

PLANT TAPHONOMY IN A LAKE AFFECTED BY VOLCANISM (AGUA DE LA ZORRA FORMATION, UPPER TRIASSIC) MENDOZA, ARGENTINA

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ABSTRACT: Volcanic eruptions have an impact on the paleoecology of plant communities and their preservation in the fossil record. The aim of this contribution is to evaluate the influence of volcanism on plant preservation in lacustrine settings via systematic sampling and chemical analyses of fossil plants in the Upper Triassic Agua de la Zorra Formation, of the Argentinian Cuyana Basin. Plant remains are not uniformly preserved throughout the Agua de la Zorra Formation and their stratigraphic distribution reflects the original spatial pattern of the plant communities. SEM-EDX analyses was used to demonstrate how volcanism affected diagenesis of the plant remains. Eight taphonomic modes were determined from biostratinomic analysis, and three preservational modes from the chemical features observed in the SEM-EDX spectra. The three preservation modes recognized by SEM-EDX analysis are more likely linked to diagenesis and are not equivalent to the taphonomic modes described based on the biostratinomic features. The Agua de la Zorra paleolake preferentially preserved plant material because of anoxic conditions in deeper parts of the lake, and a high sedimentation rate in proximal near-shore facies. The plant remains are most abundant in sandy facies deposited by high-energy flows but there is no evidence that these flows were pyroclastic nor that the plant remains were generated by volcanic trauma.

INTRODUCTION

A plant fossil assemblage, or taphoflora, is defined as an accumulation of plant parts derived from one or several organisms, deposited and entombed under the same sedimentation conditions (Spicer 1991; Greenwood 1991; Behrensmeier and Hook 1992). These processes depend on the shape of the remains and their hydrodynamic properties, the proximity of the plant communities to the depositional systems, plus a variety of factors related to the hydrological characteristics of the depositional system (Ferguson 1985; Spicer 1991). Understanding the taphonomic processes that generate particular plant fossil assemblages allows the spatial and temporal reconstruction of ancient communities (Ferguson 1985; Spicer 1991; Martín-Closas and Gómez 2004).

Volcanic eruptions have an impact on the environment and ecosystem dynamics, especially on plant communities. Volcanic events can affect the paleoecology of plant communities and their preservation in the fossil record. From an ecological view, it is possible to analyze how volcanic activity affected changes in plant communities (Wood and Del Moral 1988; Del Moral and Wood 1988, 1993; Del Moral and Grishin 1999; Swanson et al. 2013; Dale et al. 2005; Lindermeier et al. 2010). Also, the taphonomic processes and plant preservation potential are modified by how the volcanic activity alters the sedimentary environments (Spicer 1991; Behrensmeier and Hook 1992; Burnham 1993; Dale et al. 2005; Payne and Egan 2019). The incorporation of taphonomic data is essential to carry out paleoenvironmental and paleoecological reconstructions.

Lake deposits are commonly rich in different fossil remains of both plants and animals (Behrensmeier and Hook 1992). Lake geometry plays an essential role in determining the vegetation and the composition and structure of the resultant plant fossil assemblages (Spicer 1991). Deltaic-

lacustrine systems have unique features that allow the preservation of plant remains with characteristics typical of each subenvironment (Behrensmeier and Hook 1992).

Lacustrine facies models tend to differ greatly. The physical, chemical, and biological processes involved in basin-fill depend on the relationship between the accommodation rate and sediment + water supply. Ancient and modern lakes are classified into three types of lake basins: overfilled, balanced-fill, or underfilled (Carroll and Bohacs 1999; Bohacs et al. 2000; Cohen 2003; Renaut et al. 2010).

The chemometric approach conducted using a Scanning Electron Microscope (SEM) in combination with energy-dispersive X-ray spectrometry (EDX) has proved to be useful in providing diagenetic information related to different modes of preservation of fossil remains (e.g., Previtera et al. 2013; Benavente et al. 2014; Monferran et al. 2018; Previtera 2019). Although the results provided by the standard procedure are qualitative and semiquantitative, SEM-EDX allows the determination of major and minor components of different materials. Therefore applying a chemometric approach to the plant remains recovered from the Agua de la Zorra Formation could be useful to understand the diagenetic processes and to clarify whether volcanic processes affected the diagenetic chemical pathways. Here we attempt to evaluate to what degree fossil preservation is affected by volcanism in the lacustrine Agua de la Zorra Formation by (1) description of the taphonomic processes leading to megafossil plant accumulations; (2) reconstruction of the taphonomic pathways of the taphoflora to reconstruct the plant paleocommunities developed in the margins of the Agua de la Zorra paleolake; and (3) conducting a chemometric study of the plant remains to determine whether volcanism affected the diagenetic processes.

