

## Syn-Eruptive Taphoflora From The Agua De La Zorra Formation (Upper Triassic) Cuyana Basin, Mendoza, Argentina

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**ABSTRACT.** In the North of Mendoza Province, at Paramillos de Uspallata locality, Triassic sedimentary rocks outcrop. These Triassic beds are grouped in four formations: Paramillos, Agua de la Zorra, Portezuelo Bayo and Los Colorados. The Agua de la Zorra Formation is characterized by deposition in a deltaic and lacustrine system. The aims of this contribution are: **(1)** to realize a systematic study of new plant remains found in the Agua de la Zorra Formation and **(2)** to analyze the influence of the potential of preservation and the volcanism in the Agua de la Zorra taphoflora in contrast with other Triassic units. Plant remains were systematically collected and compared with taphofloras from other Triassic formations of the Cuyana Basin. The systematic study from the Agua de la Zorra Formation allowed the determination of 21 taxa, nine of which have been cited in a previous contribution and 12 were described for the first time for the Agua de la Zorra Formation. There are differences in the taxonomic diversity between the taphofloras recovered from Potrerillos and Paramillos formations and these differences are linking with differences in biostratigraphic process in each fluvial system and linked with the evidence of volcanic processes in these areas. The differences in diversity in the taphofloras of the Cacheuta and Agua de la Zorra formations can be more associated to ecological differences than variations in the taphonomic processes in each of the lake systems.

*Keywords.* Taphoflora, Volcanism, Triassic, Systematic.

**RESUMEN. Tafloflora sin-eruptiva de la Formación Agua de la Zorra (Triásico Superior) Cuenca Cuyana, Mendoza, Argentina.** En la localidad de Paramillos de Uspallata, al Norte de la provincia de Mendoza, afloran rocas sedimentarias asignadas al Triásico. Estas capas triásicas están agrupadas en cuatro formaciones: Paramillos, Agua de la Zorra, Portezuelo Bayo y Los Colorados. La Formación Agua de la Zorra se caracteriza por sedimentos depositados en un ambiente deltaico-lacustre. Los objetivos de este trabajo son: **(1)** realizar un estudio sistemático de nuevos restos fósiles de plantas colectados en la Formación Agua de la Zorra y **(2)** analizar la influencia del volcanismo en el área de Agua de la Zorra sobre el potencial de preservación de la tafloflora en la unidad en contraste con otras unidades triásicas. Los restos de plantas fueron recolectados de manera sistemática y comparados con otras taflofloras provenientes de otras formaciones triásicas de la Cuenca Cuyana. El estudio sistemático de la tafloflora de la Formación Agua de la Zorra permitió la determinación de 21 taxones, nueve de los cuales ya habían sido citados en contribuciones previas y 12 fueron descriptos por primera vez para la unidad. Se registraron diferencias en la diversidad taxonómica entre las taflofloras recuperadas de las formaciones Potrerillos y Paramillos, esas diferencias estarían relacionadas con diferencias en los procesos bioestratigráficos característicos de cada sistema fluvial y con los procesos volcánicos acontecidos en dichas áreas. Las diferencias observadas en la diversidad de las taflofloras de las formaciones Cacheuta y Agua de la Zorra pueden ser asociadas más a diferencias ecológicas que a variaciones en los procesos tafonómicos propios de cada sistema lacustre.

*Palabras claves.* Tafloflora, Vulcanismo, Triásico, Sistemática.

## 1. Introduction

Ecological responses following explosive volcanic eruption involve a variety of rapid and gradual changes. The disruptive negative effect on the environment subsequent to eruptive events, as changes in the physics-chemistry conditions and sedimentary processes and in vegetal biodiversity, have been reported (Dale *et al.*, 2005; Lindermeyer *et al.*, 2010). Ecological disturbance is “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (White and Pickett, 1985). The volcanic events have negative effects over ecological process, especially on plant communities, and affect to the sedimentary processes and taphonomic processes (Behrensmeier and Hook, 1992). Several studies evaluated the ecological disturbance and vegetation recovery in some recent models (Wood and Del Moral, 1988; Del Moral and Wood, 1988, 1993; Del Moral and Grishin, 1999; Swanson *et al.*, 2013). However, the studies regarding the fossil record are less abundant (Brea *et al.*, 2009; Poma *et al.*, 2009; Ottone *et al.*, 2011; Rößler *et al.*, 2012).

In the North of Mendoza Province, at Paramillos de Uspallata locality near Uspallata town, outcropping sedimentary rocks are referred by Harrington (1971) to the Cacheuta Group and include four formations (from base to top) Paramillos, Agua de la Zorra, Portezuelo Bayo and Los Colorados; assigned to the Triassic Period. Three of these units were influenced by the active volcanism that affected the southwest of Gondwana margin during the Permo-Triassic.

Correlation of the Paramillos de Uspallata units with the Uspallata Group outcropping at the well-known Triassic localities of Cacheuta and Potrerillos on the Mendoza River (Strelkov and Alvarez, 1984; Kokogian *et al.*, 1993; Cortés *et al.*, 1997; Stipanovic and Zavattieri, 2002) has been difficult. In this scenario, different criteria of correlation were postulated (Stipanovic *et al.*, 2002). Several authors, as Groeber and Stipanovic (1952), considered the Agua de la Zorra Formation (Paramillos de Uspallata) analogous with the Potrerillos and Cacheuta formations (at Mendoza River), whilst others, as Ramos and Kay (1991), and Kokogian *et al.* (1993) correlated the Agua de la Zorra Formation with the Las Cabras Formation (at Mendoza River).

The paleontological record of the Triassic beds of Paramillos de Uspallata is diverse and includes spinicaudatan and fishes (Geinitz, 1876; Albanesi *et al.*, 2009), trace fossils (Melchor *et al.*, 2001), reptiles (Rusconi, 1967), possible temnospondyl amphibians (Stipanovic and

Marsicano, 2002) and a permineralized forest (Brea *et al.*, 2008). Different authors described plants remains in the Paramillos and Portezuelo Bayo formations (Brea and Artabe, 1994, 1999; Brea, 1996a, 1996b, 1997, 2000; Brea *et al.*, 2009). However, only one contribution (Ottone *et al.*, 2011) dealt with the systematic study of the Agua de la Zorra Formation paleoflora.

The aims of this contribution are: (1) to present a detailed taxonomic study of new plant fossils recovered from the Agua de la Zorra Formation; and (2) to analyze the influence of the potential of preservation and the volcanism in the Agua de la Zorra paleoflora record, contrasting these parameters with those observed in other equivalent Triassic taphofloras.

## 2. Geological setting

Paramillos de Uspallata is a sub-basin of the Cuyana Basin, one of the nonmarine rift basins developed during the break-up of Pangea supercontinent (SW Gondwana) during the Triassic (Uliana and Biddle, 1988). This extensional continental basin includes fluvial and lacustrine systems (Ramos and Kay, 1991).

The sub-basin earliest infill corresponds to the Paramillos Formation. This is a volcaniclastic unit characterized by conglomerates, lithic and tuffaceous sandstones with interbedded shales and tuffs. The depositional environment of these sediments was interpreted as a highly sinuous or meandering fluvial system associated with floodplain deposits (Brea, 1995). Brea *et al.* (2009) assigned the Paramillos Formation to the late Middle Triassic based in the plant paleocommunities recorded in this area. Cingolani *et al.* (2017) analyzed zircons by the U-Pb methodology (LA-ICP-MS) and obtained approximate ages of  $239.6 \pm 1.3$  Ma (Ladinian). Overlaying the Paramillos Formation there is the Agua de la Zorra Formation. This unit is dominated by bituminous shales and marls with subordinated interbedded fine-grained sandstones and mudstones with peperitic, olivine basalts interbedded (Harrington, 1971; Brea *et al.*, 1999; Ottone *et al.*, 2011). The paleoenvironment is interpreted as a fluvial-lacustrine system with episodic incursions of lava flow in the aquatic medium (Cortés *et al.*, 1997; Ottone *et al.*, 2011). K/Ar ages of  $235 \pm 5$  Ma and  $240 \pm 10$  Ma were obtained in the basalts by Massabie (1986) and are also recorded in Linares (2007). The sedimentary record of the overlaying Portezuelo Bayo Formation is dominated by tuffaceous sandstones of fine to medium grain size with interbedded tuffs, some conglomerates and shales (Harrington, 1971; Stipanovic and Morel, 2002a). The sedimentary environment is interpreted as sinuous fluvial

system dominated by flood plain deposits. Los Colorados Formation covers the Portezuelo Bayo Formation and is characterized by sandstones with interbedded conglomerates and is referred to as Upper Triassic (Harrington, 1971; Stipanovic and Morel, 2002b).

### 2.1. Agua de la Zorra paleoenvironment

The Agua de la Zorra Formation was deposited in a deltaic and lacustrine system (Table 1, Fig. 1.1 and 1.2). Facies association AZ-a included dark greenish gray fine-grained, well-sorted massive sandstones (Sm), with vesicles of 0.5 cm in diameter and carbonate cemented nodules; light brownish gray massive muddy siltstones (Fm); moderate light gray coarse-grained, well sorted sandstones with ripple cross-stratification (Sr), and through cross-stratification pebbly sandstones (St) interpreted as lower delta plain associated with mouth bars at the delta front. The Facies association AZ-b is dominated by black, olive black, greenish red, and greenish black finely laminated mudstones (Fl); light brownish gray massive muddy siltstones (Fm), horizontally laminated fine to coarse-grained well sorted-sandstone (Sh), and massive white tuff (Tf) interpreted as prodelta to offshore lacustrine deposits.

### 3. Materials and methods

Plant remains were systematically collected in the Agua de la Zorra Formation at the Paramillos de Uspallata locality in several fieldtrips between 2015 and 2017. Eighteen fossil-bearing horizons were reported and several specimens were collected from them. The fossil-bearing horizons are identified with roman numbers from I to XVIII (Fig. 1. 2).

