



## PLANT REPRODUCTIVE STRUCTURES OF THE AGUA DE LA ZORRA AND LOS RASTROS FORMATIONS, TRIASSIC, ARGENTINA

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**ABSTRACT** – The Triassic paleofloras of Argentina are mainly known for their vegetative elements. During the last decade, several contributions have focused on the study of Triassic reproductive structures. Here, we provide new information on reproductive structures recovered from two Triassic units from the central-west of Argentina: the Agua de la Zorra Formation (Cuyana Basin) and the Los Rastros Formation (Ischigualasto-Villa Unión Basin). These specimens had been described in previous contributions, however, the taxonomic assignment of the materials remained undetermined. In this work, a redescription of the materials is provided, allowing the taxonomic assignment of the specimens. The Agua de la Zorra Formation female reproductive structures were assigned to *Matatiella* sp. (Matatiellaceae) and to *Rissikiostrobus reductus* (Podocarpaceae). The female strobilus specimen registered in the Los Rastros Formation was assigned to the genus *Umkomasia* (Umkomasiaceae). This contribution represents a step forward to a better understanding of the reproductive structures for the Triassic of Gondwana.

**Keywords:** *Matatiella*, *Rissikiostrobus*, *Umkomasia*, Gondwana, Argentina.

**RESUMO** – Estruturas reprodutivas de plantas das formações Água de la Zorra e Los Rastros, Triássico, Argentina. As paleofloras triássicas da Argentina são conhecidas por seus elementos vegetativos. Na última década, várias contribuições concentraram-se no estudo das estruturas reprodutivas triássicas. De acordo com estudos prévios, fornecemos novas informações sobre as estruturas reprodutivas recuperadas de duas unidades do Triássico do centro-oeste da Argentina: a Formação Agua de la Zorra (Bacia Cuyana) e a Formação Los Rastros (Bacia Ischigualasto-Villa Unión). Os espécimes foram descritos em contribuições anteriores e a atribuição taxonômica dos materiais permaneceu indeterminada. Neste trabalho, uma redescricao dos materiais é fornecida, permitindo a atribuição taxonômica dos espécimes. As estruturas reprodutivas femininas da Formação Agua de la Zorra foram atribuídas a *Matatiella* sp. (Matatiellaceae) e *Rissikiostrobus reductus* (Podocarpaceae). O espécime de estróbilo feminino registrado na Formação Los Rastros foi atribuído a *Umkomasia* (Umkomasiaceae). Este trabalho contribui com elementos para uma melhor compreensão das estruturas reprodutivas para o Triássico do Gondwana.

**Palavras-chave:** *Matatiella*, *Rissikiostrobus*, *Umkomasia*, Gondwana, Argentina.

### INTRODUCTION

The fossil record of Triassic plants is diverse, including vegetative parts and reproductive structures that correspond to the *Dicroidium* Flora (Balme & Helby, 1973; Zamuner *et al.*, 2001; Mays & McLoughlin, 2019). In particular, the Upper Triassic palaeofloras of Argentina are mainly known for their vegetative elements, although reproductive structures records are common (Spalletti *et al.*, 1999; Morel *et al.*, 2001; Zamuner *et al.*, 2001; Lutz *et al.*, 2011; Ottone *et al.*, 2011; Pedernera *et al.*, 2019, 2020). In some cases, the determination of the reproductive structures does not reach a specific level or remains undetermined (*e.g.* Ottone *et al.*, 2011; Pedernera *et al.*, 2019, 2020). A detailed description and a comprehensive

taxonomic and systematic study of reproductive structures are important tools for characterizing paleofloristic associations (Arce & Lutz, 2010, 2014; Gnaedinger & Zavattieri, 2017). Therefore, it is important to review the materials that have remained undetermined or that were referred to specimens of uncertain affinity, to assign them more precisely to a new taxon or an already known taxon. A better understanding of ancient biodiversity allows us to explore and analyze paleoecological and evolutionary processes. In this contribution, we provide new descriptions and taxonomic assignments to strobilus and cones recovered from two Triassic units – the Agua de la Zorra Formation and the Los Rastros Formation – and whose taxonomic assignment has remained undetermined in previous contributions (Pedernera *et al.*, 2019, 2020).