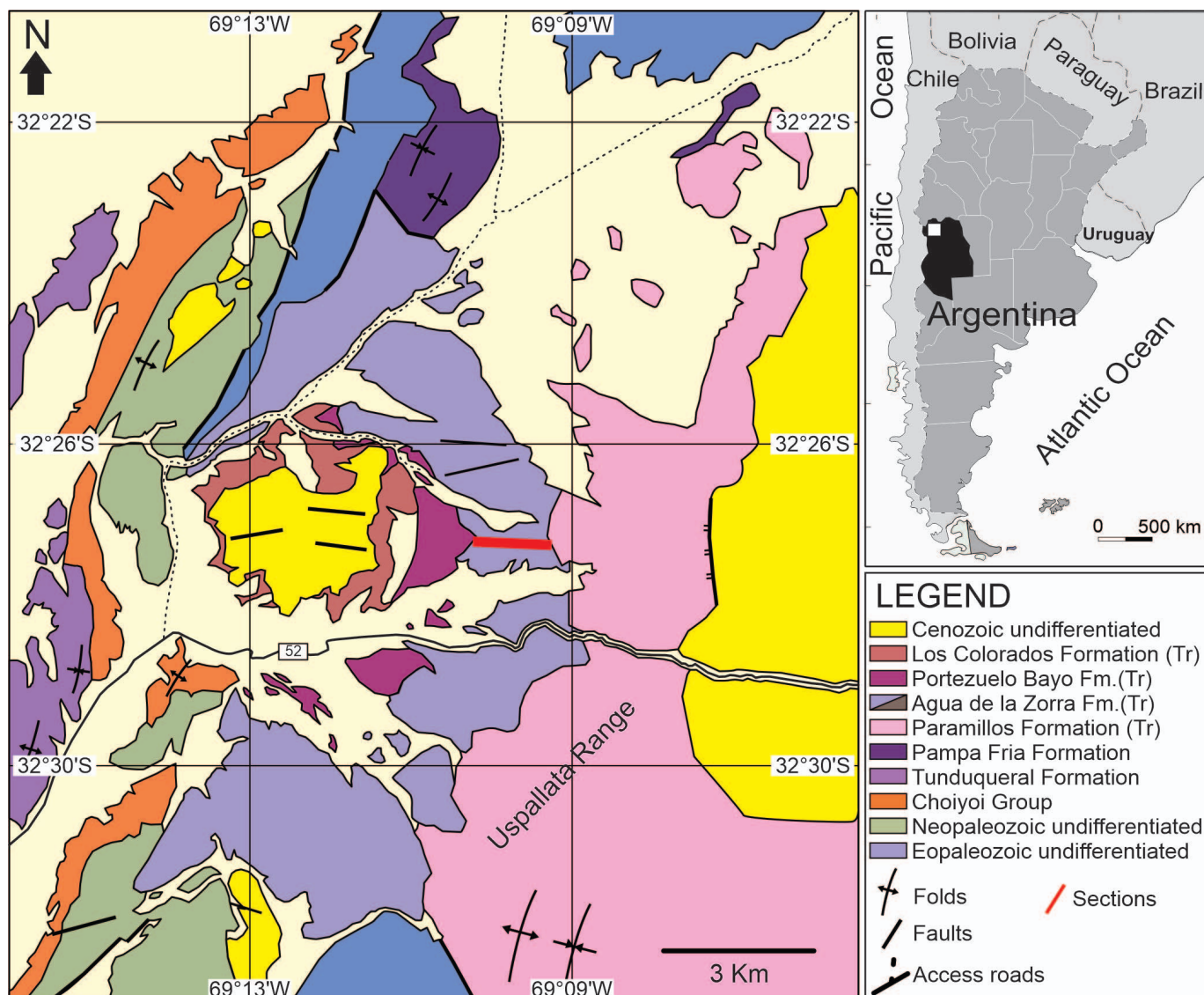


FIG. 1.—Geological map of the Paramillos de Uspallata locality, Cuyana Basin, Mendoza Province, Argentina. Modified from Pedernera et al. (2019).

GEOLOGICAL SETTING

During the Triassic, along the Gondwana western margin, long-term sediment accumulation was restricted to rift basins delimited by faults, developed during the break-up of the Pangean supercontinent (Uliana and Biddle 1988). The Cuyana Basin is one of the most extensive basins of the Center-West of Argentina. Sequences inside these basins are entirely continental and include, mainly, alluvial, river and lake deposits (Ramos and Kay 1991; Kokogian et al. 2001). In the North of Mendoza province, at the Paramillos de Uspallata locality near the town of Uspallata, outcropping sedimentary rocks are referred to the Cacheuta Group by Harrington (1971) and include four formations (from base to top) Paramillos, Agua de la Zorra, Portezuelo Bayo, and Los Colorados; all assigned to the Triassic Period (Fig. 1). These formations represent a continental succession that includes fluvial and deltaic-lacustrine paleoenvironments.