The recovered material includes leaf fragments, stems associated with leaves and reproductive structures. They are preserved as carbonaceous compressions and/or impressions in black shales and yellow mudstones from different levels of the unit. They occurred as fragmented plant elements, with variable size, densely packed or isolated, and with weak orientation preferences.

The specimens were studied with a binocular stereoscopic microscope WILD Heerbrugg M8 and they were photographed with a Canon Power Shot SD1200 IS (10 megapixels) digital camera. Reproductive structures were studied with a binocular stereoscopic microscope LEICA M60 with integrated camera Leica DMC2900.

The fossil material is 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 Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires under the prefix BAFC-Pb.

For the systematic classification we followed the proposal by Stewart and Rothwell (1993) used by Zamuner *et al.* (2001), Artabe *et al.* (2007) and Morel *et al.* (2010, 2011). In the case of ferns, we adhere with Smith *et al.* (2006) proposal, and for the identification of fructifications we follow Anderson and Anderson (2003).

### 4. Systematic paleobotany

**Subdivision Euphyllophytina Kenrick and Crane, 1997**

**Class Polypodiopsida Cronquist *et al.*, 1966**

**Order Equisetales de Candolle, 1804 ex von Berchtold and Presl, 1820**

**Family Undetermined**

**Genus *Neocalamites* Halle, 1908**

**Type species. *Neocalamites hoerensis* (Schimper, 1869) Halle, 1908**

***Neocalamites* sp.**

**Figure 2. 1,2**

**Description.** Fragmentary compressions and impressions of articulate ribbed axis, 0.9 to 11.8 cm long, up to 4 cm wide at the nodes; ribs are 0,1 cm wide and up to 0.1 cm separated on large axes; nodes displaying circular structures, 0,1 cm in diameter, interpreted as probable branches.

**Comments.** Unbranched articulate ribbed axes associated with leaves not forming a foliar sheath are currently referred to *Neocalamites*. The presence of associated sporangiophores allows different phylogenetic relationships to this taxon. Boureau (1964) included *Neocalamites* in the Family Apocalamitaceae (Radzenko, 1957), whilst Good (1975), Meyen (1987), and Escapa and Cúneo (2004) in the Family Equisetaceae (De Candolle, 1804). Recently, Elgorriaga *et al.* (2018) consider the *Neocalamites* species as a natural and independent sister group of the Equisetaceae, and not directly related to the Calamitaceae clade, as suggested by Stewart and Rothwell (1993). Following Elgorriaga *et al.* (2018), and considering that the Agua de la Zorra Formation plant fossils lack associated sporangiate organs, the suprageneric assignation of our material remains undetermined. In the studied material, the presence of nodes with no evidence of basally fused leaves forming a sheath allows the inclusion of our material in *Neocalamites*, however, pending discovery of better preserved specimens, the Agua de la Zorra material is left in open nomenclature.

TABLE 1. FACIES ASSOCIATIONS AND THEIR CHARACTERISTICS DEFINED FOR THE AGUA DE LA ZORRA FORMATION (TRIASSIC) AT USPALLATA.

Facies Association (FA)	Facies	Sedimentary structures	Bed geometry	Vertical and lateral relations	Fossil content	Processes	FA Interpretation
A	Cemented massive sandstones (Sm)	Fine-grained, well-sorted massive sandstones of dark greenish gray color (5GY4/1), with vesicles of 0.5 cm in diameter, carbonate cement interdigitations and carbonate cemented nodules	Tabular, 1-14 m thick	Underlies and overlies facies Fl	-	Diagenetically altered sandstones	
	Massive siltstones (Fm)	Massive muddy siltstones, color is light brownish gray (5YR6/1)	Tabular, 0.3-0.6 m thick	Overlies facies Sm, Sr, Fl and underlies facies Sr, St, Fl	Trace fossils	Suspension settle-out	Lower delta plain associated with mouth bars at the delta front
	Ripple cross sandstones (Sr)	Coarse-grained, well sorted sandstones, 1 cm thick sets and 2 cm thick cosets, siliciclasts are subrounded to subangular, containing angular quartz, K-feldspar and muscovite, color is moderate light gray (N6)	Tabular, 0.3 m thick	Underlies and overlies facies Fm	-	Tractive flows	
	Trough cross sandstones (St)	Pebbly sandstones with through cross stratification, sets are 5 cm thick in cosets of 20 cm thick, coarsening upwards	Tabular, 2 m thick	Underlies facies Fl and overlies facies St	-	Channelized tractive flows	
B	Finely laminated mudstones (Fl)	Finely laminated mudstones, laminae are 1 mm thick, color range from black (N1) to olive black (5Y2/1) to greenish red (5R4/2) to greenish black (5YR2/1)	Tabular, 0.5-11 m thick	Overlies facies Sm, Sh, St, Fm, Tf	Plant remains, fish scales and conchostracans		
	Massive siltstones (Fm)	Massive muddy siltstones, color is light brownish gray (5YR6/1)	Tabular, 0.3-0.6 m thick	Overlies facies Sm, Sr, Fl and underlies facies Sr, St, Fl	Trace fossils	Suspension settle-out	Prodelta to offshore lacustrine
	Horizontally laminated sandstone (Sh)	Fine to coarse-grained well sorted-sandstone, lamination is 0.5 cm thick	Tabular to lenticular, 0.3-0.6 m thick	Underlies and overlies facies Fl	-	Channelized to non-channelized tractive flows	
	Tuff (Tf)	Massive, white color (N9)	Tabular, 0.5 m thick	Underlies and overlies facies Fm.	-	Ash fall	

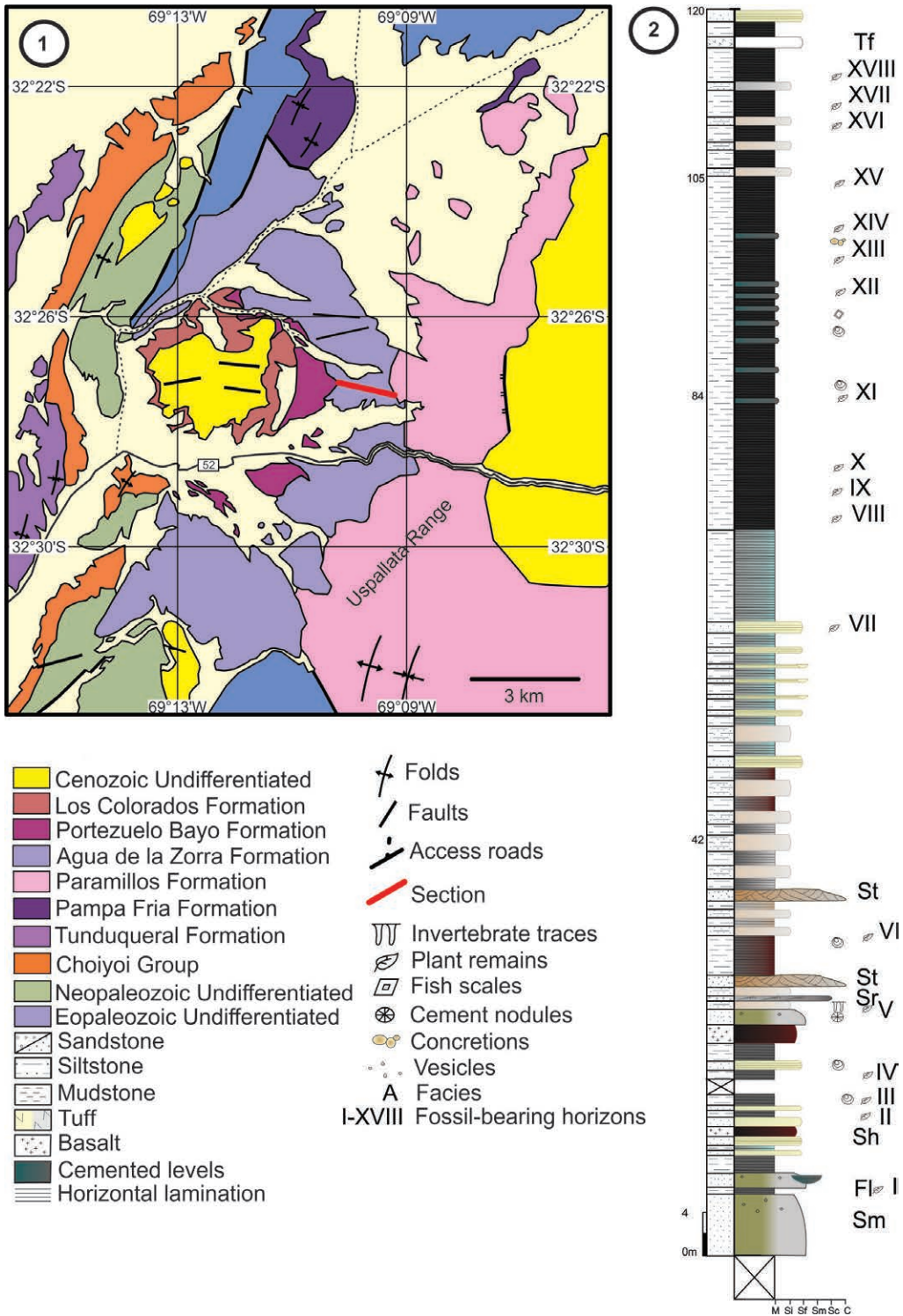


FIG. 1. 1. Geologic map of the Paramillos de Uspallata, Mendoza, Argentina. 2. Detailed stratigraphic section of Agua de la Zorra Formation at the Paramillos de Uspallata and stratigraphic provenience of materials. St, Sr, Sh, Fl, Sm, Tf are lithofacies mentioned in Table 1.

