lobed) bearing a pair of adaxial ovules, sharply pointed, 2.8 mm long and 0.7 mm in maximum width (Figs. 2.11, 3.4). Ovule, linear-elliptical (ca. 0.7 x 0.25 mm) (Figs. 2.11, 3.4).

Studied material. MCF-PBPH 089f.

Comments. The ovuliferous single lobe scale bearing a pair of adaxial ovules of the Paso Flores specimen shows features similar with the female cone associated with foliage shoot *Rissikia apiculata*, described by Townrow (1967), and with *Rissikistrobus reductus*, described by Anderson and Anderson (2003), as well as with those specimens identified by Holmes and Anderson (2013) as *Rissikistrobus* sp. A (Tab. 1).

Genus *Rissikia* Townrow, 1967

Type species. *Rissikia media* (Tenison-Woods) Townrow, 1967.

Rissikia media (Tenison-Woods) Townrow, 1967

Figures 2.9b, 3.5

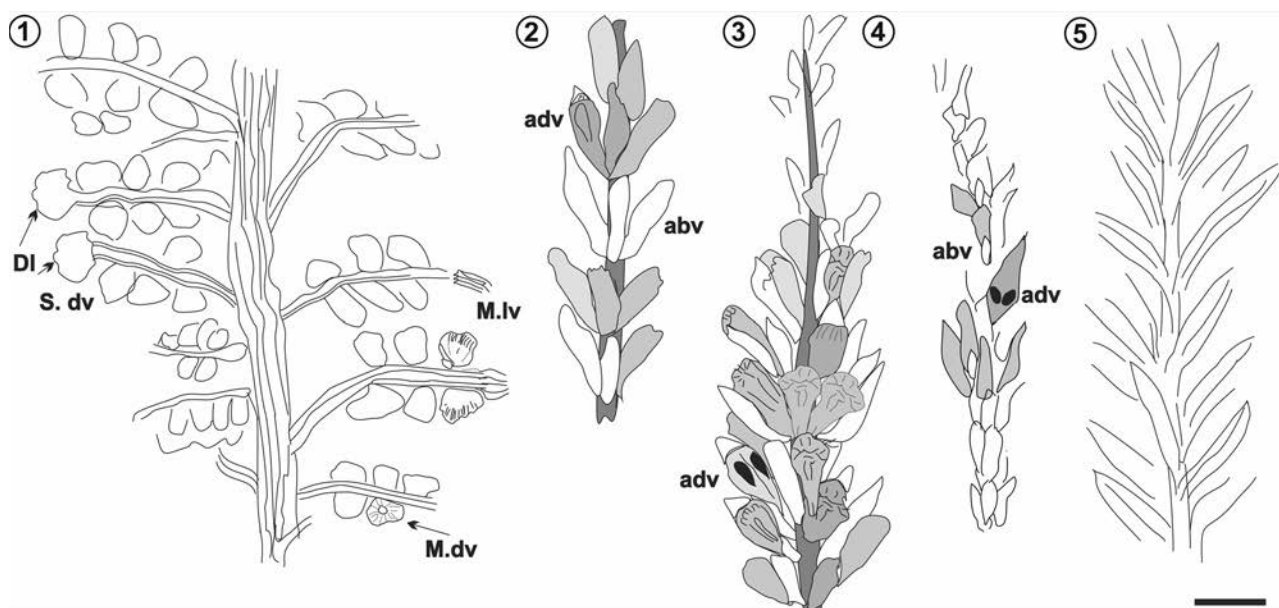


Figure 3. Line drawings. 1, *Lutanthus ornatus*, MCF-PBPH 102a. Male cone strobilus. 2–3, *Rissikistrobus plenus*, 2, young female cone, MCF-PBPH 102c; 3, mature female cone, MCF-PBPH 089b (bract/scale complexes of the megasporophylls: bracts, ovuliferous 3-lobed scale, and ovule). 4, *Rissikistrobus reductus*, MCF-PBPH 089f, female cone with ovuliferous single scale and ovule. 5, *Rissikia media*, MCF-PBPH 089a. Abbreviations: **abv**, abaxial view; **adv**, adaxial view; **DI**, distal lamina of the microsporophylls; **M.dv**, microsporangium distal view; **M.lv**, microsporangium lateral view with linear ornamentation; **ov**, ovule; **S.dv**, scale of the microsporophylls, dorsal view. Scale bar = 2 mm.

For synonymy see Troncoso *et al.* (2000) and Holmes and Anderson (2013).

Additional synonymy

2005. *Rissikia media* (Tenison-Woods) Townrow, Nielsen, p. 557–558, fig. 7.4.
 2011. *Rissikia media* (Tenison-Woods) Townrow, Lutz, Gnaedinger, Mancuso, Crisafulli, p. 581; figs. 3.18, 7.1.
 2011. *Rissikia media* (Tenison-Woods) Townrow, Morel, Artabe, Ganuza and Zúñiga p. 532–533, fig. 4.2.

Description. Foliage shoot, narrow to broadly elliptical, 15–19 mm long and 4–5 mm wide; leaflets linear to linear elliptical, 3–4 mm long and 0.5–0.6 mm wide, helically attached from 45°–50° to the rachis; apex acute and single median vein. Bases decurrent but not, or scarcely, contracted (Figs. 2.9b, 3.5).

Studied material. MCF-PBPH 048b, 089a, e.

Comments. The specimens herein described are assigned to *Rissikia media* due to their morphological features are coincident with those described by Townrow (1967), Anderson and Anderson (1989), Troncoso *et al.* (2000), Nielsen (2005), Lutz *et al.* (2011), Morel *et al.* (2011) and Holmes and Anderson (2013).

Order CORYSTOSPERMALES Petriella, 1981
 Family CORYSTOSPERMACEAE Thomas, 1933

Genus *Umkomasia* (Thomas) Klavins, Taylor and Taylor, 2002

Type species. *Umkomasia macleanii* Thomas, 1933.

Umkomasia sp.
 Figures 4.1, 5.1

Description. Ovulate cupules recurved and isolated, 13 mm wide, roundly shaped with wrinkled surface. In the upper zone of the cupule, two ridges, each of 2 mm; the lower zone of the micropyle of the seed is also observed. Ovule circular in shape, bearing a wing 1 mm wide.

Studied material. MCF-PBPH 417a.

Comments. The size of the described structure is comparable to that of the cupules of *Umkomasia* (Thomas) Klavins, Taylor and Taylor, 2002 and the megasporophylls of *Hamshawvia* Anderson and Anderson, 2003. However, these genera are different in terms of the fact that the megasporophylls of *Hamshawvia* are multiovulate while the

cupules of *Umkomasia* are uni-ovulate or bi-ovulate (Klavins *et al.*, 2002; Anderson and Anderson, 2003). The Paso Flores cupules are uni-ovulate, recurved and present a micropyle, thus being assigned to *Umkomasia*. Only two isolated cupules allowing the assignment to *Umkomasia* sp. were found in this material. However, given the shape and size of the cupules as well as their bearing of circular seeds and a medium wing size of approximately 1 mm, they are more closely comparable to those of *Umkomasia monopartite* Anderson and Anderson, 2003. A similar, though larger, rounded cupule with a wrinkled surface was recovered from the Santa Maria Formation (Triassic), Brazil (com. pers., R. Barboni).