The earliest infill in this sub-basin of the Cuyana Basin corresponds to the Paramillos Formation. This unit is volcanoclastic, characterized by a conglomerate, and lithic plus tuffaceous sandstones interbedded with shale and tuff. 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 on the plant paleocommunities recorded in this area. Recently, Cingolani et al. (2017) analyzed detrital zircons via the LA-ICP-MS U-Pb methodology and obtained an age of 239.6 ± 1.3 Ma (Ladinian). Overlying the Paramillos Formation is the Agua de la Zorra Formation. This unit is dominated by bituminous shale and marl with subordinate interbedded fine-grained sandstone and mudstone. Within the formation, peperitic olivine basalt is interbedded with lacustrine-deltaic sediments (Harrington 1971; Brea et al. 1999; Ottone et al. 2011). A Ladinian–Carnian age (K/Ar ages of 235 ± 5 Ma. and 240 ± 10 Ma.) was obtained from these basalts (Massabie 1986; Linares 2007). The sediments of the overlying Portezuelo Bayo Formation are dominated by fine- to medium-grained tuffaceous sandstones with interbedded tuff, conglomerate, and shale (Harrington 1971; Stipanovic and Morel 2002a). The Portezuelo Bayo Formation is interpreted as a sinuous fluvial system dominated by flood plain deposits. The Portezuelo Bayo Formation has not been dated. The Los Colorados Formation overlies the Portezuelo Bayo Formation and is characterized by sandstone with

interbedded conglomerate, and is referred to the Upper Triassic (Harrington 1971; Stipanovic and Morel 2002b).

The Agua de la Zorra Formation is interpreted as a deltaic-lacustrine system with episodic incursions of lava flows into an aquatic environment (Cortés et al. 1997; Ottone et al. 2011). It includes two facies association AZ-A and AZ-B (Table 1) (Pedernera et al. 2019). The AZ-A facies association presents dark greenish-gray, fine-grained, well-sorted massive sandstone (Sm), with the sandstones in contact with basalts showing various types of alteration, as 5 mm diameter vesicles and carbonate cemented nodules; light brownish-gray massive muddy siltstone (Fm); moderate-light-gray coarse-grained, well-sorted ripple cross-stratified sandstone (Sr), and pebbly trough cross-stratified sandstone (St), interpreted as representing a delta associated with mouth bars at the delta front (Pedernera et al. 2019). Facies association AZ-B is dominated by black, olive black, greenish-red, and greenish-black finely laminated mudstone (Fl); light brownish-gray massive muddy siltstone (Fm), horizontally laminated fine to coarse-grained well-sorted sandstone (Sh), and massive white tuff (Tf) interpreted as prodelta to offshore lacustrine deposits (Pedernera et al. 2019).

The Agua de la Zorra paleoflora is diverse and includes vegetative parts (fronds and simple leaves) of Equisetales (*Neocalamites*), ferns (*Cladophlebis*), Ummosiales (*Dicroidium*, *Jhonstonia*, *Xylopteris*, and *Zuberia*), Ginkgoales (*Sphenobaiera*), Voltziales (*Heidiphyllum*), Coniferales (*Rissikia*) and Gymnosperms of uncertain affinity (*Linguifolium*), including reproductive structures (strobili, ovules/seeds) (e.g., *Cordaicarpus*) (Ottone et al. 2011; Pedernera et al. 2019). Freshwater invertebrates, including conchostracans, have been described in the same lacustrine facies (Bustos Escalona et al. 2019).

MATERIALS AND METHODS

Collection of plant fossils was undertaken in several field trips between 2015 and 2017, with strict stratigraphic control (Fig. 2). Remains recovered included mega, and meso-fossil plant remains collected systematically from consecutive bedding planes every 20 cm apart through two vertical exposures in the Paramillos de Uspallata area. During collection of the material, its taphonomic attributes were recorded *in situ*.

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 name BAFC-Pb.

Taphonomic Attributes

The taphonomic attributes were used to identify and characterize the plant taphonomic modes, following the methodology proposed by Behrensmeyer and Hook (1992). The selection of the taphonomic attributes was made following the guidelines of Ferguson (1985, 2005), Spicer (1989, 1991), Gastaldo (1992), Martín-Closas and Gómez (2004) and Gastaldo et al. (2005). The selected attributes were separated into two groups: observed qualitative attributes and measured semiquantitative attributes. The qualitative attributes observed were: type of plant remnant, associated materials, and type of preservation; whereas the semiquantitative attributes measured were: articulation degree, relative abundance, *post mortem* features such as compaction and breakage; spatial pattern characteristics, such as orientation and cross-cutting; and finally, biofabric features, which include packing, sorting, and density. Each semiquantitative attribute was divided into the possible states or categories. For each category, a number between 0 and 4 was used. The values used for each category of taphonomic attributes are summarized in Table 2.

SEM-EDX Analyses

Seven samples were selected for microscopic analysis in order to evaluate the volcanic influence on the diagenetic features. These samples, identified as S1 to S7, were obtained from different stratigraphic levels with different types of volcanic influence (Fig. 2).