## GEOLOGICAL SETTING

Sedimentation in the Gondwana Western Margin during the Triassic was restricted to rift basins, developed during the break-up of the Pangean supercontinent (Uliana & Biddle, 1988). The Cuyana and Ischigualasto-Villa Unión are the most extensive basins of Center-West Argentina (Figure 1A). The successions of these basins are entirely continental and mainly include alluvial fan, river, and lake deposits. In addition, they are widely known for the good conservation of their fauna and floristic associations (Spalletti *et al.*, 1999; Marsicano *et al.*, 2001; Zamuner *et al.*, 2001; Lutz *et al.*, 2011; Mancuso *et al.*, 2014; Ezcurra *et al.*, 2017; Lara *et al.*, 2017; Pedernera *et al.*, 2021).

The Agua de la Zorra Formation (Cuyana Basin) crops out in the North of Mendoza province, in the Paramillo de Uspallata area (Harrington, 1971). This unit is interpreted as a lacustrine-deltaic system with episodic incursions of lava that flows into the aquatic environment, giving place to the development of olivine peperitic basalts interbedded with lacustrine-deltaic sediments (Harrington, 1971; Brea *et al.*, 2009; Ottone *et al.*, 2011). A Ladinian-Carnian age (K/Ar ages of  $235 \pm 5$  Ma and  $240 \pm 10$  Ma) has been obtained from these basalts (Massabie *et al.*, 1986; Linares, 2007).

The Los Rastros Formation (Agua de la Peña Group, Ischigualasto-Villa Unión Basin) outcrops in the area between the Quebrada de la Chilca and the Aguada de Ischigualasto in the Ischigualasto Provincial Park (San Juan Province), in the area of Cerro Bola, Cerro Rajado, and between the Río Gualo and the Río Chañares in the National Park Talampaya (La Rioja Province) (Mancuso & Caselli, 2012). The Los Rastros Formation was deposited in a lacustrine-deltaic system (Mancuso & Caselli, 2012; Benavente *et al.*, 2022). For the Los Rastros Formation, a Carnian age (CA-TIMS U-Pb  $234.47 \pm 0.44$  Ma) has been obtained (Mancuso *et al.*, 2020).

## MATERIAL AND METHODS

The reproductive structures were collected from the Agua de la Zorra Formation in the Paramillos de Uspallata locality (Figure 1B) and the Los Rastros Formation at the Gualo locality (Figure 1C). In both formations, the specimens were found in black finely laminated shale of the distal lacustrine facies and were preserved as coalified compressions. Initially, the taxonomic assignment of the materials has remained undetermined (Pedernera *et al.*, 2019, 2020). Therefore, a re-description of the specimens was carried out, allowing their assignment within taxa commonly known in other units from Argentina.

The specimens were observed using a LEICA M60 stereoscopic microscope, equipped with a Leica DMC2900 camera. We followed the proposal by Stewart & Rothwell (1993) to determine the systematic classification and Anderson & Anderson (2003) to identify the reproductive structures. The fossil materials are housed at the Paleobotanical Collection of the Instituto Argentino de Nivología, Glaciología y Ciencias

Ambientales (IANIGLA) in Mendoza city, Argentina, under the prefix IANIGLA-PB, and at the Paleobotanical Collection of the Facultad de Ciencias Antropológicas y Naturales de la Universidad Nacional de La Rioja (Argentina), under the acronym PULR-B.

## SYSTEMATIC PALEONTOLOGY

Order UMKOMASIALES Meyen, 1984

Family UMKOMASIACEAE Petriella, 1981

*Umkomasia* (Thomas, 1933) H.M. Anderson emend. 2019

**Type species.** *Umkomasia macleanii* (Thomas, 1933) H.M. Anderson emend. 2019.

*Umkomasia* sp.  
(Figures 2A, 3A)

**Material.** PULR-B-041.

**Provenance.** FL-VII, Los Rastros Formation.

**Description.** Compression of a cupulate female fragment of 11.04 mm in length; axis dichotomous, 0.92 mm in width; two cupules attached to the axis, one of them is fragmented, the complete cupula is 4.90 mm in length and 2.86 mm in width. A linear leave of 2.81 mm in length 0.41 mm in width was observed in the upper part of the axis. A platyspermic ovule/seed without organic connection 5.18 mm length, 3.00 mm width was also observed.