Order GINKGOALES Gorožankin, 1904

Genus *Sphenobaiera* (Florin) Harris and Millington, 1974

Type species. *Sphenobaiera spectabilis* (Nathorst) Florin, 1936.

Sphenobaiera argentinae (Kurtz) Frenguelli, 1946
 Figures 4.2, 5.2

For synonymy see Artabe (1985) and Gnaedinger and Herbst (1999).

Additional synonymy

2007. *Sphenobaiera argentinae* (Kurtz) Frenguelli, Artabe, Morel, Ganuza, Zavattieri and Spalletti, p. 292, figure 5.G.
 2011. *Sphenobaiera argentinae* (Kurtz) Frenguelli, Morel, Artabe, Ganuza and Zúñiga, p. 529, fig. 3–4.

Description. Leaf triangular in shape (wedge-shaped), 51 mm in preserved length and 18 mm at top maximum width. Basal angle of 10°. The lamina is typically dissected into two divergent and similar segments of slightly convex lateral margins 7–9 mm wide. Parallel veins up to twice dichotomous (Figs. 4.2, 5.2). Density of venation of ca. 9–10 veins per cm (Fig. 5.2).

Studied material. MCF-PBPH 052.

Comments. The specimen described from the Paso Flores Formation is morphologically coincident with those described by Frenguelli (1946), Artabe (1985), Anderson and Anderson (1989), Gnaedinger and Herbst (1999), Artabe *et al.* (2007) and Morel *et al.* (2011) as *Sphenobaiera argentinae*. With respect to *Sphenobaiera robusta* (Arber) Florin, 1936, which had been previously recorded from the Paso

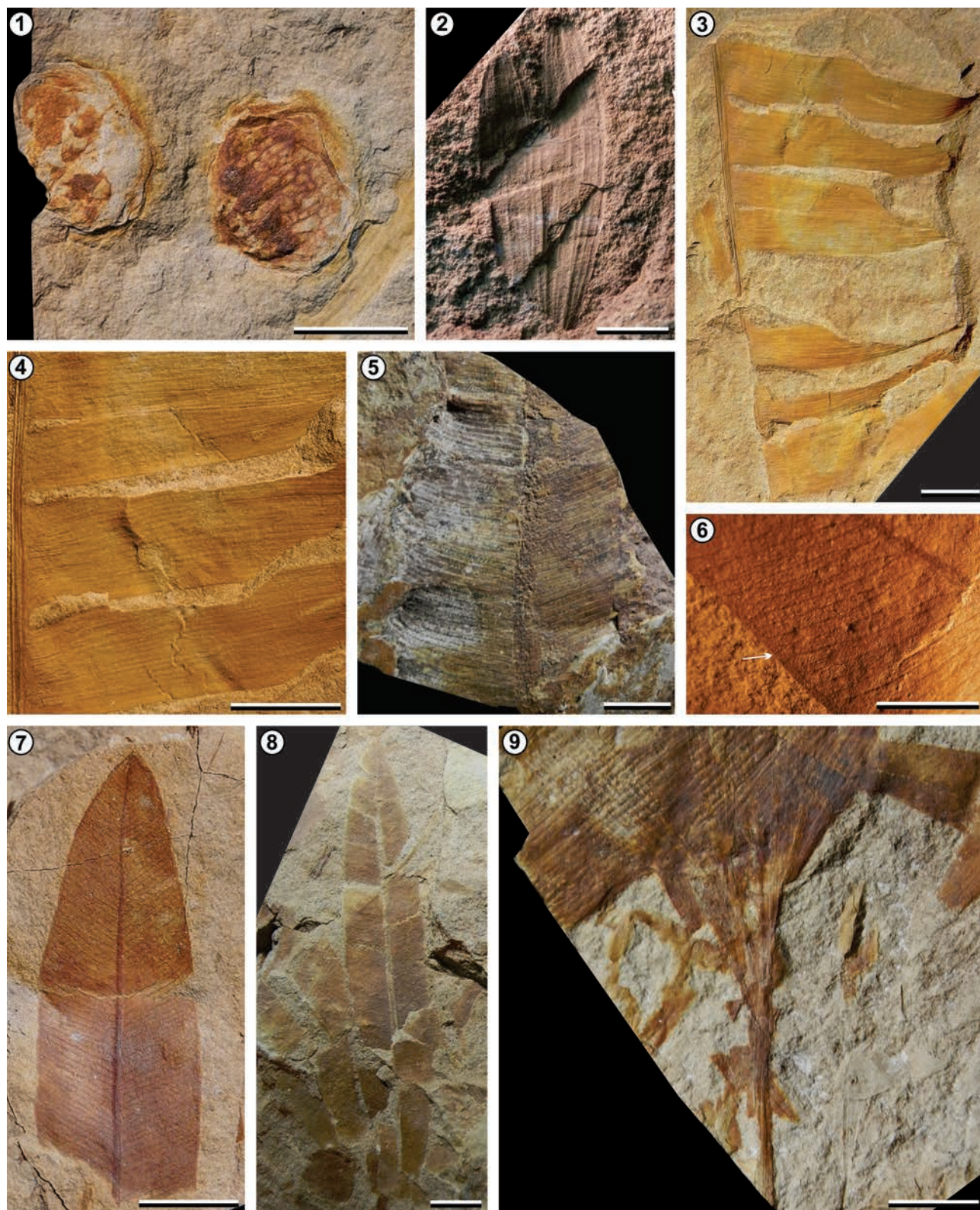


Figure 4. 1, *Umkomasia* sp., MCF-PBPH 417a. 2, *Sphenobaiera argentina*, MCF-PBPH 052. 3–4, *Pseudoctenis spatulata*, MCF-PBPH 071. 5, *Taeniopteris crassinervis*, MCF-PBPH 196. 6–8, *Yabeiella brackebuschiana*; 6–7, MCF-PBPH 064; 8, MCF-PBPH 086. 9, *Baiera triassica*, MCF-PBPH 063. Scale bars= 10 mm (1–5, 7–9), 5 mm (6).

Flores Formation (Morel *et al.*, 1999), it can be distinguished by its lamina, which is dissected into segments by two or more main incisions (Retallack, 1980; Anderson and Anderson, 1989).

Genus *Baiera* Braun, 1843

Type species. *Baiera muensteriana* (Presl in Sternberg, 1833) Heer, 1876.

Baiera triassica Gnaedinger and Zavattieri nom. nov.