The samples were carbon-coated before the examination and were mounted on double-sided carbon adhesive tape on aluminum stubs. Micrographs were obtained using a scanning electron microscope (Zeiss LEO 1450VP) at the Laboratorio de Microscopía Electrónica y Microanálisis (LabMEM) of the Universidad Nacional de San Luis (UNSL). Spectrochemical data were obtained using scanning electron microscopy (SEM) in combination with energy-dispersive X-ray spectrometry (EDAX Genesis 2000). For EDX analyses, a live acquisition time of 50 seconds was used. The energy of the excitation beam was 15 keV, and the working distance 15 mm. Point measurements by EDX were used for monitoring trends in elemental distributions. EDX measurements were performed in two selected sample areas: the fossils and the host rock.

PLANT TAPHONOMY

We identified and described eight taphonomic modes that were named with the prefix AZ followed by a number between 1 to 8. In Table 3, the qualitative attributes are summarized, and the taphonomic modes and the features that characterize each one of them are shown in Figure 3. The stratigraphic distribution of the different taphonomic modes is displayed in Figure 2.

Mode AZ-1

This mode (Fig. 4A, 4B) is characterized by small plant fragments preserved as carbonaceous compressions or impressions, isolated and dispersed, highly compacted and with a high degree of breakage. The edges of the remains have irregular and angular breaks. The materials do not display preferential orientation and are concordant to bed lamination. The relative abundance of the remains is low to moderate. The biofabric is characterized by dispersed to loosely packed, poorly to loosely sorted, and of low to moderate density. The preservation features of the remains render taxonomic assignment difficult. The plant remains of this taphonomic mode were registered in the facies association interpreted as the offshore lake (Fl facies of AZ-B facies association), and usually are commonly associated with fish scales, and Spinicaudata remains.

Interpretation.—The remains included in the mode AZ-1 are interpreted as allochthonous elements transported by fluvial processes from upstream regions of the basin. The *post mortem* and biofabric features suggest the plant material was part of the leaf litter from forest soils (Spicer 1989) produced by natural abscission of leaves during seasonal non-favorable periods (Ferguson 1985). An advanced state of decay can be interpreted from the high degree of rupture of the material during transport in traction flow, before the remains were introduced into the system (Ferguson 1985; Spicer 1975, 1981). The small-sized remains can be transported long distances (Ferguson 1985; Greenwood 1991). Probably, the remains were also broken by the action of waves within the lake before they were deposited on the lake bottom. However, the damaged edges and the degree of decomposition affect the flotation potential of the remains, and possibly the buoyancy time of these remains was short.

Mode AZ-2

Taphonomic mode AZ-2 (Fig. 4C, 4D) includes simple leaves and ovules/seeds preserved as carbonaceous compressions and impressions. The remains are isolated and dispersed with low relative abundance high

TABLE 1.—Facies associations and their characteristics defined for the Agua de la Zorra Formation (Triassic) at Uspallata. Modified from Pedernera et al. (2019).

Facies association (FA)	Facies	Sedimentary structures	Bed geometry	Vertical and lateral relations	Fossil content	Processes	FA interpretation
AZ-A	Cemented massive sandstone (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	Delta associated with mouth bars at the delta front
	Massive siltstone (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	
	Ripple cross sandstone (St)	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	
AZ-B	Trough cross sandstone (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	
	Finely laminated mudstone (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		Prodelta to offshore lacustrine
	Massive siltstone (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	
	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	