**Comments.** *Umkomasia* includes strobilus of lax paniculate form with helically attached megasporophylls bearing 1–7 pairs of opposite to sub-opposite, sessile or pedicellate cupules which are recurved, circular to ovoid, platyspermic, and split into two or more lobes. Cupules are uni- or bi-ovulate, ovules/seeds with bifid micropyle (Anderson *et al.*, 2019). This specimen was interpreted as a megasporophyll fragment and assigned as “*Strobilus* sp. A” by Pedernera *et al.* (2020); now the specimen is assigned to *Umkomasia* based on the lax paniculate form, the pedicellate cupules, and the number of megasporophylls preserved. Fragmentation and poor preservation hindered the specific assignment of the specimen.

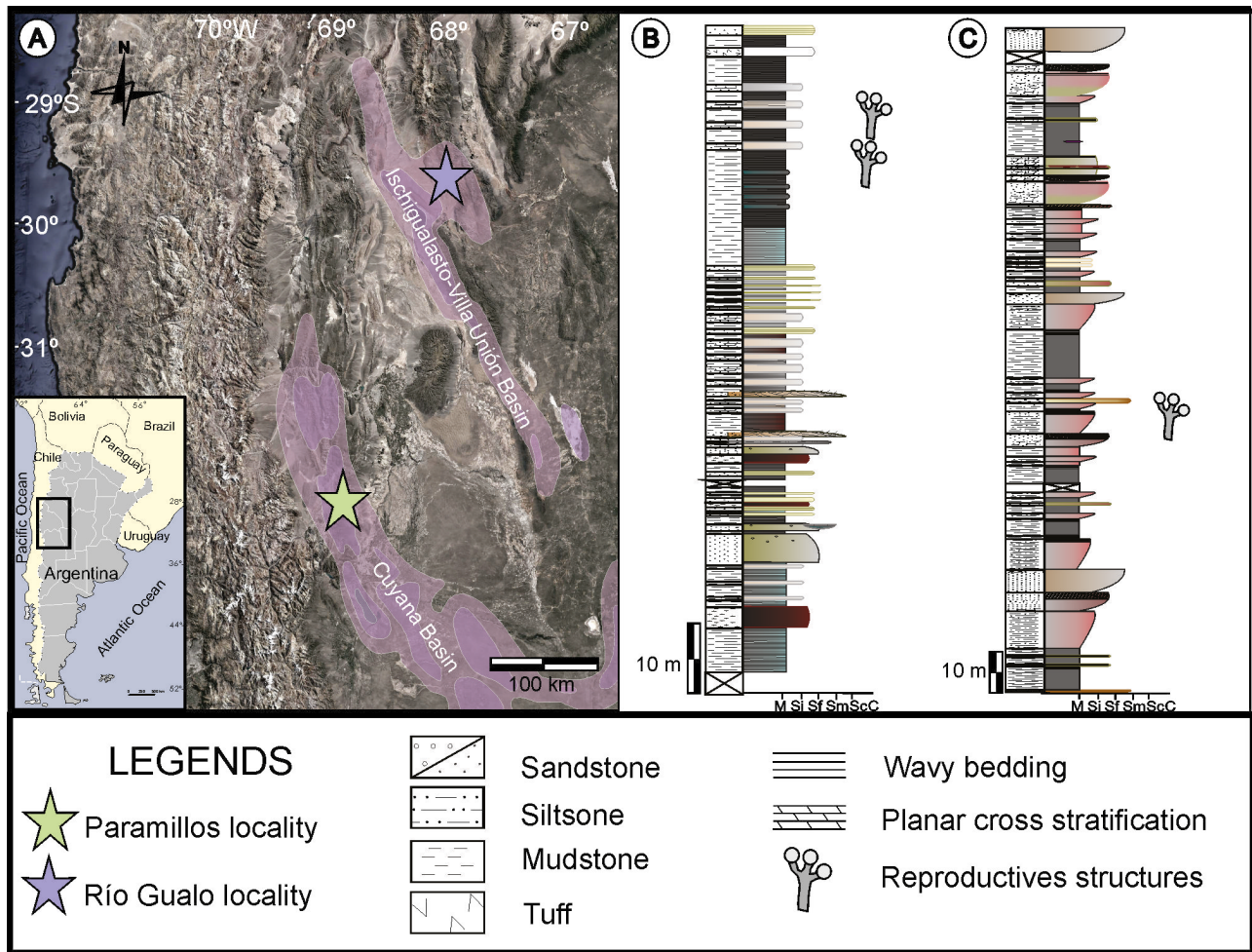
*Umkomasia* has been affiliated with the microsporangium *Pteruchus* and *Dicroidium* leaves (Thomas, 1933; Petriella, 1977, 1980, 1981; Anderson & Anderson, 2003; Anderson *et al.*, 2019). In Argentina specimens assigned to *Umkomasia* have been reported in the Potrerillos, Cortaderita, and Paso Flores formations (Cuyana Basin) (Artabe *et al.*, 2001; Gnaedinger & Zavattieri, 2017; Bodnar *et al.*, 2020).