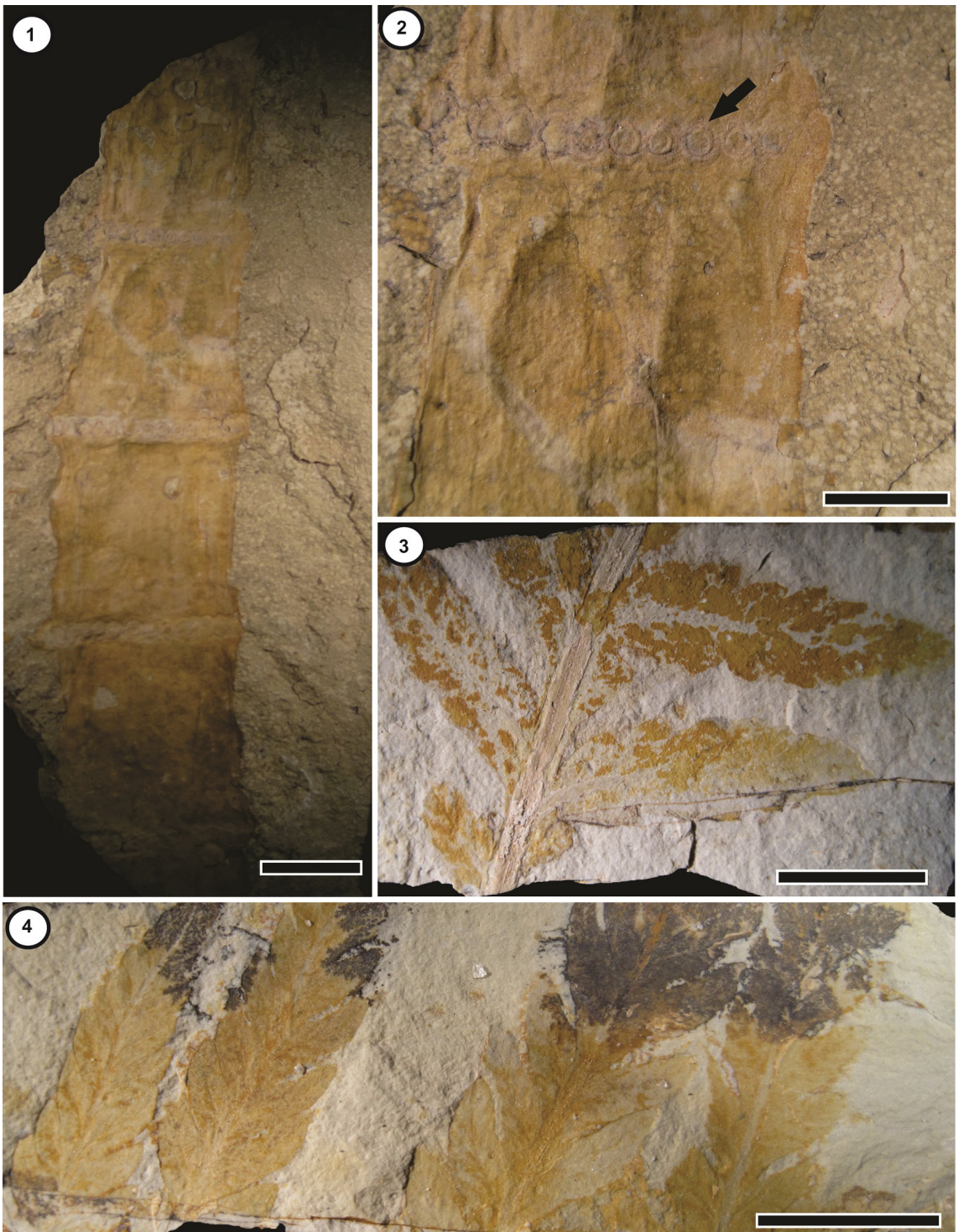


FIG. 2. 1. *Neocalamites* sp Halle, 1908, IANIGLA-PB-679. Scale bar=1 cm. 2. Detail of nodes the arrow mark incertion branch's structure. Scale bar=0.5 cm. 3. *Cladophlebis* sp. Cf. *C. mesozoica* Frenguelli, 1947. IANIGLA-PB-682 Scale bar=1 cm. 4. *Cladophlebis kurtzii* Frenguelli, 1947. IANIGLA-PB-681 Scale bar=1 cm.

**Order Osmundales Link, 1833****Family Osmundaceae Martynov, 1820****Genus *Cladophlebis* Brongniart, 1849 emend.**

Frenguelli, 1947

**Type species. *Cladophlebis albertsii* (Dunker, 1846)**

Brongniart, 1849

*Cladophlebis kurtzi* Frenguelli, 1947

Figure 2. 4

**Synonymy in Herbst (1971)**

**Description.** Fragmentary impressions of bipinnate fronds bearing subopposite subcircular and elongate pinnules, attached with an angle ca. 45°. Pinnules decurrent at the base, entire margins and apex slightly rounded. With a single mid-vein and badly preserved secondary venation, but in some specimens, it is possible to see secondary veins forking near the insertion area with the mid vein.

**Comments.** The genus *Cladophlebis* was created by Brongniart (1849) to refer to sterile filiciform fronds of the Paleozoic and Mesozoic that can not be assigned with certainty to a natural family, however, it is known that some species correspond to the family Osmundaceae (Boureau and Doubinger, 1975). Nevertheless, *Cladophlebis* leaves are also present in Cyatheaceae and Dennstaediaceae (Villar de Seoane, 1996), and in ferns of uncertain affinity (Carrizo *et al.*, 2011). *Cladophlebis* leaves of the Agua de la Zorra Formation are referred to the Osmundaceae because Cyatheaceae and Dennstaediaceae records begin in the Jurassic (Smith *et al.*, 2006).

The species *Cladophlebis kurtzi* Frenguelli, 1947 includes laminate, alternate, well spaced, lanceolate pinnules with entire margins, and secondary veins bifurcating once near the base. As noted by Frenguelli (1947), the presence of smaller, triangular-ovate pinnules of acute apex and confluent bases, as seen in the Agua de la Zorra material, indicates a distal position in the pinnate leaves.

***Cladophlebis* sp. cf. *C. mesozoica* Kurtz in**

Bodenbender, 1911 ex Frenguelli, 1947

Figure 2. 3

**Synonymy in Herbst (1971)**

**Description.** The specimen is an impression of fragment of a bipinnate frond bearing subopposite, broadly attached pinnules, 1.5-2 cm long, 0.5 cm wide; pinnules constricted anadromically and decurrent catadromically with entire to slightly lobed margin, a rounded apex, and badly preserved secondary venation.

**Comments.** This species includes alternate shallowly lobed pinnules, bearing two forked secondary veins. The morphology of pinnules is variable in relation of their position in the pinnae, diffculting the assignment of fragmentary material (Herbst, 1971).

**Class Gymnospermopsida *sensu* Stewart and Rothwell, 1993****Order Umkomasiales Meyen, 1984****Family Umkomasiaceae Petriella, 1982**

**Remarks.** Umkomasiaceae was traditionally known as *Corystospermaceae* (Thomas, 1933), a descriptive name, not based on a validly published fossil-generic name. Descriptive family names are proscribed by the Code (Art. 18.1 of the ICN) (Doweld, 2017; Turland *et al.*, 2018).

Umkomasiaceous leaves are morphologically variable, but shear similar cuticles, so, several authors (Townrow, 1957; Bonetti 1966; Archangelsky, 1968; Anderson and Anderson, 1970, 1983; Holmes and Ash, 1979) refer all of them to the genus *Dicroidium*. However, considering that the preservation of mummified remains is relatively scarce, another group of authors (Frenguelli, 1943, 1944; Retallack 1977; Petriella, 1979; Artabe, 1985, 1990; Morel, 1994; Gnaedinger and Herbst, 1998a) discriminated different genera of distinctive morphology as *Dicroidium*, *Johnstonia*, *Xylopteris* and *Zuberia*. This contribution stands this last position.

**Genus *Dicroidium* Gothan, 1912****Type species. *Dicroidium odontopteroides***

(Morris, 1845) Gothan, 1912

***Dicroidium argenteum* (Retallack) Gnaedinger in**

Gnaedinger and Herbst, 2001

Figure 3. 1

**Synonymy in Retallack (1977) and in Gnaedinger and Herbst (2001)**

**Description.** Frond fragments up to 6 cm long with subopposite, subcircular pinnules displaying slightly constricted bases, entire margins and a rounded apex.

**Comments.** The Agua de la Zorra Formation specimens fit well with the forms figured by Retallack (1977) and Gnaedinger and Herbst (2001).

***Dicroidium crassum* (Menéndez) Petriella, 1979**

Figure 3. 6

**Synonymy in Retallack (1977) and Gnaedinger and Herbst (1998a, 2001).**

**Description.** Fragments of dichotomously divided fronds up to 5.5 cm long with subopposite, subcircular pinnules at ca. 45° to rachis.

**Comments.** The species include monopinnate fronds with equidimensional to rhomboid pinnules, constricted to sometimes subpetiolae at base, acute at apex, with obtuse apical inclination, and lacking midrib (Menéndez, 1951; Petriella, 1979; Gnaedinger and Herbst 1998a; Lutz et al., 2011).

***Dicrodium odontopteroides* (Morris) Gothan, 1912**

**Figure 3. 2**

**Synonymy in Retallack (1977) and in Gnaedinger and Herbst (2001)**

**Description.** Fragments of dichotomously divided frond up to 2.5 cm long with subcircular, subopposite pinnules enlarged at base, entire margins, rounded at apex, and odontopteroid venation.

**Comments.** Following Gnaedinger and Herbst (1998a, 2001), we consider that all species varieties, as previously defined by Retallack (1977), Petriella (1979), and Anderson and Anderson (1983), represent the morphological variability of a single taxon.