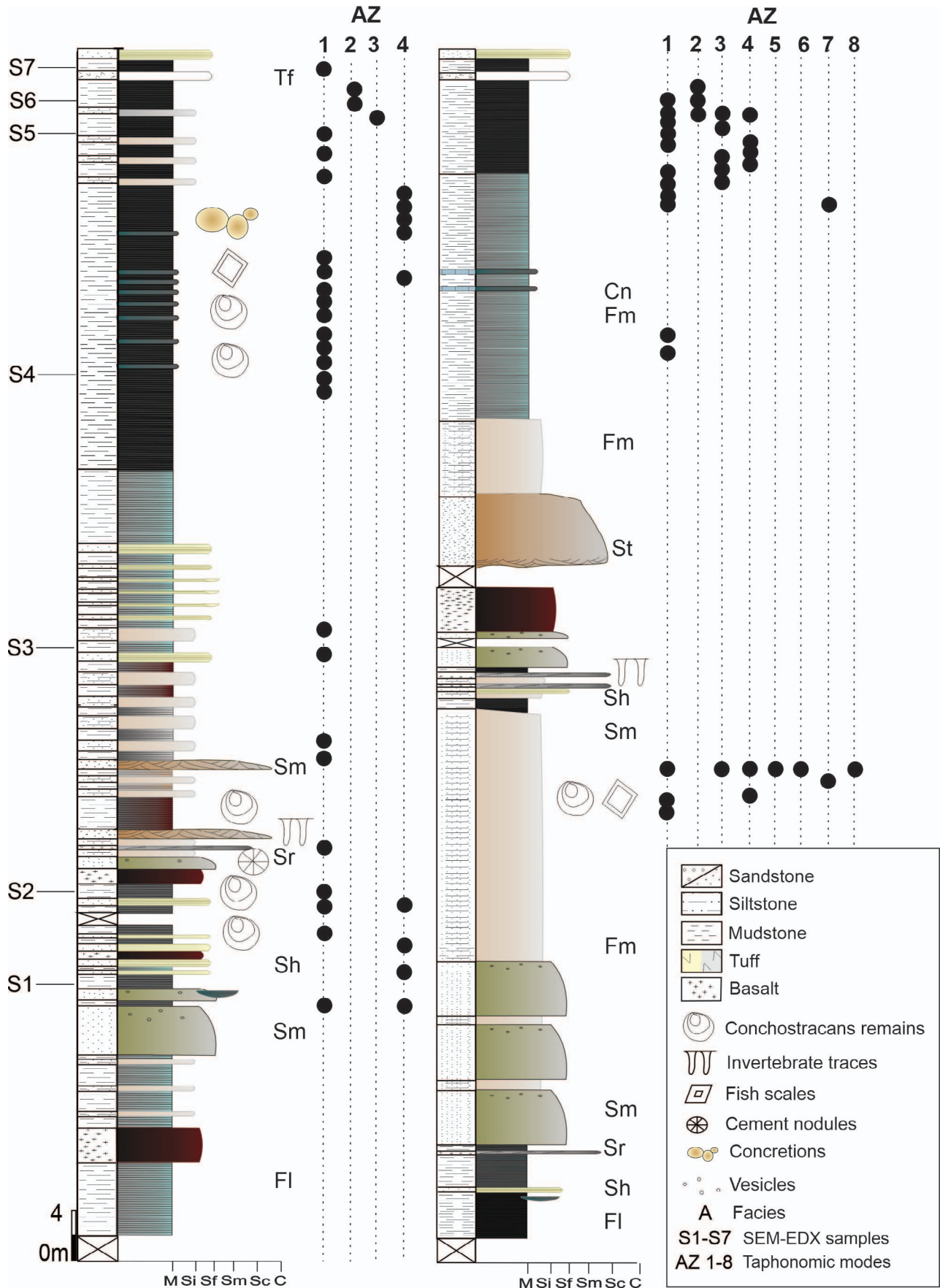


TABLE 2.—*Taphonomic attributes and proposed states.*

Semiquantitative taphonomic attributes	Possible states
Remains	Type of remains recorded
Taxa	Taxa recorded
Association of material	Associated material recorded
Mode of fossilization	Carbonaceous compression, impression, mummification, silicification, permineralization, preservation of hard part.
Degree of articulation	Isolated and dispersed (0) Associated but dispersed (1) Disarticulated but associated (2) Articulated (3)
Relative abundance	Low (0) Low to moderate (1) Moderate (2) Moderate to high (3) High (4)
Postmortem modification	Absence (0)
Compaction	Low (1)
Breakage	Moderate (2) Moderate to High (3) High (4)
Spatial pattern	
Orientation	Without preferential orientation (0) Preferential orientation (1)
Cross-cutting	Concordant (0) Discordant (1)
Biofabric	
Packing	Dispersed (0) Dispersed to loosely packed (1) Loosely packed (2) Loosely to densely packed (3) Densely packed (4)
Sorting	Poorly sorted (0) Poorly to loosely sorted (1) Loosely sorted (2) Loosely to well sorted (3) Well sorted (4)
Density	Low (0) Low to moderate (1) Moderate (2) Moderate to high (3) High (4)
Host sediment	Claystone (0) Fine sandstone (1) Medium sandstone (2) Coarse sandstone (3) Conglomerate (4)

level of compaction, and low level of breakage. The materials do not exhibit preferential orientation and are concordant to bed lamination. The taxa identified are *Heidiphyllum*, *Linguifolium*, and ovules/seeds referred to the genus *Cordaicarpus*. The remains preserved in this taphonomic mode were registered in the F1 facies of AZ-B facies association interpreted as the offshore lake.

Interpretation.—Mode AZ-2 includes remains interpreted as allochthonous elements transported by aerial dispersion. The leaves associated

with this mode were referred to the genera *Heidiphyllum* and *Linguifolium*, and the ovules/seeds were referred to the genus *Cordaicarpus*. Based on their usual preservation in the form of accumulations of complete leaves, *Heidiphyllum* and *Linguifolium* are considered to be seasonally deciduous trees (Artabe et al. 2001; Bomfleur et al. 2011, 2013). Although the production of deciduous leaves is greater than the production of perennial leaves, the preservation potential of deciduous plants is lower (see Ferguson 1985; Spicer 1991). These accumulations are interpreted as leaves distributed by the action of wind (Ferguson 1985; Spicer 1991).