Figures 4.9, 6.1, 3–5, 7.1

1876. *Baiera taeniata* Geinitz, lam. 2, fig. 10.

1937. *Ginkgo taeniata* (Geinitz) Frenguelli, fig. 3, lam. 3, fig. 8.

1999. *Sphenobaiera taeniata* (Geinitz) Morel, Ganuza and Zúñiga p. 398–399; fig. 5f.

Description. Fragmentary impressions of petiolate (petiole 21 mm in preserved length, 1.7 mm wide), symmetrical and triangular leaves of which the most complete is 50 mm long of maximum length, 46 mm wide and with a sharp basal angle (60°–70°) (Figs. 4.9, 6.1, 3–5, 7.1). The deeply dissected lamina bifurcates three times forming 6 to 8–10? narrow and elongated segments with parallel margins. The first incision is deep, matching the base sheet 2.5 mm from the base of the leaf lamina and dividing it into two basal halves 1–2 mm wide. The second incision is deep too (about 1 cm from the base sheet), forming segments 4–7 mm wide. The third incision is 20 mm or 18 mm deep, forming terminal segments with rounded apices 2–3 mm wide. Venation bifurcates up to four times, with a density of up to 4 veins in terminal segments (Fig. 6.1).

Studied material. MCF-PBPH 063, MCF-PBPH 417a.b.

Comments. The criteria specified by Gnaedinger and Herbst (1999, p. 282, fig. 1) and Bauer *et al.* (2013, p. 541), which was then updated by Barboni and Dutra (2015: tab. 1, p. 421), is herein followed in order to include the specimens from the Paso Flores Formation described in this contribution within the genus *Baiera*. *Baiera triassica* Gnaedinger and Zavattieri nom. nov. was proposed after the nomenclatural revision of the Argentinian specimens previously identified as *Baiera taeniata* Geinitz, 1876; *Ginkgo taeniata* (Geinitz) Frenguelli, 1937 and *Sphenobaiera taeniata* (Geinitz) Morel, Ganuza and Zúñiga, 1999 (see Gnaedinger and Zavattieri, 2017). This species differs from others described for the Triassic of Gondwana in the acute basal angle of its lamina,

its number of segments and the depth of its incisions. Figure 6 illustrates the morphological variability that characterizes both the specimens described herein and those analyzed by Geinitz (1876), Frenguelli (1937) and Morel *et al.*, (1999). It also differs from *Baiera africana* Baldoni, 1980 (already recorded from the Paso Flores Formation) by the presence of numerous linear segments, a small acute basal angle and a subrounded to retuse apex. Furthermore, the Argentinian specimens described by Artabe *et al.* (1998) (Llantenes Formation), and Morel *et al.* (1999) (Paso Flores Formation), and assigned to *Baiera furcata* (Lindley and Hutton) Braun, 1843, are distinguished by their lamina, which is dissected by more incisions.

Order CYCADALES Dumortier, 1829

Genus *Pseudoctenis* Seward, 1911

Type species. *Pseudoctenis eathiensis* (Richards) Seward, 1911.

Pseudoctenis spatulata du Toit, 1927

Figures 4.3–4, 5.3–4

For synonymy see Gnaedinger (1999).

Additional synonymy

2003. *Pseudoctenis* cf. *spatulata* du Toit, Leppe and Moisan, p. 478, fig. 4A–D.

Description. Fragment of leaf, 104 mm long preserved. Pinnae 7 to 11 mm wide at the base; wider posteriorly, up to 10–14 mm. This character and the basal constriction confer an oblong-elongate shape to the pinnae (Figs. 4.3–4, 5.3–4). A laminar wing is observed (Figs. 4.4, 5.4). The rachis is 1.2 mm wide. The angles of insertion of the pinnae to the rachis are of 70°–80°, with variable distance among them ranging from 2.5 to 3 mm at the base of the fronds. Veins dichotomize mainly at the base and in the middle part of the pinna (Fig. 4.4). From the rachis, 9 to 12 oblique veins emerge in the lower half of the pinna and run nearly parallel along the length of the pinna until 16–22 veins occur in the distal part of the pinnae (Figs. 4.4, 5.4).

Studied material. MCF-PBPH 071.

Comments. The morphological features and measurements herein described are closely similar to those described for the species by du Toit (1927), Artabe (1985), Anderson and

Anderson (1989), Gnaedinger (1999) and Leppe and Moisan (2003), among others.

Pseudoctenis carteriana (Oldham) du Toit, 1927 and *Pseudoctenis falconeriana* (Morris) Bonetti, 1968 (Tabs. 6–7), which had been previously recorded from the Paso Flores Formation (Morel *et al.*, 1992, 1999; Ganuza *et al.*, 1995), differ from *P. spatulata* described above, by the lack of the constriction in the basal part of the pinna (Artabe, 1985; Gnaedinger, 1999).

PTERIDOPHYLLA *Incertae Sedis*

Venation patterns on extant plants are strongly correlated with leaf shapes probably exclusively determined by genes (Dengler and Kang, 2001; Roth-Nebelsick *et al.*, 2001; Laguna *et al.*, 2008). According to Laguna *et al.* (2008), the primary veins to be formed in all leaves of a species are the same, enabling the identification of plants on the bases of the leaves venation patterns. Gnaedinger and Herbst (2004a) proposed the use of the “venation pattern” to differentiate

species within a fossil genus (even to identify middle leaf fragments) and demonstrated that the venation patterns of *Taeniopteris* Brongniart, 1832, *Yabeiella* Ôishi, 1931 and *Linguifolium* (Arber) Retallack, 1980 consist of an alternating sequence of different types of lateral veins (Gnaedinger and Herbst, 2004a, fig. 2). It is according to these proposals that we differentiate species of *Taeniopteris* and *Yabeiella*.

Genus *Taeniopteris* Brongniart, 1832

Type species. *Taeniopteris vittata* Brongniart, 1832.

Taeniopteris crassinervis (Feistmantel) Walkom, 1917

Figures 4.5, 5.5–6, Table 2

For synonymy see Artabe (1985), and Sen Gupta (1986).

Additional synonymy

1998. *Taeniopteris crassinervis* (Feistmantel) Walkom, Gnaedinger and Herbst, p. 58, fig. 3a–b; Lám. 1, fig. k.

Description. Middle to upper part (apex) of a leaf fragment,

TABLE 2— Venation pattern of *Taeniopteris crassinervis*.