Family MATATIELLACEAE Anderson & Anderson, 2003

*Matatiella* Anderson & Anderson, 2003

**Type species.** *Matatiella roseta* Anderson & Anderson, 2003.

*Matatiella* sp.  
(Figures 2B, 3B)



**Figure 1.** Study areas and stratigraphic sections with the location of the materials. **A**, the Cuyana and Ischigualasto-Villa Unión basins. Stars mark the location of the Agua de la Zorra Formation and the Los Rastros Formation; **B**, stratigraphic section of the Agua de la Zorra Formation at the Paramillos de Uspallata locality; **C**, stratigraphic section of the Los Rastros Formation at the Río Gualo locality. **Abbreviations:** M, mudstone; SI, siltstone; SF, fine-grained sandstone; Sm, thin-bedded, medium-to-fine-grained sandstone; Sc, medium-to-thick bedded coarse-grained sandstone; C, conglomerate.

**Material.** IANIGLA-PB-739.

**Provenance.** FL-II, Agua de la Zorra Formation.

**Description.** A fragment of a lax female strobilus 12.64 mm in length and 1.33 mm in width. The main axis with pedunculate megasporophylls, apparently planar, bearing three ovules/seeds peduncles. Platyspermic ovules/seed, oval-shaped, 2.00–2.12 mm in width, 2.30–2.52 mm in length. The apex and base rounded. Ovules/seeds fragmented, surrounded by cupules.

**Comments.** *Matatiella* includes linear-cylindrical shape strobilus, megasporophylls simple, pedunculated, enclosed by a thin protective membrane (Anderson & Anderson, 2003). This genus usually is compared to *Peltaspermum*, however, megasporophylls of *Peltaspermum* present radial symmetry while in *Matatiella* they are bilaterally symmetrical. The specimen was described for the first time as “Strobilus sp. A” by Pedernera *et al.* (2019). Based on the diagnosis of the genus (Anderson & Anderson, 2003), the material was assigned to *Matatiella* considering the bilateral symmetry of megasporophylls. The fragmentation and bad preservation of the specimen hindered the specific assignment.

*Matatiella* was included in Ginkgoopsida (Anderson & Anderson, 2003). In Argentina, *Matatiella* specimens also were described from the Los Rastros Formation (Arce & Lutz, 2010) and the Monina Formation (Drovandi *et al.*, 2020).