The linear and oblanceolate shape (such as *Heidiphyllum* and *Linguifolium* leaves) and the membranous wing surrounding the inner body of *Cordaicarpus* ovules/seeds are more likely to be transported by aerial dispersion than by water. The morphological features of the materials limited breakage and the absence of other *post mortem* modifications support wind transport to the lake (Spicer 1991). Elements can spend several days, even months, floating on the surface of a lake, and be transported offshore until their deposition on the bottom (Spicer 1981, 1991; Spicer and Wolfe 1987; Gastaldo 1992).

Mode AZ-3

This mode (Fig. 4E) includes simple leaves and axis fragments preserved as carbonaceous compressions and impressions. Remains are isolated dispersed, and have low relative abundance. The materials exhibit a high degree of compaction, and the degree of breakage is moderate to high. The remains show no signs of preferential orientation and are concordant with stratification. The materials are scattered, poorly sorted, and present in low density. The plants preserved can be associated with fish scales. The taxa recorded in association with this mode are *Neocalamites*, *Taeniopteris*, and *Sphenobaiera*. The plant remains of this taphonomic mode were registered in the facies association interpreted as the offshore lake environment (F1, Facies association AZ-B).

Interpretation.—The remains of the mode AZ-3 are interpreted as allochthonous and parautochthonous materials. The degree of breakage observed is linked to transportation by traction currents. The specimens referred to *Taeniopteris* and *Sphenobaiera* are interpreted as parautochthonous and allochthonous materials due to their arboreal and shrubby habits in forests around the fluvial-lacustrine system. On the other hand, the *Neocalamites* remains were considered parautochthonous as the *Neocalamites* communities would have developed in the margins of the rivers and lake (Anderson and Anderson 2018). In general, the edge of the leaf lamina has irregularities and angular breaks as the product of the transport in water flow; however, occasionally, we observed rounded and regular marks of a kind that can have been attributed to predatory insect-plant interactions (Labandeira et al. 2007).

Mode AZ-4

This mode (Fig. 4F–4H) includes axis and fronds preserved as compressions, and impressions. The remains are articulated, and the relative abundance of the materials is low to moderate. Also, the elements present a high degree of compaction, and a moderate degree of breakage. They lack preferential orientation and are concordant to bed lamination. The remains are characterized by being dispersed to loosely packed, poorly sorted, and with low to moderate density. Occasionally, they are associated with fish scales, and spinicaudatan remains. The taxa referred to this taphonomic mode include *Neocalamites* sp., *Cladophlebis* spp., *Dicroi-*

Fig. 2.—Detailed stratigraphic sections of Agua de la Zorra Formation at the Paramillos de Uspallata with distribution of taphonomic modes and stratigraphic position of samples analyzed by SEM-EDX. Colors in the sections represent the colors of each facies, following the Munsell color chart. The black circles represent the stratigraphic location of samples assigned to each taphonomic modes and their distribution across the sections.

TABLE 3.—Qualitative taphonomic attributes of each taphonomic mode.

Taphonomic modes	Qualitative taphonomic attributes			
	Type of remains	Taxa	Associated materials	Mode of fossilization
AZ-1	Debris	Indetermined	Fish scales and spinicaudata	Carbonaceous compressions and impressions
AZ-2	Simple leaves and reproductive structures	<i>Heidiphyllum</i> , <i>Linguifolium</i> y <i>Cordaicarpus</i>	-	Carbonaceous compressions and impressions
AZ-3	Simple leaves and axis	<i>Taeniopteris</i> , <i>Sphenobaiera</i> y <i>Neocalamites</i>	Fish scales and spinicaudata	Carbonaceous compressions and impressions
AZ-4	Fronds, axis and reproductive structures	<i>Cladophlebis</i> , <i>Dicroidium</i> , <i>Johnstonia</i> , <i>Xylopteris</i> , <i>Zuberia</i> y <i>Neocalamites</i>	Fish scales and spinicaudata	Carbonaceous compressions and impressions
AZ-5	Fronds	<i>Xylopteris</i> , <i>Dicroidium</i> y <i>Cladophlebis?</i>	-	Compressions and impressions
AZ-6	Axis	<i>Neocalamites</i>	-	Mold-cast
AZ-7	Fronds	<i>Zuberia</i>	-	Compressions and impressions
AZ-8	Fronds	<i>Xylopteris</i>	-	Compressions and impressions

dium spp., *Johnstonia* spp., *Xylopteris* spp., and *Zuberia* spp. The plant remains of this taphonomic mode were recorded in the F1 facies of AZ-B facies association interpreted as the offshore lake environment.

Interpretation.—The remains referred to as taphonomic mode AZ-4 are interpreted as allochthonous and parautochthonous materials. The *post*

mortem attributes observed denote transport by traction currents. However, fronds and axes assigned to this mode exhibit less fragmentation than the remains recorded in mode AZ-3. This suggests a lower transport distance than for the AZ-3 remains (Ferguson 1985; Spicer 1991; Martín-Closas and Gómez 2004).