<i>Paso Flores Formation. MCF-PBPH 196 (Figs. 4.5, 5.6a)</i>										%
S	2	1		2	2		1	1	1	43
Dc		1	1	2	2	1		1		38
D2				2			1		1	19
A										
<i>Paso Flores Formation. MCF-PBPH 196 (Figs. 4.5, 6.5b)</i>										%
S	2	1	2		1		2	2		50
Dc		2		1		1		1	2	35
D2			1		1		1			15
A										
<i>El Tranquilo Group. CTES-PB 8176 (Gnaedinger and Herbst, 1998: fig. 3b)</i>										%
S		1	1	2						37
Dc	1		1		1	1				37
D2				2		1				27
A										

A, anastomosing veins; Dc, dichotomized veins once at different height of their path in the leaf lamina; D2, dichotomized veins twice in one or both pair of veins; S, simple veins. The order in which the veins forms is S, Dc, D2, A.

ca. 49 mm of preserved length and 36 mm in the wider basal portion, progressively narrowing upwards, up to 21 mm wide (Figs. 4.5, 5.5–6). Base and apex not preserved. Distinct midrib 2.5 mm wide at base, gradually narrowing to 1.09 mm towards the apex. Margins slightly undulate (Figs. 4.5, 5.5–6). Lateral veins disposed at angles of 80°–90° from the midrib. Venation patterns: alternating groups of simple veins (43–50%), with veins that dichotomize either once immediately from the midrib or at various distances across the lamina (35–38%) as well as with veins that dichotomize twice (15–19%) (Figs. 4.5, 5.6). Density of venation: 14–16 veins/cm near the margin (Figs. 4.5, 5.5–6).

Studied material. MCF-PBPH 190, 196.

Comments. The described morphological features and dimensions agree with those provided by Walkom (1917) for the species *Taeniopteris crassinervis* (Feistmantel) Walkom, 1917 and are furthermore coincident with those described for the species by Artabe (1985), Sen Gupta (1986) and Gnaedinger and Herbst (1998).

The “venation pattern” data for *Taeniopteris crassinervis*, which is based on the type of lateral veins and the emergence sequence from the midrib, is illustrated in Table 2. Such data, which was obtained from the Paso Flores material, is compared with that of the El Tranquilo (Santa Cruz Province) specimens (Gnaedinger and Herbst, 1998).

The main and most notable features of *T. crassinervis* as compared to most of the other fossil species of the genus *Taeniopteris* are that the veins either dichotomize once immediately from the midrib or at various distances across the lamina and that there are veins that dichotomize twice (Gnaedinger and Herbst, 2004a). When compared with other *Taeniopteris* species sharing the same venation pattern (alternating simple veins with groups of veins dichotomized once and twice), *T. crassinervis* stands out mainly by the distribution of the types of veins in the groups and percentages as well as by the venation density and the angle disposition of the veins (Tab. 3).

This species is distinguished from *Taeniopteris lentriculi-*

TABLE 3— Comparison between *Taeniopteris* species from Gondwana that share the character of the venation pattern (alternation of simple veins with vein groups dichotomized once and twice).

		<i>Taeniopteris</i> <i>homerifolius</i>	<i>Taeniopteris</i> <i>thomsoniana</i>	<i>Taeniopteris</i> <i>vittata</i>	<i>Taeniopteris</i> <i>crassinervis</i>	
Veins angle*		75°	85–90°	50–60° 80°	80–90°	
Venation pattern	<i>Veins type (number)</i>	<i>S</i>	1–2	1–2	1–2	
	<i>Dc</i>	1–5	1–3	1–7	1–2	
	<i>D2</i>	1	1–2	1–2	1–2	
	<i>A</i>		1–2			
	<i>Veins type (percentage)</i>	<i>S</i>	34–36	25–26	6–15	37–50
	<i>D1</i>	60–62	52–57	50–73	37–38	
	<i>D2</i>	4	8–11	12–44	15–27	
	<i>A</i>		4–7			
Veins density		10–12	28–36	24–28	14–16	

*middle part of the leaf. Data taken from Gnaedinger and Herbst (2004a). Explanation of abbreviations in Table 2.

forme (Etheridge) Walkom, 1917, previously recorded from the Paso Flores Formation (Ganuza *et al.*, 1995; Morel *et al.*, 1999), by the fact that it presents numerous simple veins of which a few dichotomize once at the emergence from the midrib (Shirley, 1898; Walkom, 1917; Artabe, 1985; Anderson and Anderson, 1989).

Genus *Yabeiella* Ôishi, 1931

Type species. *Yabeiella brackebuschiana* (Kurtz) Ôishi, 1931.

Yabeiella brackebuschiana (Kurtz) Ôishi, 1931

Figures 4.6–8, 5.7–8, Table 4

For synonymy see Stipanovic *et al.* (1996).

Additional synonymy

2004. *Yabeiella brackebuschiana* (Kurtz) Ôishi, Gnaedinger and Herbst, p. 54–55, figs 3.G–H, 5. E–F.

2007. *Yabeiella brackebuschiana* (Kurtz) Ôishi, Artabe, Morel, Ganuza, Zavattieri and Spalletti, p. 296, fig. 5.D.

2011. *Yabeiella brackebuschiana* (Kurtz) Ôishi, Morel, Artabe, Ganuza and Zúñiga, p. 533, fig. 4.5.

2011. *Yabeiella brackebuschiana* (Kurtz) Ôishi, Lutz, Gnaedinger, Mancuso and Crisafulli, p. 582, fig. 2.11, 7.11.