**Genus *Johnstonia* Walkom, 1925**

**Type species. *Johnstonia coriacea* (Johnston, 1886) Walkom, 1925**

***Johnstonia coriacea* (Johnston) Walkom, 1925**

**Figure 3. 3**

**Synonymy in Retallack (1977)**

**Description.** Compressions and impressions of fronds with a dichotomously forked rachis, margin entire, leaf blade relatively broad, rounded at apex, midrib always discernible. 2.5-6 cm in length and 0.5 cm in width. Venation not preserved.

***Johnstonia dutoitii* (Townrow) Retallack, 1977**

**Figure 3. 4**

**Synonymy in Retallack (1977) and Gnaedinger and Herbst (2001)**

**Description.** Fragments of pinnatifid fronds up to 6 cm long with a dichotomously forked rachis, margin of the leaf blade slightly lobed. Venation is not preserved.

**Comments.** The species includes symmetrical pinnatifid fronds of lobate to rounded margins and secondary veins coalescent to the margin (Retallack, 1977).

***Johnstonia* sp. cf. *J. serrata* Retallack 1977**

**Figure 3. 7**

**Synonymy in Retallack (1977)**

**Description.** Compressions of fragments of pinnatifid asymmetric low lobes fronds. 1.5-4.5 cm in length and 0.4-1 cm in width. Venation taeniopteroid.

**Comments.** *Johnstonia serrata* includes pinnatifid fronds with asymmetric lobes, shallow incisions in the apex margin, and taeniopteroid venation (Retallack, 1977). The doubtful assignment is due to the bad preservation of the material.

**Genus *Xylopteris* Frenguelli, 1943 emend. Stipanovic and Bonetti in Stipanovic et al., 1996**

**Type species. *Xylopteris elongata* (Carruthers)**

**Frenguelli, 1943**

***Xylopteris argentina* (Kurtz) Frenguelli 1943 emend.**

**Stipanovic and Bonetti in Stipanovic et al. 1996**

**Figure 3. 5**

**Synonymy in Retallack (1977), Gnaedinger and Herbst (1998a) and Ottone et al., (2011)**

**Description.** Impressions and compressions of 3-7 cm in length with linear pinnules having a coenopteroid venation.

**Comments.** The genus *Xylopteris* includes bifurcate, pinnate or pinnatifid fronds, mono-, bi- or tripinnate, having linear pinnules (Frenguelli, 1943; Stipanovic et al., 1996; Ottone, 2006; Barboni et al., 2016). For specific discrimination within the genus we follow the criteria of Ottone (2006) and Ottone et al. (2011).

The species *Xylopteris argentina* includes monopinnate, linear, bi- or trifurcate fronds with linear pinnules and simple, usually coenopteroid, venation (Kurtz, 1921; Stipanovic et al., 1996; Ottone et al., 2011). Specimens described herein agree with the diagnosis proposed by Frenguelli (1943) and the emendation of Stipanovic and Bonetti in Stipanovic et al. (1996).

***Xylopteris elongata* (Carruthers) Frenguelli, 1943**

**Figure 3. 11**

**Synonymy in Ottone et al. (2011)**

**Description.** Impressions of fronds up to 4 cm long with alternate to subopposite pinnae bearing linear pinnules of coenopteroid venation.

**Comments.** This species comprises irregularly bipinnate fronds with a dichotomously forked rachis bearing linear, simple or bifurcate foliar segments interpreted as pinnae (Carruthers, 1872; Ottone et al., 2011).



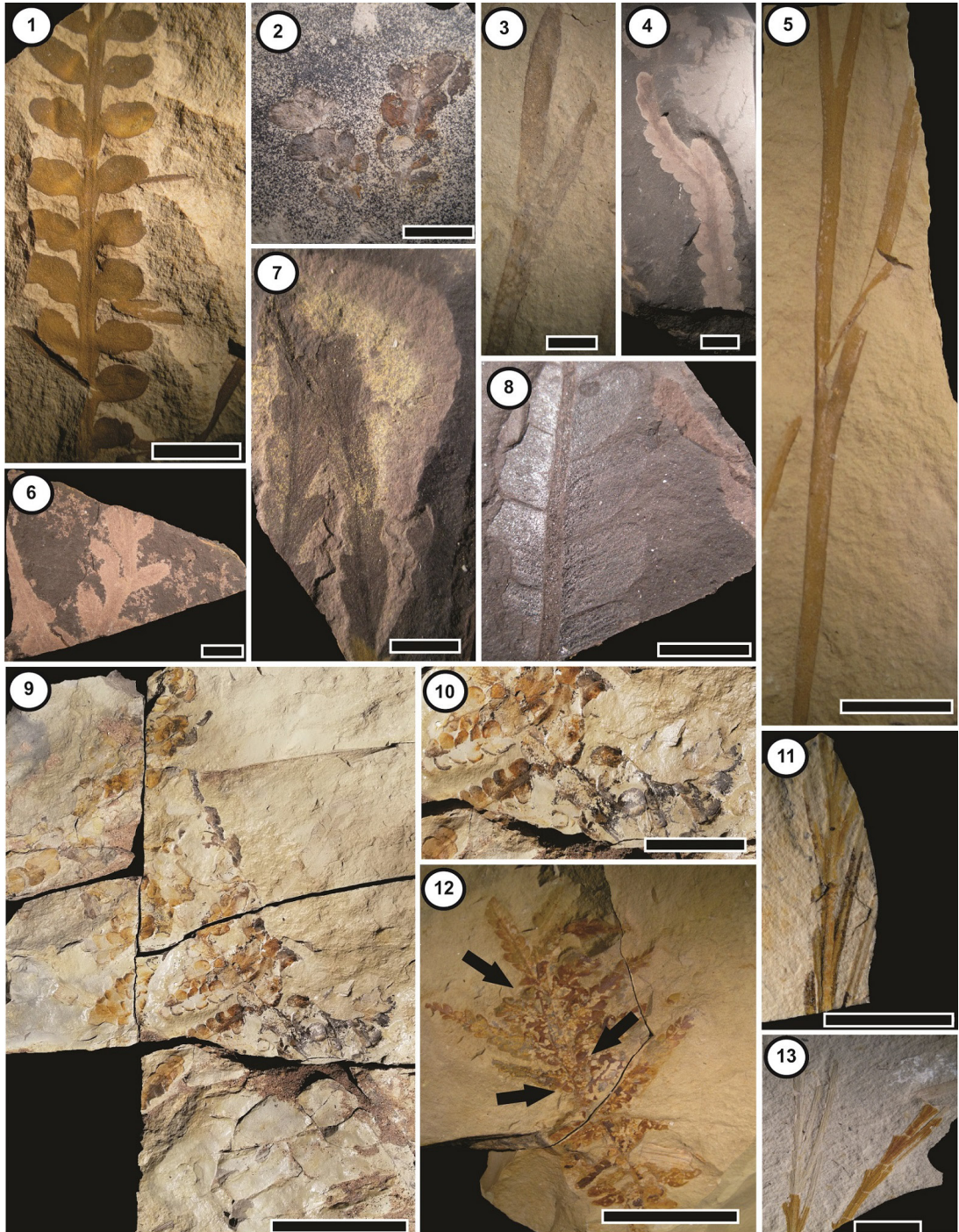


FIG. 3. 1. *Dicroidium argenteum*. Gnaedinger in Gnaedinger and Herbst, 2001. IANIGLA-PB-683. Scale bar=1 cm. 2. *Dicroidium odontopteroides* Gothan, 1912. IANIGLA-PB-686. Scale bar=1cm. 3. *Johnstonia coriacea* Walkom, 1925. IANIGLA-PB-692. Scale bar=1cm. 4. *Johnstonia dutoitii* Retallack, 1977. IANIGLA-PB-693. Scale bar=1cm. 5. *Xylopteris argentina* Frenguelli emend. Stipanovic and Bonetti en Stipanovic *et al.* 1996. IANIGLA-PB-699. Scale bar=1cm. 6. *Dicroidium crassum* Petriella, 1979. IANIGLA-PB-697. 7. *Johnstonia sp. c.f. J. serrata* Retallack 1977. IANIGLA-PB-697. Scale bar=0.5cm. 8. *Zuberia feistmanteli* Frenguelli, 1943. IANIGLA-PB-705. Scale bar=1cm. 9. *Zuberia zuberi*. Frenguelli, 1943. IANIGLA-PB-736. Scale bar=5cm. 10. *Zuberia zuberi*. Frenguelli, 1943. IANIGLA-PB-736. Scale bar=1cm. 11. *Xylopteris elongata* Frenguelli, 1943. IANIGLA-PB-697. Scale bar=1cm. 12. *Zuberia zuberi*. Frenguelli, 1943. BAFC-Pb 27201. Arrow mark intercalary pinules. Scale bar=2cm. 13. *Xylopteris elongata* Frenguelli, 1943. IANIGLA-PB-702. Scale bar=1cm.

**Genus *Zuberia* Frenguelli 1943 emend. Artabe, 1990****Type species. *Zuberia zuberi* (Szajnocha, 1889)****Frenguelli, 1943*****Zuberia feistmantelii* (Johnston) Frenguelli, 1943****Figure 3. 8****Synonymy in Artabe (1990)**

**Description.** Fragments up to 5.5 cm long of bipinnate fronds, bearing opposite to subopposite sub-quadrangularpinnules. The pinnules are isodiametric, width greater than 0.6 cm. The venation is of the odontopteroid type. Sub-quadrangular interpinnules.

**Comments.** The genus *Zuberia* comprises bifurcate, imparipinnate, bipinnate, bipinnatifid or tripinnatifid fronds with rectangular, rhomboid or orbicular pinnules of odontopteroid venation, having, as a diagnostic character, intercalary pinnules (Frenguelli, 1943, 1944; Artabe, 1990). The species *Zuberia feistmantelii* includes bifurcate bipinnate fronds with relatively large, ca. 1 cm long, opposite to subopposite, subquadrangular pinnules of odontopteroid venation and greater than 0.6 cm (Artabe, 1990).