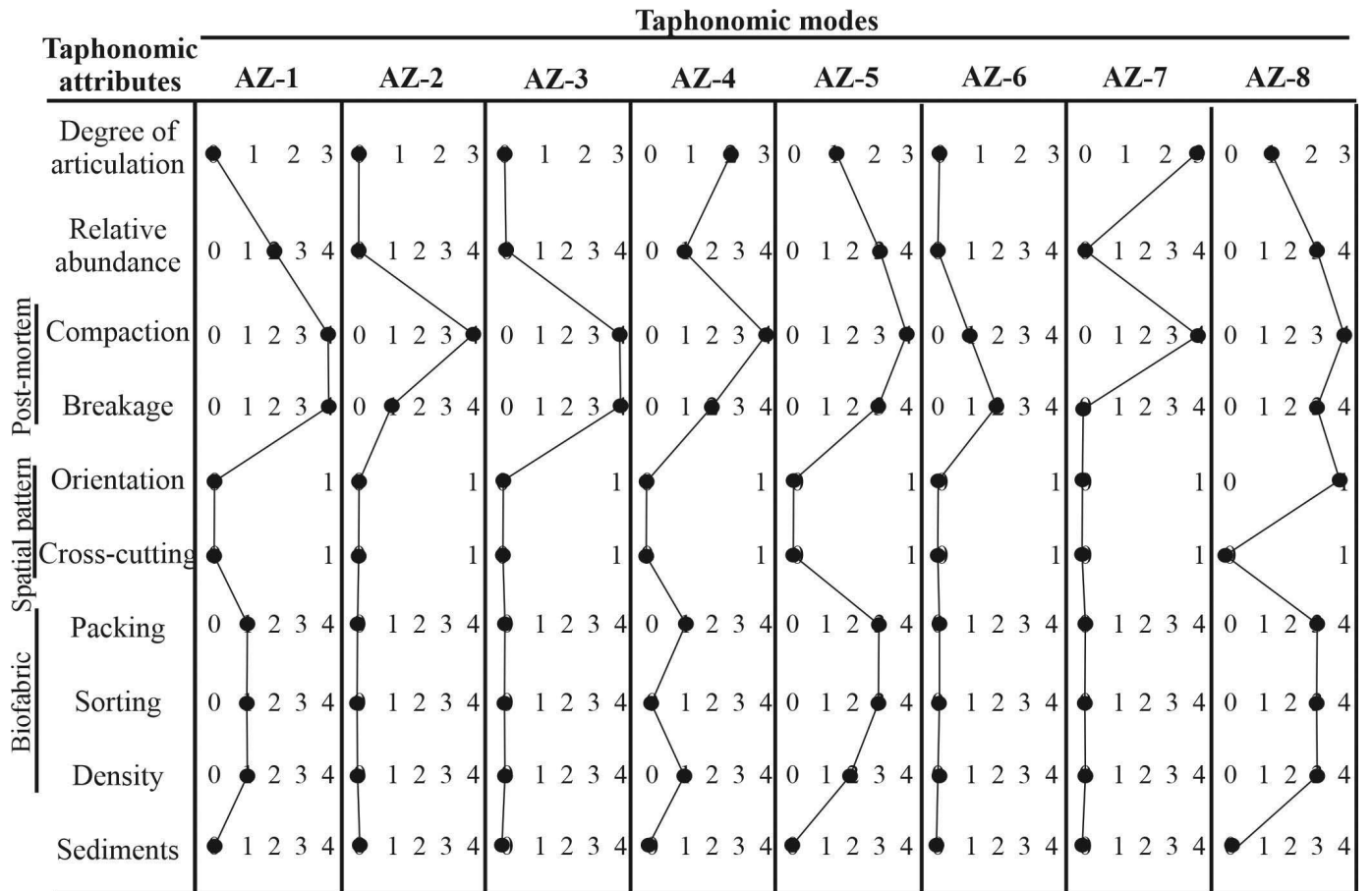


FIG. 3.—Characterization of semi-quantitative taphonomic attributes in each of the taphonomic modes identified in the Agua de la Zorra Formation.



Mode AZ-5

This mode (Fig. 5A) includes frond fragments, and possible reproductive structures (cupules?) preserved as impressions and compressions. The degree of articulation varies between associated, but dispersed, material and disarticulated but associated remains. The relative abundance of remains is moderate to high and with a high degree of compaction, and fragmentation is moderate to high. The materials do not display preferential orientation, and the remains are concordant with stratification. The remains are loosely to densely packed, poorly sorted to well-sorted, and occur in moderate density. The taxa represented in this taphonomic mode mostly belong to Umkomasiales, and the genus *Xylopteris* is the most abundant taxon. This taphonomic mode was registered in Fm facies from the facies association AZ-A.