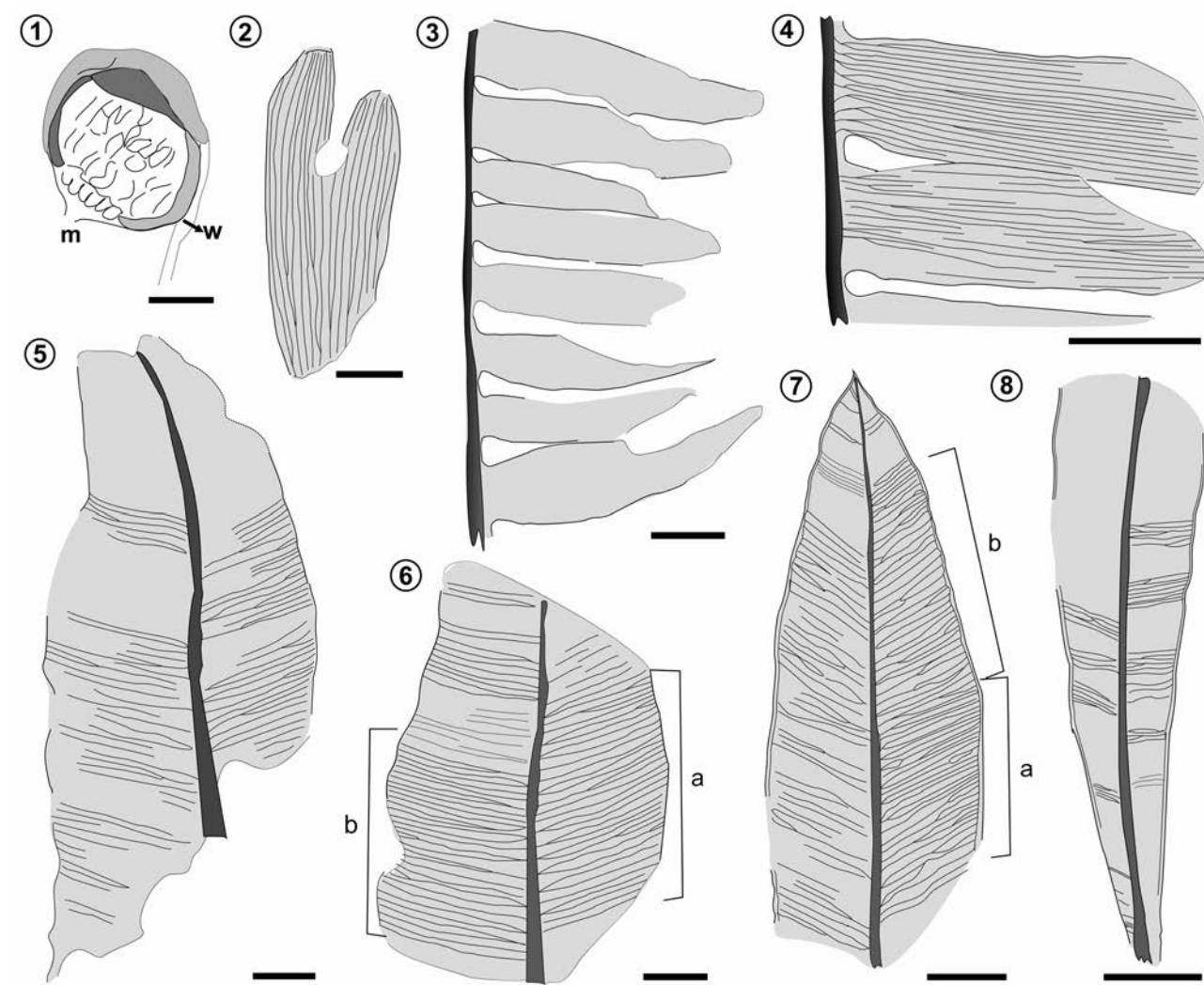


Figure 5. Line drawings. 1, *Umkomasia* sp., MCF-PBPH 417a. 2, *Sphenobaiera argentina*, MCF-PBPH 052. 3–4, *Pseudoctenis spatulata*, MCF-PBPH 071. 5–6, *Taeniopteris crassinervis*; 5, MCF-PBPH 190; 6, MCF-PBPH 196. 7–8, *Yabeiella brackebuschiana*; 7, MCF-PBPH 064; 8, MCF-PBPH 179. Scale bars= 5 mm (1), 10 mm (2–8).

2013. ?*Yabeiella brackebushiana* (Kurtz 1921) Ôishi, Holmes and Anderson, p. 60, fig.13A–C, 14A, B.

2015. *Yabeiella brackebuschiana* (Kurtz) Ôishi, Morel, Artabe, Ganuza, Bodnar, Correa, and Spalletti, p. 463–464.

Description. Simple leaves, lanceolate in shape, of a length of more than 100 mm and a width of 12–16 mm in the middle part of the leaf (Figs 4.6–8, 5.7–8). Apex acuminate, base gradually narrowing (Fig. 5.7–8). Midrib vein wide, 2 mm in width, striate. Lateral veins at an angle of 65°–70° from the midrib. Venation patterns: groups of 1–2 simple veins (27%) alternating with groups of 1–2 veins that dichotomize once (37%) and veins that dichotomize twice (10%) as well as groups of 1–2 or more veins that anastomose (26%) (Fig. 5.7). On the laminar margin, lateral veins are fused to the adjacent veins in arches forming a clear marginal vein (Figs. 4.6, 5.7–8). Vein density: 16 veins/cm near laminar margin.

Studied material. MCF-PBPH 064, 086, 092, 171a, 174a–b, 175a, 179, 198.

Comments. In the present work we follow the criteria suggested by Stipanovic *et al.* (1996) and Gnaedinger and Herbst (1998, 2004b) in order to distinguish the five species of *Yabeiella*. The “venation pattern” as a specific distinctive feature and the comparisons between the percentages of vein types for the most closely related species, *i.e.*, *Y. brackebuschiana*, *Yabeiella wielandi* Ôishi, 1931 and *Yabeiella*

mareyesiaca (Geinitz) Ôishi, 1931, are illustrated in Tables 4–5. The Paso Flores specimens are thereafter assigned to *Y. brackebuschiana*.

Other taxa identified from the Paso Flores Formation at the Cañadón de Pancho locality

The associated recorded taxa (systematically assigned with the numbers of new material and references), which were identified from the upper part of the Paso Flores Formation at the Cañadón de Pancho locality and previously described for the unit, are listed in Table 6. The results of this analysis reveal that most of such taxa represent new records for this locality, except for *Dicroidium lancifolium* (Morris) Gothan, 1912; *Dicroidium odontopteroides* (Morris) Gothan, 1912; *Sphenobaiera robusta* (Arber) Florin, 1936 and *Heidiphyllum elongatum* Retallack, 1981 (Artabe *et al.*, 1994; Ganuza *et al.*, 1995).

CONCLUSIONS

Based on the study of the new paleoflora collected from the upper section of the Paso Flores Formation, at the Cañadón de Pancho locality, western region of the Collón Curá River, southern extreme of the Neuquén Basin, the following conclusions can be drawn:

A. First records of taxa from the Triassic of Argentina. The

TABLE 4– Venation patterns of *Yabeiella brackebuschiana*.

Paso Flores Formation. MCF-PBPH 064 (Figs. 4.6, 5.7a)								%
S	2		1		1		1	26
D1			1		2		1 2 2 1	47
D2				1			1	11
A		1					1 1	16
Paso Flores Formation. MCF-PBPH 064 (Figs. 4.6, 5.7b)								%
S					2		1 2	23
D1			2			1	2 1 1	34
D2	1		1		1			14
A		2			1		1 2	29

A, anastomosing veins; *D1*, dichotomized veins once; *D2*, dichotomized veins twice in one or both pair of veins; *S*, simple veins. The order in which the veins forms is S, D1, D2, A. The venation pattern of the specimen was obtained in two sections of the lamina (a and b) and it shows in Figure 5.7.

TABLE 5— Comparison between *Yabeiella* species from Gondwana.

		<i>Yabeiella</i> <i>brackebuschiana</i>	<i>Yabeiella</i> <i>wielandi</i>	<i>Yabeiella</i> <i>mareyesiacca</i>
Shape		<i>lanceolate</i>	<i>elongate-spatulate</i>	<i>lanceolate</i>
Apex		<i>acuminate</i>	<i>rounded</i>	<i>obtusely rounded</i>
Veins angle *		65–70	50–60	80–90
Venation pattern	<i>Veins type (number)</i>	S	1–2	1–3 (4)
		D1	1–2	1–3 (6)
		D2	1	
		A	1–2	1–3
	<i>Veins type (percentage)</i>	S	23–26	38–48
		D1	34–47	48–50
		D2	11–14	
		A	16–29	4–12
Veins density		12–16	15–16	20–26

*middle part of the leaf. Data taken from Gnaedinger and Herbst (2004a). Explanation of abbreviations in Table 4.