Order CONIFERALES Engler, 1897

Family PODOCARPACEAE Endlicher, 1847

*Rissikistrobus* Anderson & Anderson, 2003

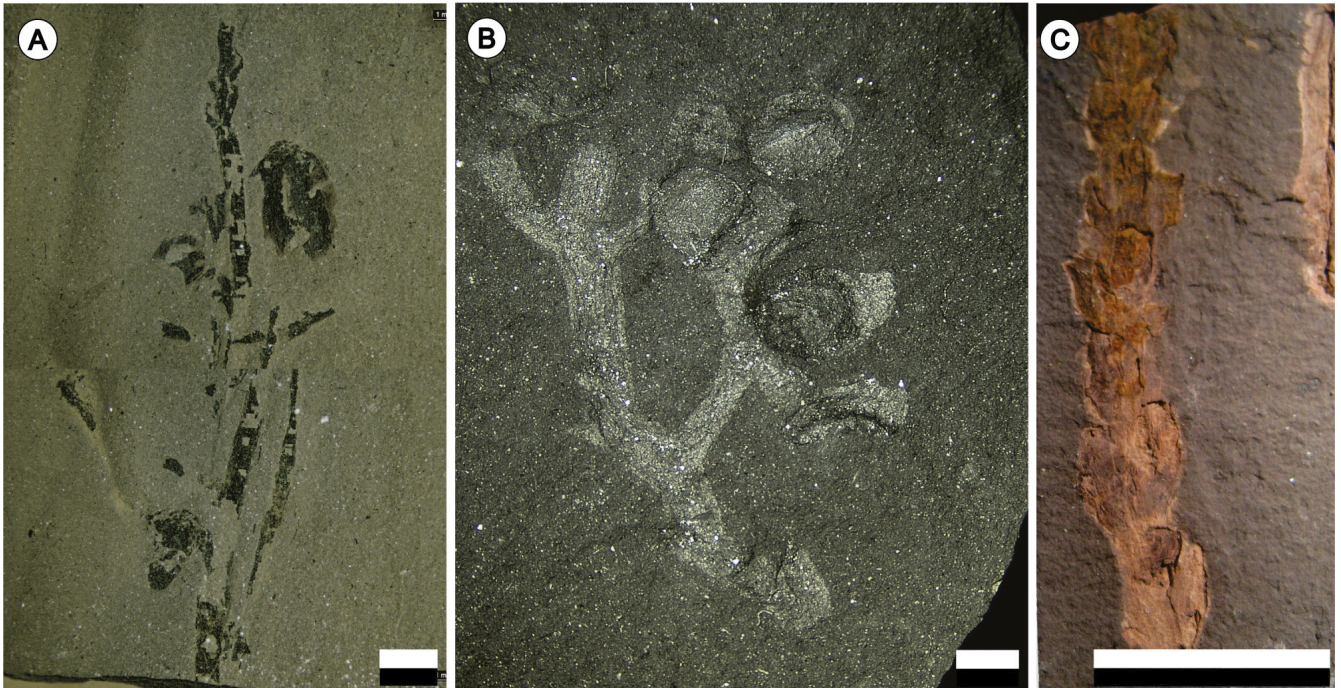
**Type species.** *Rissikistrobus plenus* Anderson & Anderson, 2003.

*Rissikistrobus reductus*  
(Figures 2C, 3C)