***Zuberia zuberi* (Szajnocha) Frenguelli, 1943****Figure 3. 9, 10, 12****Synonymy in Artabe (1990)**

**Description.** Fragments up to 4.5 cm long of bipinnate fronds bearing opposite to subopposite quadrangular to sub-quadrangular pinnules and rounded interpinnules, showing a badly preserved venation. The size of pinnules and interpinnules are smaller than 0.5 cm.

**Comments.** This species is characterized by the bifurcate bipinnate fronds with relatively small, up to 0.5 cm in length, opposite to subopposite, subquadrangular pinnules of odontopteroid venation (Artabe, 1990).

**Order Cycadales Dumortier, 1829****Genus *Taeniopteris* Brongniart, 1828 emend. Cleal and Rees, 2003****Type species. *Taeniopteris vittata* Brongniart, 1828*****Taeniopteris* sp.****Figure 4.5**

**Description.** Impressions and compressions of leaf fragments, 1.7-4 cm in length, 0.5-1.1 cm width, with a simple entire-margined lamina bearing a rigid midvein, 0.1-0.3 cm wide; lateral veins approximately perpendicular to midvein, dichotomizing near 1/2 lamina and reaching margin.

**Comments.** van Konijnenburg-van Cittert et al. (2017, p. 101-102) interpretation of the genus is followed here

in. This artificial taxon could also be positioned in the Jurassic-Cretaceous Pentoxylales (Césari et al. 1998; Sharma, 2001). We refer the Agua de la Zorra material to the Cycadales because the Pentoxylales are unknown in the Triassic of South America (Sharma, 2001). The specimens described herein were assigned to the genus *Taeniopteris* by their venation features (Anderson and Anderson, 1989). The specific attribution of the studied material is hindered by the poor preservation of the specimens.

**Order Ginkgoales Gorozankin, 1904**

**Remarks.** The great morphological variability of fossil leaves, also present in extant *Ginkgo biloba* Linnaeus 1771, make difficult the assignment of fossil material. In this sense the taxonomical criterion of Gnaedinger and Herbst (1999, p. 281-282) is followed here in.

**Genus *Sphenobaiera* Florin, 1936 emend. Harris and Millington in Harris et al., 1974****Type species. *Sphenobaiera spectabilis*****(Nathorst, 1906)****Florin, 1936*****Sphenobaiera* sp.****Figure 4. 6**

**Description.** Impressions of fragments of wedge-shaped, lobed leaf, up to 2.8 cm in length; lamina forking, at least, one time, dichotomy occurring within 1.4 cm from base at an angle of 45° to give two segments, 10 cm in width; venation parallel reaching distal margin; petiole quite undiscernable.

**Comments.** The genus includes fan-shaped leaves without petiole; close comparison of this form with previously described species is hindered by the fact that only one, fragmentary specimen was encountered.

**Order Voltziales Andreanszky, 1954****Family Voltziaceae Arnold, 1947****Genus *Heidiphyllum* Retallack, 1981****Type species. *Heidiphyllum elongatum* (Morris) Retallack, 1981*****Heidiphyllum elongatum* (Morris) Retallack, 1981****Figure 4. 3,4**

**Synonymy in Retallack (1981), Anderson and Anderson (1989) and Troncoso et al., (2000)**

**Description.** Compressions and impressions of obovate/lanceolate to linear leaves fragments, 4 cm in length, and 0.3-0.5 in width, bearing 4 to 8 veins simple, parallels. The bases of leaves are not preserved.

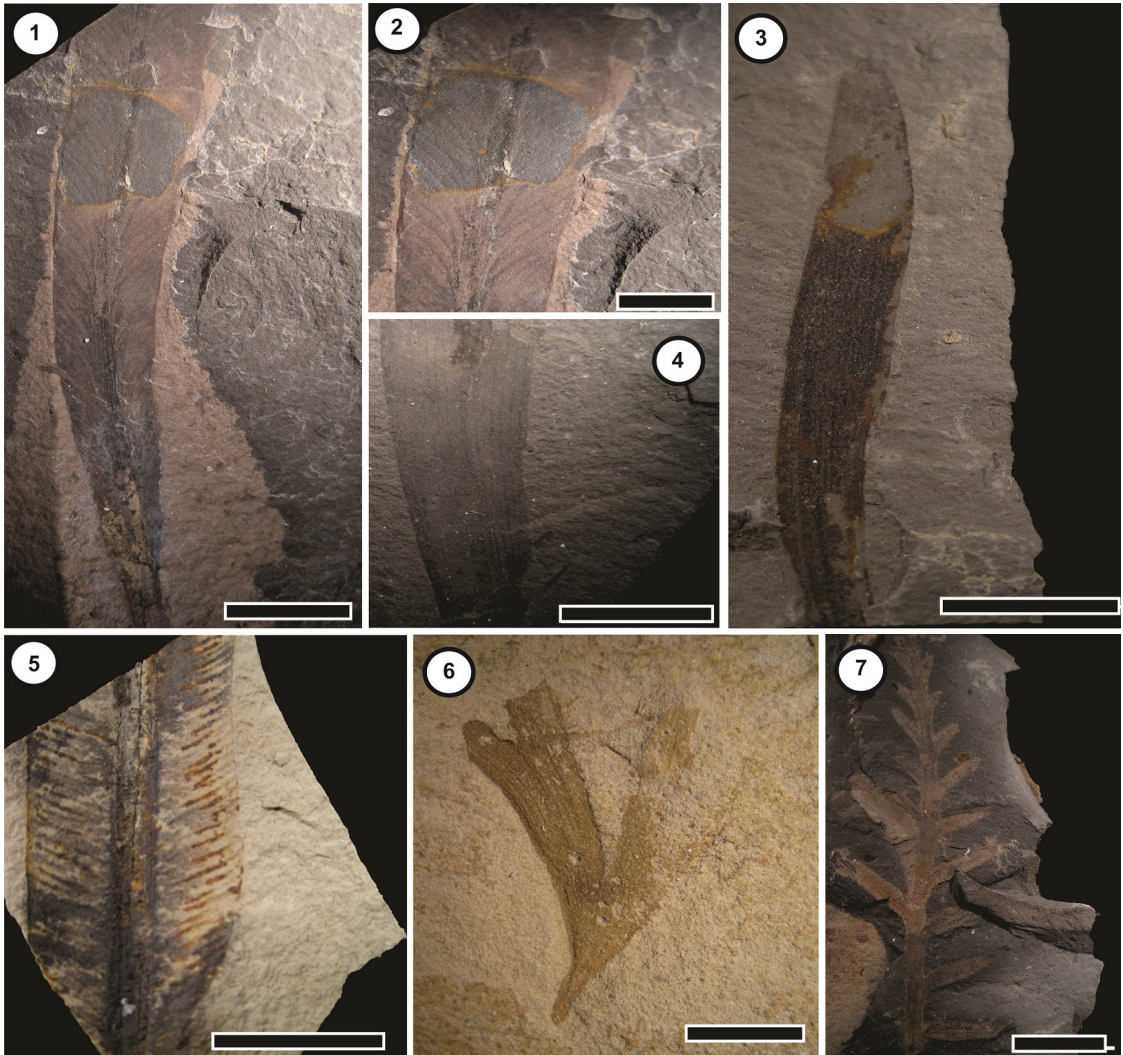


FIG. 4. 1-2. *Linguifolium patagonicum*. Gnaendinger & Herbst 1998. IANIGLA-PB-727. Scale bar=1cm. 3-4. *Heidiphyllum elongatum* Retallack 1981. IANIGLA-PB-716 y 711. Scale bar=1cm. 5. *Tueniopteris* sp. Brongniart 1828. IANIGLA-PB-711 Scale bar=1cm. 6. *Sphenobaiera* sp. Florin, 1936. IANIGLA-PB-715. Scale bar=1cm. 7. *Rissikia media* Townrow, 1967. IANIGLA-PB-723. Scale bar=1cm.

**Comments.** *Heidiphyllum elongatum* is characterized by possess apetiolate, linear-elliptical to linear-oblongate leaves with entire margins, apex subacute to rounded and parallel venation only forking at the base of the leaf (Retallack, 1981; Anderson and Anderson 1989). Troncoso *et al.* (2000) highlights the polymorphic character of this species.

**Order Coniferales Engler, 1897**  
**Family Podocarpaceae Endlicher, 1847**  
**Genus *Rissikia* Townrow, 1967**  
**Type species. *Rissikia media* (Tenison-Woods)**

**Townrow, 1967**

***Rissikia media* (Tenison-Woods) Townrow, 1967**

**Figure 4. 7**

**Synonymy in Holmes (1982), Anderson and Anderson (1989) and Troncoso *et al.* (2000)**

**Description.** Compressions and impressions of shoots; 2-6 cm in length and 0.2 cm in width; leaves with one single midvein, simple, linear, alternated to subopposite, slightly constricted basally, attached laterally to the axis and separated each other 0.2-0.3 cm.

**Comments.** The characteristics of the specimens described herein are consistent with the description of Townrow (1967). *Gymnospermopsida incertae sedis*

**Genus *Linguifolium* Arber, 1913 emend. Retallack, 1980**

**Type species. *Linguifolium lillianum* Arber, 1913**

***Linguifolium patagonicum* Gnaedinger and Herbst, 1998b**

**Figure 4. 1,2**

**Description.** The studied material includes compressions and impressions of petiolate, linear-spathulate leaf fragments, up to 8.5 cm in length, and 1.3 cm of maximum width; petiole distinctive, 0.2 cm in width; midvein, 0.1-0.2 cm in width; lateral veins emerge forming an acute angle ( $5^{\circ}$ - $15^{\circ}$ ) to midvein and fork at least one time.

**Comments.** The Agua de la Zorra Formation specimens show the most critical features of the species described by Gnaedinger and Herbst (1998b).