Lutanthus male cone (Voltziales) and the *Rissikistrobus* female cone (Podocarpaceae) represent new records for the Triassic of Argentina. Since the *Lutanthus* male cone was first described for the Late Triassic (Carnian) in Southern Africa (Anderson and Anderson, 2003), the Paso Flores specimen therefore constitutes its second record for Gondwana. The Paso Flores *Rissikistrobus* female cone corresponds to the third record of the species in the Triassic of Gondwana (in South Africa, by Anderson and Anderson, 2003; in Australia, by Holmes and Anderson, 2013) and is hereby recorded in co-occurrence with the foliage shoot *Rissikia*.

B. On the affiliation of organs. The recognition of the *Lutanthus* male cone in the Paso Flores Formation may contribute to elucidate its probable affinity to Voltziales (with at least four pollen cone genera, see Introduction) and thus help acknowledge that there is still a hiatus of unrecognized conifer species in the Triassic of Gondwana. Further studies should be carried out in order to confirm the different inferred affiliations as regards Voltziales (Anderson and Anderson, 2003; Anderson *et al.*, 2007; Bomfleur *et al.*, 2011, 2013). Within Podocarpaceae, the *Rissikistrobus* female

cone recovered in co-occurrence with the foliage shoot *Rissikia* again confirms the inferred affiliation. The Voltziales and Podocarpaceae herein described provide data on the distribution of both groups in Gondwana.

C. First records of taxa from the Paso Flores Formation. Six fossil taxa are hereby described for the first time: foliage of *Sphenobaiera argentina*, *Pseudoctenis spatulata*, *Rissikia media*, *Yabeiella brackebuschiana*, *Taeniopteris crassinervis* and *Umkomasia* sp. (Tab. 7).

D. First records of fossil taxa from the Quemquemtreu area, at the Cañadón de Pancho locality. Eleven fossil species, which had been previously described from other outcropping localities of the Paso Flores Formation, were recorded for the first time from this upper section of the unit. They are: *Asterotheca rigbyana*, *Marattiopsis muensteri*, *Cladophlebis kurtzii*, *Cladophlebis indica*, *Dictyophyllum (Dictyophyllum) tenuifolium*, *Goepfertella stipanicicii*, *Dicroidium incisum*, *Pachydermophyllum praecordillerae*, *Baiera furcata* and *Pseudoctenis falconeriana* (Tabs. 6–7).

E. Nomenclatural revision. The new name, *Baiera triassica* Gnaedinger and Zavattieri nom. nov., is hereby introduced in order to replace *Baiera taeniata* (Geinitz, 1876), *Ginkgo*

TABLE 6– Taxa identified from the upper part of the Paso Flores Formation at Cañadón de Pancho locality.

Species.	Studied material (this work)	Paleofloristic localities of the Paso Flores Fm (previous records)	Reference
<i>Order MARATTIALES Prantl, 1874</i>			
Astrothea rigbyana <i>Herbst, 1977 (Fig. 7.2)</i>	MCF-PBPH 118a-b, 173, 182, 184, 419	Western margin of the Limay river, Lomas de Ranquel Huao (Neuquén)	Morel et al. (1992, 1999)
Marattiopsis muensteri <i>(Goepfert) Schimper, 1869 (Figs. 7.3–4)</i>	MCF-PBPH 048b, 084, 102, 115b, 421, 423, 426	Western margin of the Limay river (Neuquén)	Morel et al. (1999)
<i>Order OSMUNDALES Bromhead, 1840</i>			
Cladophlebis indica <i>(Oldham and Morris) Feistmantel, 1877</i>	MCF-PBPH 075	Lomas de Ranquel Huao, western margin of the Limay river (Neuquén)	Frenguelli (1947); Morel et al. (1992, 1999)
Cladophlebis kurtzii Frenguelli, 1947	MCF-PBPH 115	Lomas de Ranquel Huao (Neuquén); *Type locality (Río Negro)	Morel et al. (1992, 1999)
<i>Order FILICALES Dumortier, 1829</i>			
Dictyophyllum (D.) tenuifolium <i>(Stipanovic and Bonetti)</i> <i>Bonetti and Herbst, 1964</i>	MCF-PBPH 055, 047,070a, 091a.	*Type locality (Río Negro), western margin of the Limay river and Lomas de Ranquel Huao (Neuquén)	Bonetti and Herbst (1964); Spalletti et al. (1988); Arrondo et al. (1991); Morel et al. (1992, 1999)
Goepertella stipanivicii <i>Herbst, 1993 (Fig.7.5)</i>	MCF-PBPH 093, 087	Lomas de Ranquel Huao (Neuquén)	Bonetti and Herbst (1964); Herbst (1993); Morel et al. (1999).
<i>Order CORYSTOSPERMALES Petriella, 1981</i>			
Dicroidium odontopteroides <i>(Morris) Gothan, 1912 (Fig. 7.6)</i>	MCF-PBPH 099a, 180	Lomas de Ranquel Huao, western margin of the Limay river, Cañadón de Pancho (Neuquén)	Morel et al. (1992); Ganuza et al. (1995); Morel et al. (1999)
Dicroidium incisum <i>(Frenguelli) Anderson</i> <i>and Anderson, 1970 (Fig. 7.7)</i>	MCF-PBPH 054a,	Western margin of the Limay river (Neuquén)	Morel et al. (1999)
Dicroidium lancifolium <i>(Morris) Gothan, 1912</i>	MCF-PBPH 098, 099b	Lomas de Ranquel Huao (Neuquén); Cañadón de Pancho and western margin of the Limay river (Neuquén) *Type locality (Río Negro)	Morel et al. (1992); Ganuza et al. (1995); Morel et al. (1999)
<i>Order PELTASPERMALES Meyen, 1987</i>			
Pachydermophyllum praecordillerae <i>(Frenguelli) Retallack, 1981</i>	MCF-PBPH 426a	Lomas de Ranquel Huao (Neuquén)	Morel et al. (1992)
<i>Order GINKGOALES Gorožankin, 1904</i>			
Sphenobaiera robusta <i>(Arber) Florin, 1936</i>	MCF-PBPH 174c	Cañadón de Pancho, western margin of the Limay river (Neuquén)	Frenguelli (1937); Artabe et al. (1994); Morel et al. (1999)
Baiera furcata <i>(Lindley and Hutton) Braun, 1843</i>	MCF-PBPH 171b-c	Western margin of the Limay river (Neuquén)	Morel et al. (1999)
<i>Order VOLTZIALES sensu Rothwell, Mapes and Hernandez-Castillo, 2005</i>			
Heidiphyllum elongatum <i>(Morris) Retallack, 1981 (Fig.7. 8)</i>	MCF-PBPH 063b, 070b	Lomas de Ranquel Huao, Cañadón de Pancho, western margin of the Limay river (Neuquén)	Morel et al. (1992, 1999); Ganuza et al. (1995)
<i>Order CYCADALES Dumortier, 1829</i>			
Pseudoctenis carteriana <i>(Oldham) du Toit, 1927</i>	MCF-PBPH 054c	Lomas de Ranquel Huao and Cañadón de Pancho (Neuquén)	Morel et al. (1992) Ganuza et al. (1995)
P. falconeriana <i>(Morris) Bonetti, 1968</i>	MCF-PBPH 056	Western margin of the Limay river (Neuquén)	Morel et al. (1999)
<i>For the outcropping localities mentioned, see Fig. 1. *Type locality has been mentioned in referred papers as "cerro Mariana and/or eastern side of the Limay river", which encompass the Paso Flores Formation outcrops along the eastern margin of the Limay river within Estancia Paso Flores (Río Negro province).</i>			