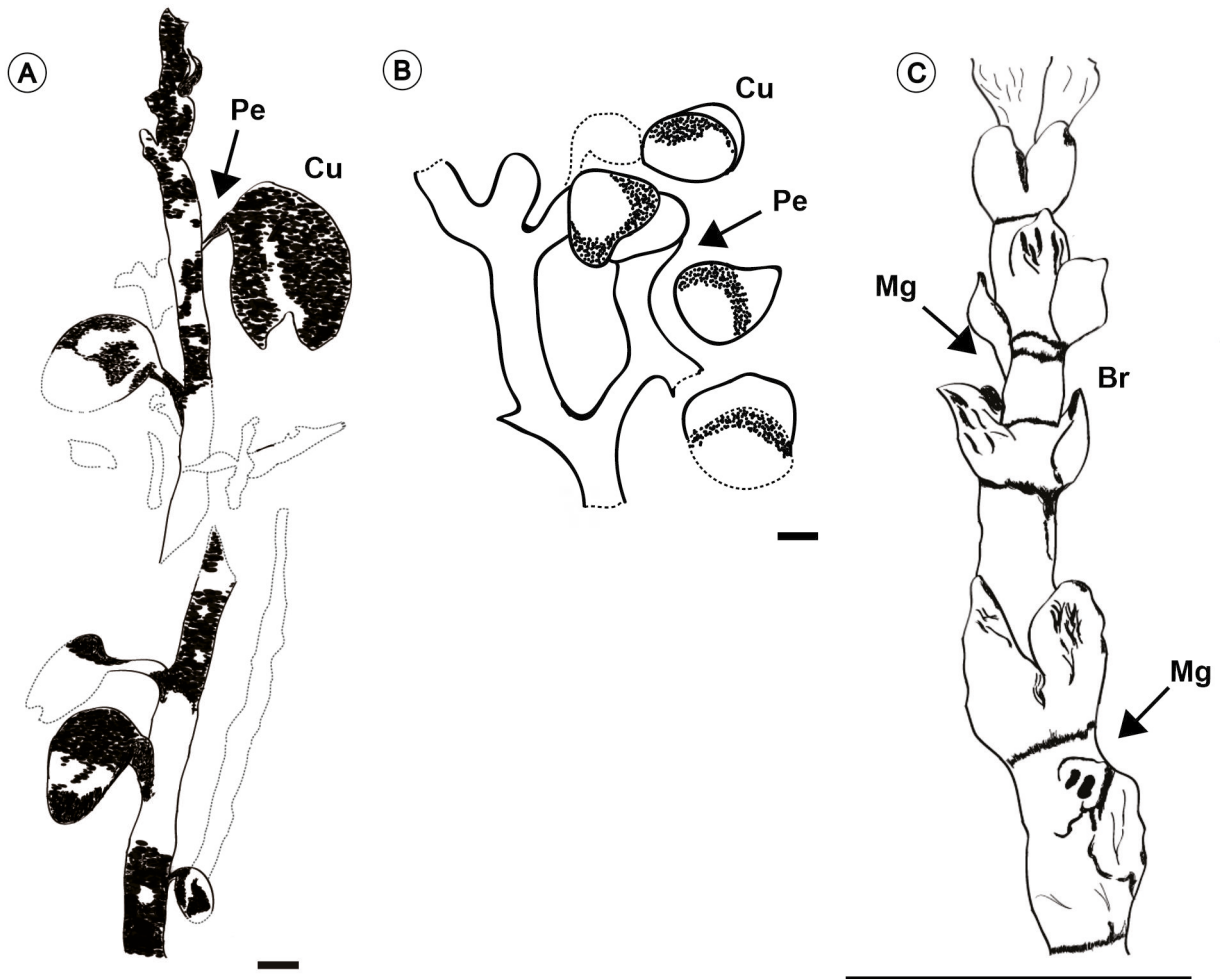
**Material.** IANIGLA-PB-722.

**Provenance.** FL-I, Agua de la Zorra Formation.

**Description.** Compression of a cone fragment, linear, 30 mm in length and 5 mm in width; bearing spirally arranged 11 bracts/scales complexes and ovules; bract/scales complex



**Figure 2.** Strobili and cones. **A**, *Umkomasia* sp. PULR-B-041; **B**, *Matatiella* sp. IANIGLA-PB-739; **C**, *Rissikiostrobus reductus* IANIGLA-PB-722. Scale bars = 1mm.



**Figure 3.** Line drawings. **A**, *Umkomasia* sp. PULR-B-041; **B**, *Matatiella* sp. IANIGLA-PB-738; **C**, *Rissikiostrobus reductus* IANIGLA-PB-722. Abbreviations: Pe, peduncle; Cu, cupules; Mg, megasporangium; Br, bracts/scales. Scale bars = 1 mm.

lobate up to 5.8 mm in length and 2.8 mm in width. Bracts with a single lobule and ovules oval-shaped, 3 mm in width, 6 mm in length, with peduncle, megasporangium, and integument, 1 mm in width, are occasionally recognizable.

**Comments.** *Rissikistrobus* includes linear shape compact pinalean-like female cones, with bract/scale complexes of 1–3 lobes bearing a pair of adaxial ovules on each lobe. Megasporophylls with spirally arranged, and cone units consisting of ovuliferous bract/scale complexes and naked ovules (Anderson & Anderson, 2003). Three species have been described in the Molteno Formation: *R. plenus*, *R. semireductus*, and *R. reductus* (Anderson & Anderson, 2003). *Rissikistrobus plenus* species show an ovuliferous scale consisting of 3 nearly similar-sized lobes. *Rissikistrobus semireductus* shows an ovuliferous scale consisting of a large central lobe and two very reduced lateral lobes, while *R. reductus* is characterized by the lone central lobe. The specimen studied here was described for the first time as “Strobilus sp. B” by Pedernera *et al.* (2019). After reanalyzing the specimen, it was reinterpreted and assigned to *Rissikistrobus reductus* based on the morphology of bracts that only showed a developed central lobe (Anderson & Anderson, 2003).