**Genus *Cordaicarpus* Geinitz, 1862 emend.**

**Archangelsky, 2000**

**Type species. *Cordaicarpus cordai* Geinitz, 1862.**

***Cordaicarpus* sp. A**

**Figure 5. 1**

**Description.** Ovules/seeds compressions, flattened, oval, 0.6 cm in width, 0.6 cm in length; sarcotesta filmy,

narrow, surrounding an inner, oval, thick walled body (megasporeangium); sarcotesta narrowing to one end (basal chalaza?); micropylar channel not preserved.

**Comments.** *Cordaicarpus* sp. A superficially resembles many species of the genus, however, the poor preservation of the studied material hindered its specific designation.

***Strobilus* sp. A**

**Figure 5. 2**

**Description.** Compression of an incomplete strobilus?; axis dichotomous, 5 cm in length and 0.2 cm in width; cupules? 0.5 cm in diameter.

**Comments.** This fossil remain is interpreted as a probable megasporophyll fragment, however, the attachment area of cupules? on axis is not clearly distinguishable.

***Strobilus* sp. B**

**Figure 5. 3**

**Description.** Compression of a strobilus fragment of linear shape, bearing spirally arranged megasporophylls; cone units include bract/scales complexes and ovules; bract/scales complex lobate (it is difficult to discriminate between bract and scale due to preservation), bearing ovules or sterile?; ovules oval-shaped, 0.3 cm wide, 0.6 cm length, with peduncle, megasporeangium, and integument, 0.1 cm wide, occasionally recognizable.

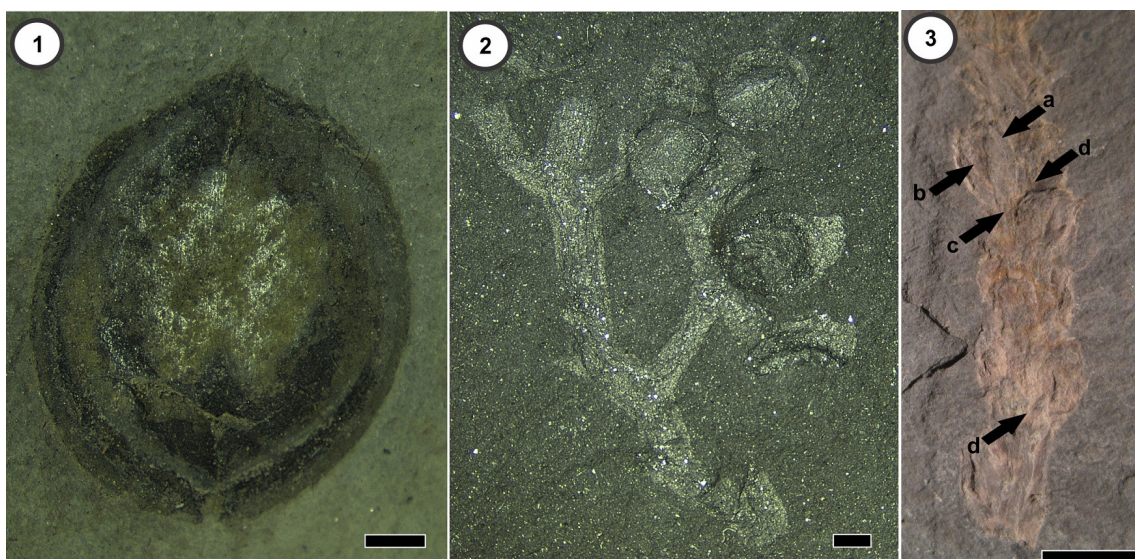


FIG. 5. 1. *Cordaicarpus* sp. A. IANIGLA-PB-737 Scale bar=1 mm. 2. *Strobilus* sp. A. IANIGLA-PB-738. Scale bar=1mm. 3. *Strobilus* sp. B. IANIGLA-PB-722. Scale bar=0.5 cm. a. megasporangium, b. integument, c. peduncle, d. bractes/scales.

**Comments.** Linear-shaped cones bearing megasporophylls of lobed scales were referred by Anderson and Anderson (2003) to *Rissikistrobus*. Cones of Paleozoic Majonicaceae and Utrechtaceae (Walchiaceae) also have megasporophylls with lobed scales (Taylor *et al.*, 2009).

## 5. Discussion

The Cuyana Basin is formed by several sub-basin, which due to the lack of continuous outcrops and the scarcity of fossiliferous information, the correlations among their successions have mainly relied on lithostratigraphy and equal distribution of depositional environments (*e.g.* Yrigoyen and Stover, 1970; Strelkov and Alvarez, 1984; Ramos and Kay, 1991; López-Gamundí and Astini, 2004). In this way, some authors linked all depocenters by lithological similarities and proposed an equivalent infilling history for the whole basin, reflected in the use of a unified nomenclature (*e.g.* Yrigoyen and Stover, 1970; Strelkov and Alvarez, 1984; Ramos and Kay, 1991; López-Gamundí and Astini, 2004). However, other authors (*e.g.* Baldis *et al.*, 1982, Brea *et al.*, 2009; Mancuso *et al.*, 2010; Ottone *et al.*, 2011; Barredo *et al.*, 2012) have considered that separate outcrops represent independent depocenters with a separated geological history, even during the last rifting stage.

Particularly in Mendoza Province, the Potrerillos and Paramillos de Uspallata areas, located in different sub-basins, include a fluvial-lacustrine succession named as Potrerillos-Cacheuta and Paramillos-Agua de la Zorra, respectively. Both successions are chronostratigraphically equivalent constrained to Middle-Upper Triassic based on U-Pb SHRIMP in the Potrerillos Formation (239.2±4.5 Ma and 230.3±2.3 Ma; Spalletti *et al.*, 2008), the U-Pb (LA-ICP-MS) in the Paramillos Formation (239.6±1.3 Ma; Cingolani *et al.*, 2017), and K/Ar in the Agua de la Zorra Formation (235±5 Ma and 240±10 Ma; Massabie, 1986; Ramos and Kay, 1991; Linares, 2007). In addition, both successions are interpreted as fluvial systems that transitionally pass to lacustrine environment during the synrift stage (Kokogian *et al.*, 1993, 2001; Spalletti *et al.*, 2005).

The Argentine Triassic megaflores are dominated by the Umkomasiaceae (also known as Corystospermaceae), an endemic Gondwanan family that includes different genera of leaves as *Dicroidium*, *Johnstonia*, *Xylopteris* and *Zuberia*, but *Dicroidium* is the most abundant genus in the Triassic paleoflores (Zamuner *et al.*, 2001; Stipanovic and Archangelsky, 2002). The *Dicroidium* Flora includes also cosmopolitan taxa referred to the Equisetales (*Neocalamites*, *Equisetites*), Lycopsidea (*Pleuromeia*),

Osmundales (*Cladophlebis*), Peltaspermales (*Lepidopteris*, *Scytophyllum*), Cycadales (*Pterophyllum*, *Anomozamites*, *Ctenis*, *Pseudoctenis*, *Taeniopteris*), Ginkgoales (*Ginkgoites*, *Baiera*, *Sphenobaiera*) and Voltziales (*Heidiphyllum*) (Zamuner *et al.*, 2001; Stipanovic and Archangelsky, 2002).

As we mentioned previously, only one contribution (Ottone *et al.*, 2011) deal with the systematic study of the Agua de la Zorra Formation paleoflora. On Table 2 we show the relationship between taxa cited for the Agua de la Zorra Formation by Ottone *et al.* (2011) and taxa described in this contribution.

The megaflores content of the Potrerillos-Cacheuta succession is quite diverse and include more than 100 species

**TABLE 2. RELATIONSHIP BETWEEN TAXA CITED FOR AGUA DE LA ZORRA FORMATION AND DESCRIBED THEM IN THIS WORK. \***

Species	Ottone <i>et al.</i> (2011)	This contribution
<i>Neocalamites</i> sp.	X	X
<i>Cladophlebis kurtzi</i>		X
<i>C. sp. cf. C. mesozoica</i>	X	X
<i>Dicroidium argenteum</i>		X
<i>D. crassum</i>		X
<i>D. odontopteroides</i>	X	X
<i>D. sp. cf. D. prolongatum</i>	X	
<i>Johnstonia coriacea</i>		X
<i>J. dutoitii</i>		X
<i>J. stelzneriana c.f. J. serrata</i>	X	X
<i>J. stelzneriana c.f. J. stelzneriana</i>	X	
<i>Xylopteris elongata</i>	X	X
<i>X. argentina</i>	X	X
<i>Zuberia feistmanteli</i>		X
<i>Z. zuberi</i>		X
<i>Linguifolium patagonicum</i>		X
<i>Taeniopteris</i> sp.		X
<i>Sphenobaiera</i> sp.		X
<i>Heidiphyllum elongatum</i>		X
<i>Rissikia media</i>		X
<i>Cordaicarpus</i> sp A	X	X
Strobils sp A		X
Strobils Sp B		X

\*Data taken from Ottone *et al.* (2011).

(Table 3). They are dominated by the Ummosasiaceae (*Dicroidium* and *Xylopteris*), ferns (*Cladophlebis*) and Equisetales (*Neocalamites*) (Kurtz, 1921; Stipanovic and Bonetti, 1969; Morel, 1991, 1994; Morel and Artabe, 1993; Brea, 1995, 1997; Brea and Artabe, 1999; Stipanovic et al., 1996; Kokogian et al., 2000; Spalletti et al., 2005). On the other hand, the Paramillos-Agua de la Zorra megafloora assemblage is less diverse and only includes 32 species (Table 3). Conifer (*Agathoxylon*) and Ummosasiaceae trunks (*Cuneumxylon*) are common in the Paramillos Formation whilst leaves of Ummosasiaceae (*Dicroidium* and *Xylopteris*) and ferns (*Cladophlebis*) are dominant in the Agua de la Zorra Formation (Darwin, 1846; Conwentz, 1885; Stappenbeck, 1910; Kurtz, 1921; Du Toit, 1927; Groeber, 1939; Windhausen, 1941; Harrington, 1971; Brea and Artabe, 1994, 1999; Brea, 1996a, 1996b, 1997, 2000; Brea et al., 2009; Ottone et al., 2011).