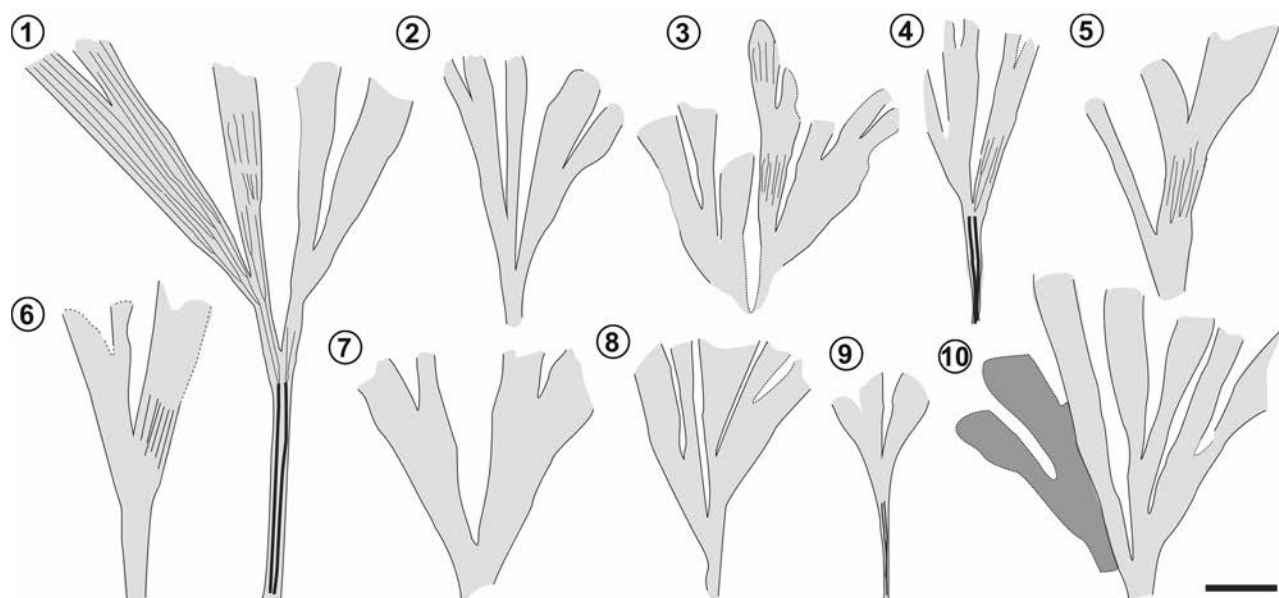


Figure 6. Line drawings. *Baiera triassica*. 1, 3–5, specimens from Cañadón de Pancho section, Paso Flores Formation. 1, MCF-PBPH 063a; 3, MCF-PBPH 417a; 4, MCF-PBPH 063b; 5, MCF-PBPH 417b; 2, 7–9, specimens from the Paso Flores Formation by Frenguelli (1937: lam. 3, fig. 8); 6, specimens from the Carrizal Formation (Maraves Basin) by Geinitz (1876: lam. 2, fig. 10); 10, specimens from type locality, Paso Flores Formation by Morel *et al.* (1999: fig. 5F). Scale bar= 10 mm.