Anderson & Anderson (2003) suggested the link between *Rissikistrobus* and *Rissikia* foliage (Podocarpaceae). In Argentina, *Rissikistrobus plenus* and *Rissikistrobus reductus* have been registered in the Paso Flores Formation (Gnaedinger & Zavattieri, 2017).

## DISCUSSION

### Taxonomic remarks

Poor preserved ovules/seeds were recovered from the Agua de la Zorra Formation (Table 1). This bad preservation has hindered the specific taxonomic assignment of the materials and their botanical affinity (Ottone *et al.*, 2011). Previous studies have registered ovules/seeds that were assigned to *Cordaicarpus* (Pedernera *et al.*, 2019). In addition, two types of strobili with undetermined generic assignment have been registered (Pedernera *et al.*, 2019). Frenguelli (1944) mentioned the presence of reproductive structures referable to the genus *Pteruchus*, *Umkomasia*, and *Cardiopteridium* in the Los Rastros Formation. Arce & Lutz (2010, 2014) have reported more specimens referred to *Acevedoa*, *Umkomasia*, *Peltaspermun*, *Matatiella*, and *Telemachus*. Pedernera *et al.* (2020) made references to ovules/seeds (referred to *Cordaicarpus* and *Samaropsis*), and to strobilus undetermined. Recently, Beltrán *et al.* (2021) described reproductive structures referred to as the genus *Dordrechtites*.

Even though the materials presented here had already been described in previous publications (Pedernera *et al.*, 2019, 2020), the taxonomic assignment of the materials remained undetermined, and redescription of the materials have allowed the taxonomic assignment of the specimens. *Strobilus* sp. A (Pedernera *et al.*, 2019) was assigned to genus *Matatiella*, while *Strobilus* sp. B (Pedernera *et al.*, 2019) was

**Table 1.** Plant taxa recorded in the Los Rastros and Agua de la Zorra formations. \*indicates taxa referred to reproductive structures. In gray are the taxa from the present study. Data taken from Frenguelli (1948), Spalletti *et al.* (1999), Zamuner *et al.* (2001), Lutz *et al.* (2011), Ottone *et al.* (2011), Arce & Lutz (2010, 2014) and Pedernera *et al.* (2019, 2020).

Taxa	Los Rastros Formation	Agua de la Zorra Formation
Isoetales		
<i>Pleuromeia</i> sp.	X	
Equisetales		
<i>Equisetites fertilis</i>	X	
<i>Neocalamites carrerei</i>	X	
<i>N. ischigualasti</i>	X	
<i>N. ramaccionii</i>	X	
<i>Neocalamites</i> sp.	X	X
<i>Phyllothea australis</i>	X	
Filicopsida		
<i>Cladophlebis kurtzi</i>		X
<i>C. mesozoica</i>	X	X
<i>C. mendozaensis</i>	X	
<i>C.</i> sp. cf. <i>C. mesozoica</i>	X	X
<i>C.</i> sp. A		X
Umkomasiales		
<i>Dicroidium argenteum</i>	X	X
<i>D. crassum</i>	X	X
<i>D. dubium</i>	X	

Table 1. Cont.

<i>D. lancifolium</i>	X	
<i>D. lineatum</i>	X	
<i>D. nondichotoma</i>	X	
<i>D. obtusifolium</i>	X	
<i>D. odontopteroides</i>	X	X
<i>D. sp. cf. D. prolongatum</i>		X
<i>Johnstonia coriacea</i>	X	X
<i>J. dutoitii</i>	X	X
<i>J. stelzneriana</i>	X	X
<i>Xylopteris elongata</i>	X	X
<i>X. argentina</i>	X	X
<i>X. densifolia</i>	X	
<i>X. rigida</i>	X	
<i>Zuberia feismantelii</i>	X	X
<i>Z. zuberi</i>	X	X
<i>Z. sahinii</i>	X	
<i>Z. brownii</i>	X	
<i>Umkomasia sp.*</i>	X	
<i>Rhexoxylon sp.</i>	X	
Peltaspermales		
<i>Pachydermophyllum papillosum</i>	X	
<i>P. praecordillerae</i>	X	
<i>P. pinnatum</i>		
<i>Peltaspermum monodiscum*</i>	X	
Petriellales		
<i>Rochipteris alexandriana</i>	X	
Cycadales and Cycaoideales		
<i>Kurtziana cacheutensis</i>	X	
<i>Taeniopteris sp.</i>		X
Ginkgoales		
<i>Baiera africana</i>	X	
<i>Baiera pontifolia</i>	X	
<i>B. schenkii</i>	X	
<i>Sphenobaiera argentinae</i>	X	
<i>S. sectina</i>	X	
<i>S. helvetica</i>		
<i>S. insecta</i>	X	
<i>Sphenobaiera sp.</i>		X
Czekanowaskiales		
<i>Czekanowskia rigali</i>	X	
<i>Czekanowskia sp.</i>	X	
Voltziales		
<i>Heidiphyllum clarifolium</i>		
<i>H. elongatum</i>	X	X
<i>Heidiphyllum. sp.</i>		
<i>Cycadocarpium andium*</i>	X	
<i>Telemachus elongatus*</i>	X	