Differences in the taxonomic diversity are markedly evident when comparing the fluvial systems represented by Potrerillos and Paramillos formations (Table 3, Figure 6). The Potrerillos Formation represents a braided fluvial system, which passes upward to moderately-high sinuosity fluvial system with wide development of floodplain and deltaic plain (Kokogian et al. 1993; Zamuner et al., 2001; Spalletti et al., 2005; Lara et al., 2017), and preserves 67 species (Table 3, Fig. 6, Fig. 7.1). The high sinuosity fluvial system, in which channel-filling sand bodies are associated with mud-dominated floodplain deposits (Brea et al. 2008) of the Paramillos Formation only preserves 10 species (Table 3, Figure 6 and figure 7.1). The differences in the megafloora record could reflect compositional changes in the parental paleocommunity, and/or different environmental and/or preservation conditions.

**TABLE 3. RELATIONSHIP BETWEEN TAXA CITED FOR THE POTRERILLOS, CACHEUTA, PARAMILLOS AND AGUA DE LA ZORRA FORMATIONS.\***

Species	Potrerillos Fm.	Cacheuta Fm.	Paramillos Fm.	Agua de la Zorra Fm.
<i>Muscites Guescelini</i>	X			
<i>Pleuromeia</i> sp.	X	X	X	
<i>Neocalamites carrerei</i>	X	X	X	
<i>Neocalamites</i> sp.				X
<i>Neocalamostachys arrondoi</i>	X		X	
<i>Nododendron suberosum</i>	X		X	
<i>Nododendron</i> sp.	X			
<i>Phyllothea asutralis</i>	X			
<i>Phyllothea gracilis</i>	X			
<i>Equisetites fertilis</i>	X			
<i>Asterothea truempyi</i>	X			
<i>Cladophlebis copiosa</i>	X			
<i>C. kurtzi</i>	X	X	X	X
<i>C. mesozoica</i>	X	X	X	X
<i>C. mendozaensis</i>	X	X	X	
<i>Cladophlebis</i> sp. cf. <i>C. mesozoica</i>				X
<i>Cladophlebis</i> sp.	X	X		X
<i>Coniopteris potrerillensis</i>	X			
<i>C. harringtonia</i>	X			
<i>Lobifolia dejerseyi</i>	X			
<i>Glossopteris longicaulis</i>	X			
<i>Dicroidium argenteum</i>	X			X
<i>D. crissum</i>	X			X
<i>D. dubium</i>	X			

Table 3 continued.

Species	Potrerrillos Fm.	Cacheuta Fm.	Paramillos Fm.	Agua de la Zorra Fm.
<i>D. lancifolium</i>	X	X		
<i>D. odontopteroides</i>	X	X		X
<i>D</i> sp. cf. <i>d. prolongatum</i>				X
<i>D. pinnis-distantibus</i>		X		
<i>Johnstonia coriácea</i>	X	X		X
<i>J. dutoitii</i>				X
<i>J. stelzneriana</i>	X	X		X
<i>Xylopteris elongata</i>	X			X
<i>X. argentina</i>	X	X		X
<i>X. spinifolia</i>		X		
<i>Zuberia feistmanteli</i>	X	X		X
<i>Z. zuberi</i>	X	X		X
<i>Z. sahinii</i>		X		
<i>Umkomasia cacheutensis</i>		X		
<i>Umkomasia</i> sp.	X			
<i>Pteruchus simmondsi</i>	X	X		
<i>Pteruchus</i> sp.	X			
<i>Fanerotheca dichotoma</i>		X		
<i>Feruglóa samaroides</i>	X	X		
<i>Cuneumxylon spallettii</i>	X		X	
<i>Lepidopteris madagascariensis</i>	X			
<i>Pachydermophyllum dubium</i>	X			
<i>P. praecordillerae</i>	X			
<i>P. pinnatum</i>	X			
<i>Antevsia exstans</i>	X			
<i>Sphenopteris jocoliensis</i>	X			
<i>Dejerseya lunensis</i>				
<i>Lingufolium patagonicum</i>				X
<i>Rochipteris</i> sp.	X			
<i>Pseudoctenis falconeriana</i>		X		
<i>Kurtziana brandmary</i>	X			
<i>K. cacheutensis</i>	X	X		
<i>Taeniopteris</i> sp.				X
<i>Nilssonía taeniopteroides</i>		X		
<i>Pterophyllum</i> sp.		?		
<i>Baiera bidens</i>	X			
<i>B. cuyana</i>	X			
<i>B. rollerii</i>	X			
<i>Sphenobaiera argentinae</i>	X	X		
<i>S. taeniata</i>	X			

\* Data taken from Darwin, 1846; Brea and Artabe, 1994, 1999; Brea, 1995, 1996a, 1996b, 1997, 2000; Brea *et al.*, 2009; Ottone *et al.*, 2011 Kutz, 1902, 1921; Stipanovic and Bonetti, 1969; Stipanovic, 1982; Morel, 1991, 1994; Morel and Artabe, 1993; Morel *et al.*, 2010, 2011; Stipanovic *et al.*, 1996; Kokogian *et al.*, 2000; Spalleti *et al.*, 2005.

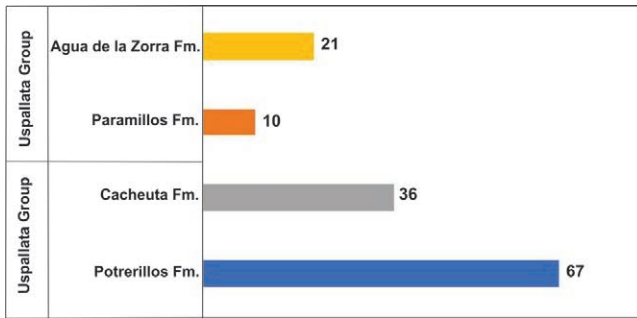


FIG. 6. Number of species in the Potrerillos, Cacheuta, Paramillos and Agua de la Zorra formations of flucial-lacustrine sequence of Cuyana.

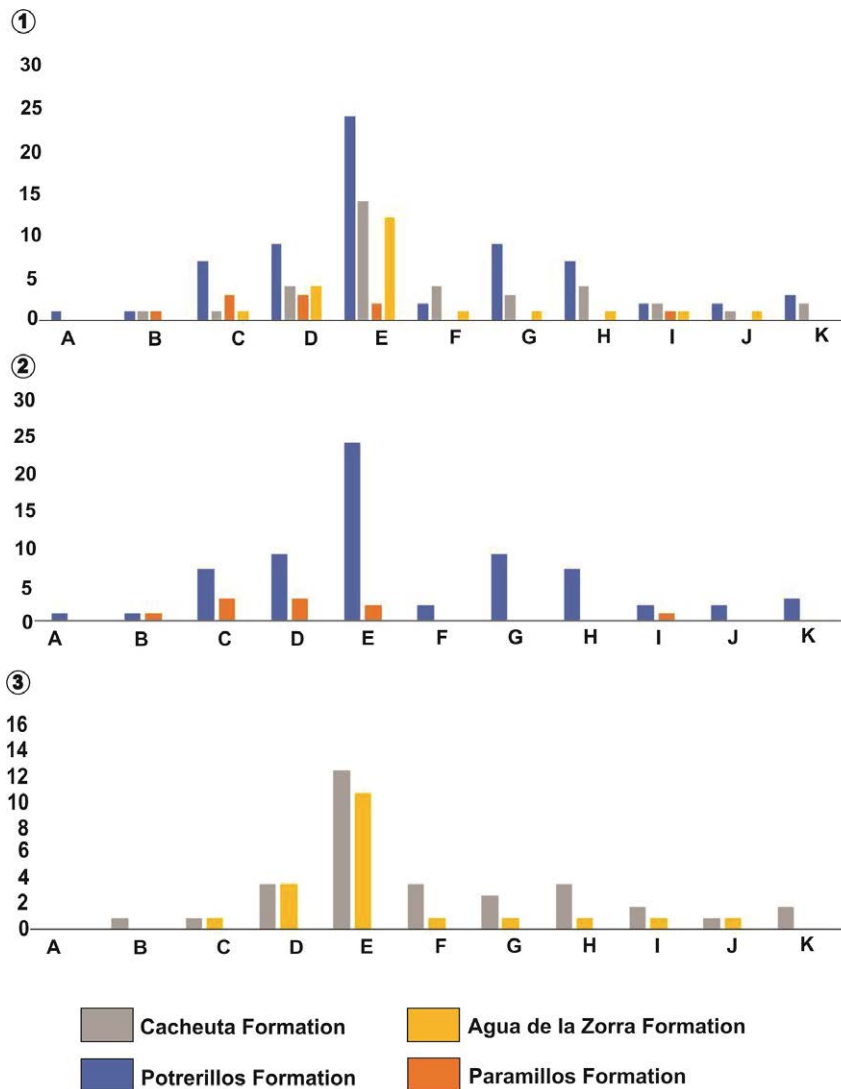


FIG. 7. 1. Number of species for taxonomic groups in the Potrerillos, Cacheuta, Paramillos and Agua de la Zorra formations. 2. Comparison between the number of species registered in the Potrerillos and Paramillos formations. 3. Comparison between the number of species registered in Cacheuta and Agua de la Zorra formations. **References.** A: Briofitas, B: Isoetales, C: Equisetales, D: Filicales, E: Pteridospermales, F: Cycadales and Cycadeoideas, G: Ginkgoales and Czekanowskiales, H: Voltziales, I: Coniferales, J: Gimnospermosidas *I.S.*, K: Gnetales.