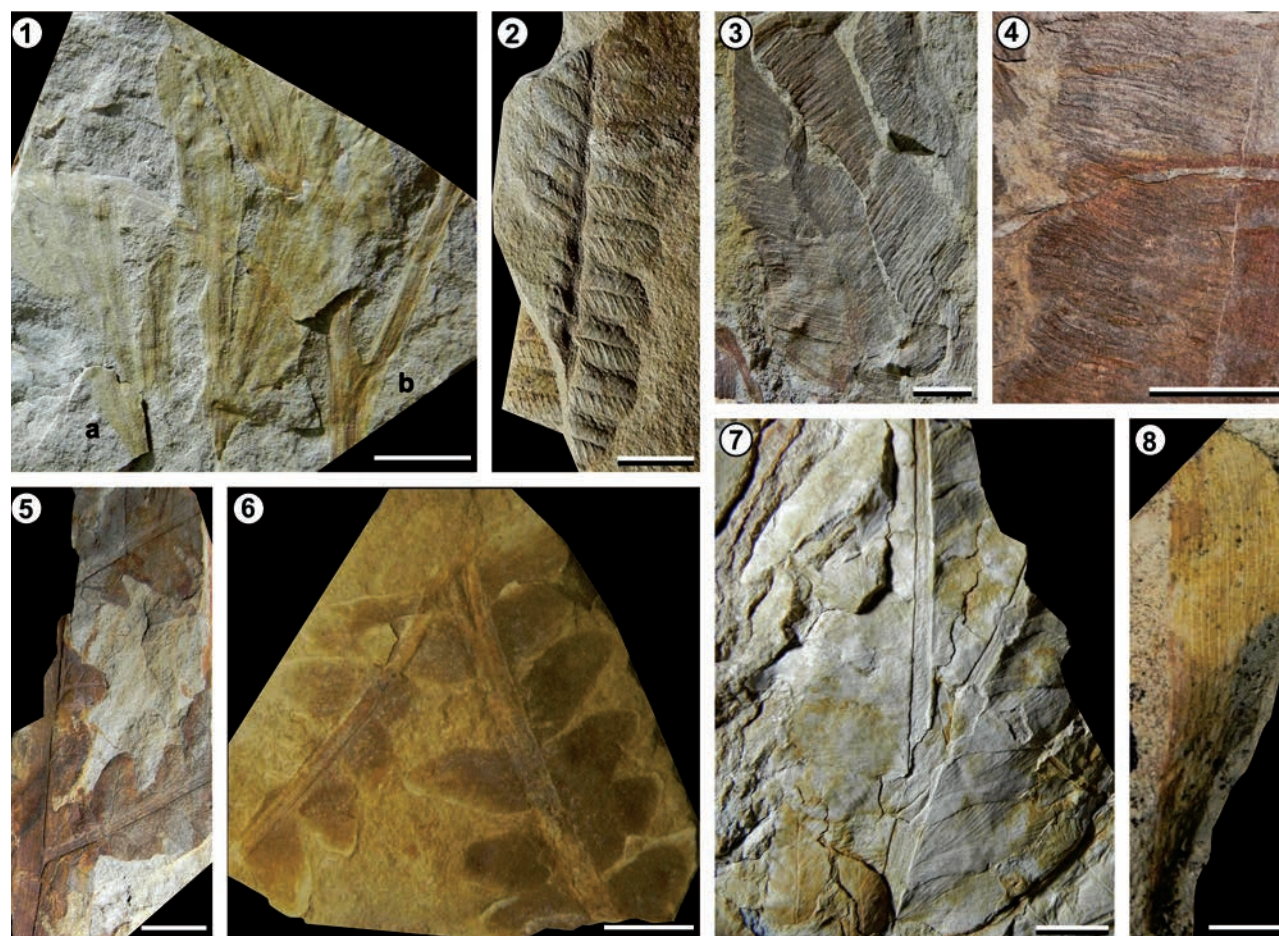


Figure 7. 1, *Baiera triassica*, MCF-PBPH 417a–b. 2, *Asterotheca rigbyana*, MCF-PBPH 184. 3–4, *Marattiopsis muensteri*, 3, MCF-PBPH 102; 4, MCF-PBPH 426. 5, *Goeppertella stipanicicij*, MCF-PBPH 093. 6, *Dicroidium odontopteroides*, MCF-PBPH 099a. 7, *Dicroidium incisum*, MCF-PBPH 054a. 8, *Heidiphyllum elongatum*, MCF-PBPH 070b. Scale bars= 10 mm (1, 3–8), 5 mm (2).

TABLE 7— Paleofloristic record of the Paso Flores Formation.

Localities	A	B	C	D
<i>Asterotheca rigbyana</i>	X	X		●
<i>Marattiopsis muensteri</i>	X			●
<i>Cladophlebis grahami</i>	X			
<i>C. kurtzii</i>	X	X		●
<i>C. mendozaensis</i>		X		
<i>C. indica</i>	X	X		●
<i>Coniopteris harringtoni</i>		X		
<i>Dictyophyllum (D.) tenuifolium</i>	X	X		●
<i>Dictyophyllum (T.) rothi</i>	X	X		
<i>Goeppertella stipanicicii</i>	X			●
<i>Dicroidium crassum</i>			X	
<i>D. incisum</i>	X			●
<i>D. odontopteroides</i>	X	X	X	●
<i>D. lancifolium</i>	X	X	X	●
<i>Zuberia sahnii</i>			X	
<i>Zuberia zuberi</i>			X	
<i>Johnstonia stelzneriana</i>			X	
<i>Xylopteris elongata</i>			X	
<i>Xylopteris rigida</i>			X	
<i>Scleropteris grandis</i>	X		X	
<i>Pachydermophyllum praecordillerae</i>		X		●
<i>Heidiphyllum elongatum</i>	X	X	X	●
<i>Rissikia media</i>				N
<i>Ginkgoites matatiensis</i>	X			
<i>Baiera africana</i>	X	X		
<i>Baiera furcata</i>	X			●
<i>Baiera triassica (=Baiera taeniata)</i>	X			●
<i>Sphenobaiera argentina</i>				N
<i>Sphenobaiera robusta</i>	X		X	●
<i>Nilssonsonia taeniopteroides</i>			X	
<i>Pseudoctenis carteriana</i>	X	X	X	●
<i>P. falconeriana</i>	X			●
<i>P. spatulata</i>				N
<i>Yabeiella brackebuschiana</i>				N
<i>Taeniopteris crassinervis</i>				N
<i>T. lentriculiformis</i>	X		X	
<i>Kurtziana cacheutensis</i>		X		
<i>Solenites vimineus</i>	X			
<i>Czekanowskia rigali</i>				
<i>Cycadodocarpidium andium</i>			X	
<i>C. majus</i>			X	
<i>Linguifolium arctum</i>	X			
<i>L. lilleanum</i>			X	
<i>L. tension-woodsii</i>	X			
<i>Cordaicarpus sp.</i>	X		X	
<i>Umkomasia sp.</i>				N
<i>Lutanthus ornatus</i>				N
<i>Rissikistrobus reductus</i>				N
<i>Rissikistrobus plenus</i>				
<i>Protocircoporoxylon marianaensis</i>	X			

A. Paso Flores (Type locality) ("cerro Mariana and/or eastern side of the Limay river"), Río Negro; B. Lomas and Cañadón de Ranquel Huaco, Neuquén; C. Cañadón de Pancho, Neuquén; D. Cañadón Pancho, Neuquén (this works) (Modified from Morel et al., 1999). Species marked with N are new for the Formation.

taeniata (Frenguelli, 1937) and *Sphenobaiera taeniata* (Morel *et al.*, 1999), which are homonymous species based on their nomenclatural revision (Gnaedinger and Zavattieri, 2017).

F. On the composition of the paleoflora of the Paso Flores Formation. Nine fossil taxa are hereby added to the 41 taxa previously described for this formation (Tab. 7). Such new paleobotanical data extends the paleoflora diversity record to the uppermost part of the formation at the western area of the Collón Curá River as well as that of the Triassic floras of Argentina. Remains of Marattiales, Filicales, Crystospermales, Peltaspermales, Ginkgoales, Cycadales, Voltziales, Coniferales (Podocarpaceae) and another *incertae sedis* constitute the plant fossil groups recorded from this Formation. All of these groups are also represented in the microflora even though Isoetales, Equisetales and Gnetales representatives were only registered in the palynoflora assemblages (Zamuner *et al.*, 2001).

G. On the age of the paleoflora of the Paso Flores Formation. As remarked by Morel *et al.* (1999), the paleofloristic assemblages recorded from the Cañadón de Pancho locality and those collected from other localities in Neuquén Province can be assigned to the late Late Triassic age. The uppermost section of the Paso Flores Formation at Cañadón de Pancho, southern Neuquén Province, yields well-preserved microfloral assemblages recorded in co-occurrence with the well-preserved megafloral remains of *Dicroidium* Flora. Zavattieri and Volkheimer (2002) analyzed the chronostratigraphically known distribution of the 25 species recorded for the first time in the palynoflora of the Paso Flores Formation at the Cañadón de Pancho locality and dated the microflora as latest Triassic (latest Norian–“Rhaetian”), thus representing the youngest Triassic palynoflora known in Argentina.

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