Table 1. Cont.

<i>Telemachus</i> sp.*	X	
Coniferales		
<i>Rissikia media</i>	X	X
<i>Rissikiostrobus reductus</i> *		X
Gymnospermopsida incertae sedis		
<i>Acevedoa rastroensis</i> *	X	
<i>Cordaicarpus</i> sp.*	X	X
<i>Dejerseya lunensis</i>	X	
<i>Dejerseya lobata</i>	X	
<i>Desmiophyllum</i> sp.	X	
<i>Dordrechtites elongatus</i> *	X	
<i>Dordrechtites</i> sp.*	X	
<i>Harringtonia argentinica</i>	X	
<i>Lingofolium patagonicum</i>		X
<i>Matatiella roseta</i> *	X	
<i>Matatiella</i> sp.*		X
<i>Pelourdea polyphylla</i>	X	
<i>P. problematica</i>	X	
<i>Pelourdea</i> sp.	X	
<i>Pterorrachis ambigua</i>	X	
<i>Sphenopteris</i> sp. A	X	
<i>Samaropsis</i> sp.*	X	
<i>Phoenicopsis</i> sp.	X	
Gnetales		
<i>Yabeiella brackebuschiana</i>	X	
<i>Y. mareyesiacae</i>	X	
<i>Y. spatulata</i>	X	
<i>Yabeiella</i> sp.	X	

assigned to *Rissikistrobus reductus*. This is the first record of the *Matatiella* and *Rissikistrobus* for the Agua de la Zorra Formation (Table 1). Finally, the *Strobilus* sp. A (Pedernera *et al.*, 2020) was assigned to *Umkomasia* sp. Although there were already references to reproductive structures in other locations from the Los Rastros Formation, it is the first record of *Umkomasia* in the Rio Gualo area (Table 1).

### Taphonomic remarks

In both units, Agua de la Zorra and Los Rastros formations, the reproductive structures were found in distal lacustrine facies and are preserved as impressions and compressions. The specimens are articulated and have moderate breakage. In addition, they present a high degree of compaction, lack preferential orientation, and lie concordant to the bed lamination. The elements are interpreted as allochthonous elements. Their moderate degree of breakage suggests a fresh state of the remains when entrained, which gives them higher resistance to breakage during transport. The moderate degree

of breakage also could indicate a much shorter transport time and distance (Ferguson, 1985; Spicer & Parrish, 1986; Spicer, 1991). Lack of preferential orientation evidence and its arrangement consistent with stratification plans suggest that these materials would have remained floating, until deposition by settling (Pedernera *et al.*, 2021).

### CONCLUSIONS

The systematic and taxonomic redescription and re-assignment of materials published as undetermined specimens provide a better understanding of the characterization of the palaeofloristic associations of the units. This contributes to the knowledge of reproductive structures for the Triassic of Gondwana. *Strobilus* sp. A and *Strobilus* sp. B mentioned by Pedernera *et al.* (2019) from the Agua de la Zorra Formation were assigned to *Matatiella* sp. and to *Rissikistrobus reductus* respectively; and the *Strobilus* sp. A from the Los Rastros Formation presented by Pedernera *et al.* (2020) was assigned

to *Umkomasia* sp. These taxa represent the first record of female reproductive structures in the Agua de la Zorra Formation and the Los Rastros Formation in the Gualo Area.

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