Plants have a limited number of potential depositional sites, and plant preservation is restricted by the sediment supply rate, accommodation space, and groundwater fluctuation, therefore depend on the tectonic and climatic conditions (Behrensmeyer and Hook, 1992; Spicer, 1991; Demko *et al.*, 1998; Gastaldo *et al.*, 2005; Gastaldo and Demko, 2011). The Potrerillos and Paramillos fluvial systems show a well-developed flood plain in relatively few channel belts reflecting that the generation of accommodation space was at least equal to the rate of sediment supply. The Potrerillos megaflora was mainly composed of leaves preserved as carbonaceous compressions and/or impressions (Morel *et al.*, 2010, 2011), related to the floodplain and crevasse splay (Zamuner *et al.*, 2001; Spalletti *et al.*, 2005; Lara *et al.*, 2017). A relatively high groundwater position enhance the preservation potential of plant remains (Retallack, 1984). The abundance and diversity of the Potrerillos Formation fossil plants could reflect similar characters of the original flora, but also rely in the presence of a high position to the water table. The Paramillos Formation preserved an *in situ* fossil forest (Darwin Forest) developed on a volcanoclastic floodplain (Darwin, 1846; Brea and Artabe, 1994, 1999; Brea, 1996a, 1996b, 1997, 2000; Brea *et al.*, 2009; Ottone *et al.*, 2011). Sedimentological evidences (sediment supply and accommodation space) suggest similar condition of deposition than in the Potrerillos Formation, however the poor preservation of leaves would suggest the existence of a potential fluctuated groundwater.

The Potrerillos and Paramillos fluvial successions were influenced by volcanism that affected the southwest Gondwana margin during the Permo-Triassic. The Potrerillos Formation recorded several tuff and tuffaceous sandstones (which were used to obtain absolute age for the unit). The Paramillos Formation included tuff and tuffaceous sandstone but also basalt flows (Massabie, 1986; Ramos and Kay, 1991; Poma *et al.*, 2009, Cingolani *et al.*, 2017). Moreover, the Darwin Forest seems to be buried by a diluted, subaerial, cool and wet base surge pyroclastic flow (Brea *et al.*, 2008).

Volcanism produces disruption in the surrounding environments with negative effect in plant biodiversity, and changes in the physical-chemical conditions into sedimentary environment. In consequence, vegetation affected by volcanism (debris flows, pyroclastic flows, lahars, air-fall tephra, lava flows) suffers a catastrophic devastation (Behrensmeyer and Hook, 1992; Spicer, 1991; Dale *et al.*, 2005) and the dynamics of the fluvial and lacustrine systems are disrupted.

A volcanic explosion is considered as an ecological disruption (White and Pickett, 1985; Dale *et al.*,

2005), and the process of gradual ecological change after disturbance is named succession (Thoreau, 1993). Primary succession is the ecological restoration process in entirely denuded areas and cleansed of biota, as occur in areas affected by lava flow (Dale *et al.*, 2005). In the forest cases, the succession can may take thousands of years (*e.g.*, Grishin *et al.* 1996). Post-eruption, the soil is deeply disturbed by ash fall, pyroclastic flow, and/or lava flow (LaManna and Ugolini, 1987). The ecological succession of the vegetal communities must be adapted to the new stressed post-eruption conditions. Thus, the ecological restoration in the first stage in the succession will be very slow, show low taxonomic diversity, poor development of biomass and communities of limited structural complexity (Del Moral and Wood, 1993; Dale *et al.* 2005). The low diversity and abundance recorded at the Paramillos Formation could be related with the first stage of post-eruption ecological succession. Besides, in the first stage of the ecological succession opportunist, generalist, fast growing, r-strategist species, generally ferns, dominated the community (Spicer, 1991), a kind of herbaceous plants that require specific conditions (low energy, anoxia or disoxya) to preserve.

In contrast to fluvial systems of Potrerillos and Paramillos, the lacustrine systems represented by Cacheuta and Agua de la Zorra formations show almost the same taxonomic diversity (Table 3, Figure 7.2). The Cacheuta Formation preserve 36 species, whereas the Agua de la Zorra Formation 22 species (Table 3, Fig. 6), both in deep lacustrine systems. Despite of the taxonomic diversity is similar, the number of genera in different taxa are quite variable (Fig. 7.1). The Cacheuta taphoflora is dominated by different species of *Dicroidium* with subordinate ferns (*Cladophlebis*) (Table 3) and the Agua de la Zorra taphoflora is dominated by fronds of Umkomasiaceae (*Dicroidium* and *Xylopteris*), ferns as (*Cladophlebis*) and Equisetales (*Neocalamites*) (Table 2, Figure 7.3).

Both Cacheuta and Agua de la Zorra lacustrine systems are characterized by the development of deep offshore facies, with anoxic bottom and delta progradation in the lacustrine facies (Spalletti *et al.*, 2005; Ottone *et al.*, 2011, Pedernera *et al.*, 2016, 2017). Furthermore, both succession recorded volcanic rocks, tuff and tuffaceous sandstones levels in Cacheuta and tuff and tuffaceous sandstone, sills and basalt flows (which were used to obtain absolute age for the unit) in Agua de la Zorra (Massabie, 1986; Ramos and Kay, 1991, Linares 2007). The peperitic beds interbedded in the Agua de la Zorra lacustrine facies, currently interpreted as basaltic lava flow episodic incursion in the water body is a main difference between both secessions (Ottone *et al.*, 2011).

In both Cacheuta and Agua de la Zorra successions, the presence of a high water table that enhanced the preservation potential of vegetal elements is evident. Both lacustrine successions are dominated by laminated bituminous mudrocks related to offshore facies, and include carbonaceous compressions of disarticulated, isolated, fragmented simple or compound leaves (Morel, 1994, 2010, 2011; Ottone *et al.*, 2011; Pedrera *et al.*, 2016). When more distal is the Cacheuta and Agua de la Zorra delta facies, more variable is the size, and higher the articulation degree, density package, and preferential orientation of vegetal remains (Pedrera *et al.*, 2016). In the case of Agua de la Zorra, the main specimens recovered in these facies are related to Umkomasiaceae compound leaf remains referred to *Xylopteris* (Figure 8). Lacustrine anoxic bottoms are environments where the rate of decay and/or biodegradation of plant remains are significantly lower than that in the oxygenated environments. Thus, a lacustrine anoxic bottom enhances the preservation of organic plant remains (Behrensmeier and Hook, 1992; Spicer, 1991; Gastaldo and Demcko, 2011). However, the amount of plant remains that arrived to the lake offshore by flotation or dispersion are less numerous than those preserved in areas closer to the coast or with deltaic influence (Spicer, 1991). Therefore, the relative abundance of plant remains in offshore facies does not reflect the diversity of the plant paleocommunities associated with the lacustrine systems. In contrast, in the oxygenated delta and marginal palustrine environments, where there is a consequently higher rate of decay, the preservation potential would be linked to factors as the rate of sediment supply or the water table fluctuation (Retallack 1984; Behrensmeier and Hook, 1992; Spicer, 1991; Gastaldo and Demcko, 2011).

Lacustrine systems influenced by volcanism present increase in the rate of sediment supply linked with unusual ash fall supply, which also triggers changes in the original chemical composition of lake waters (Behrensmeier and Hook, 1992; Spicer, 1991). Ash fall also plays a major role in plant preservation; the ash layers restrict oxygen and limit the action of detritivores, that are buried rapidly, preserving delicate plant remains (Burnham and Spicer, 1986; Spicer, 1991).

The Cacheuta Formation includes tuff levels and the Agua de la Zorra Formation also includes peperitic basalts (Ottone *et al.*, 2011). The peperite levels resulted by interaction between lava and water/sediment, the basalts disturbed the sediments of the bottom of the lake but sediments and plant remains entombed therein remained termally unaffected (Ottone *et al.*, 2011). The evidences of alteration produced by temperature of the basalts in the sediments

and plant remains (both micro- and macro-remains) are not present in all the sections studied. Therefore, the shift in diversity in the taphofloras of the Cacheuta and Agua de la Zorra taphoflora can be mainly related to ecological differences than variations in the taphonomic processes in each of the lake systems (Table 3).

## 6. Conclusions

The systematic study of a taphoflora recovered from the Agua de la Zorra includes 21 taxa, 12 of them referred in the unit by the first time (one species of the fern leaf *Cladophlebis*; two species of *Dicroidium*, two species of *Johnstonia*, and two species of *Zuberia*, all Umkomasiaceae leaves; the cycadalean *Taeniopteris*; the ginkgoalean *Sphenobaiera*; conifers as *Heidiphyllum*, and *Rissikia*; together with other gymnosperms as *Linguifolium*, strobils and ovules/seeds).

The comparison of the chronostratigraphically equivalent Middle-Upper Triassic taphofloras influenced by the active volcanism from southwest of Gondwana margin, shows clear differences. The Paramillos and Potrerillos taphoflora, both related to fluvial environments, are markedly different in taxonomic diversity, due mainly to preservation potential linked to groundwater position that in Potrerillos was high enhancing the plant preservation and in Paramillos was fluctuated resulted in a poor preservation of leaves. Moreover, the low diversity and abundance recorded in the beginning of the Paramillos post-eruption, ecological succession can explain the scarcity of the taphoflora. The Cacheuta and Agua de la Zorra taphoflora show a similar taxonomic diversity in spite of the Agua de la Zorra lacustrine systems are affected by basaltic lava flow episodic incursions in the water body. These disturbed basalts unaffected sediments and plant remains entombed in the bottom of the lake. The differences are an effect of variation in the ecological paleocommunities.

## Acknowledgements

The authors wish to thanks to E.L. Bustos Escalona and C. Sancho for they support during the fieldstrips. We thanks to A.B. Arcucci, María de los Angeles Gómez and E. Previterra for the critical reading of the manuscript and they constructive comments. We are also grateful to M. Brea and J. Bodnar for their critical review of the submitted manuscript. This research was supported by grants PICT-2013-0805 (Agencia Nacional de Promoción Científica y Tecnológica) and PIP 112-201501-00613-CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas). This is the contribution R-278 of the Instituto de Estudios Andinos Don Pablo Groeber.

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