Interpretation.—The remains of the mode AZ-5 were interpreted as allochthonous elements. The biofabric attributes, packing, sorting, and density suggest that materials were deposited abruptly during a flood event (Renaut et al. 2010). The hydrodynamic characteristics of different leaf morphologies result in sorting in the distribution of leaves inside the lacustrine system. Leaves that are linear and narrow in shape are usually deposited in the proximal areas of lacustrine systems (e.g., prodelta) (Spicer 1989, 1991). The dominance of *Xylopteris* remains in the AZ-5 mode indicate that deposition of these materials occurred in proximal parts of the lower delta.

Mode AZ-6

This mode is characterized by an axis fragment referred to the genus *Neocalamites* (Fig. 5B), preserved as a mold-cast in three dimensions, isolated and dispersed, with relatively low abundance. The remains show low compaction and moderate breakage. The remains lack preferential orientation and lie concordant to beds. The biofabric features include those of dispersed packing, poor sorting, and low density. Remains referred to the mode AZ-6 were registered in Fm facies from facies association AZ-A.

Interpretation.—AZ-6 mode includes exclusively an axis fragment referred to *Neocalamites* interpreted as a parautochthonous element, transported a short distance by traction. The specimen is preserved as a cast-mold in three dimensions. The sediment that fills the axis fragment is the same as the host rock, suggesting that the fill of the axis cavity was synchronous with entombment of the axis (Spicer 1991). High sedimentation rate could explain the taphonomic features observed in this taphonomic mode. This material was deposited in the lower delta.

Mode AZ-7

The mode AZ-7 (Fig. 5C) includes large frond fragments referred to *Zuberia zuberi* preserved as compressions or impressions. The specimens are articulated and with low relative abundance. They present a high degree of compaction and breakage. These materials do not show preferential orientation and are concordant to bed stratification. The remains are dispersed, poorly sorted, and have low density. AZ-7 materials were registered in Fl facies.

Interpretation.—The remains included in mode AZ-7 were interpreted as allochthonous elements, produced by trauma. Trauma can be recognized in the fossil record by the combination of high articulation and low breakage (Ferguson 1985; Martín-Closas and Gómez 2004). Trauma introduces fresh material into the system. The fresh material has a higher resistance to transport than does partially degraded material, and consequently, the remains have less damage and higher articulation (Ferguson 1985). Remains of taphonomic mode AZ-7 were deposited in offshore facies (Fl, facies association AZ-B).

Mode AZ-8

This mode (Fig. 5D, 5E) includes frond fragments preserved as compressions or impressions. The remains are associated but dispersed; the relative abundance is moderate to high. Compaction is high, and breakage moderate to high. The remains are preferentially oriented and concordant to the bed lamination. The remains are loosely to densely packed and loosely to well-sorted (by shape; linear forms, as *Xylopteris*, dominate) and abundant. This taphonomic mode was registered in Fm facies from the facies association AZ-A.

Interpretation.—The taphonomic attributes observed are very similar to those that characterize mode AZ-5. However, AZ-8 is distinguished by the material having a preferred orientation. The biofabric attributes, packing, sorting, and density, observed in this mode suggest that allochthonous materials were deposited suddenly by a flow event (Renaut et al. 2010). The long and narrow planar leaf laminae remains (as is the case of *Xylopteris*) are more easily oriented by the effects of water flow (Spicer 1991). The evidence of current flow in the preferential orientation in the AZ-8 remains suggests that the deposition and entombment occurred in proximal parts of the delta.

SEM-EDX ANALYSES RESULTS

Samples selected for chemical analysis were collected from Fl facies from different stratigraphic levels. Three groups were identified based on chemistry observed in the spectra obtained by SEM-EDX analysis (Fig. 6). Group 1 (G1) includes the samples S1, S4, and S7. The samples were taken from different horizons near the base and near the top of the section. The spectra of this group are similar for the fossil and the host rock. Both fossil and host rock spectra display a strong dominance of Si and O and low concentration of C, and a high abundance of Na, Mg, Al (Fig. 6A, 6B).

Group 2 (G2) includes S3 and S5 samples, located in the middle and upper part of the section. The spectra of this group are characterized by a difference in composition the fossils and the host rock. The fossil EDX spectra show similar high-intensity peaks of C and O, in contrast with the host rock spectra that show significant differences between C and O peaks. The peak intensity of Si is similar in the fossil and host rock spectra (Fig. 6C, 6D).

Group 3 (G3) is represented by samples S2 and S6, which are located close to the bottom and top of the unit, respectively. These samples exhibit remarkable difference between fossil and host rock EDX spectra. The high-intensity peak of C characterized the fossil spectra, with a lower intensity peak of O and Si, while high-intensity peak of Si, with lower O, characterized the host rock spectra (Fig. 6E, 6F).

FIG. 4.—Taphonomic modes AZ-1 to AZ-4. **A**) Outcrop photograph showing remains of the mode AZ-1. **B**) Photograph showing a fragment of *Dicroidium* sp., of the mode AZ-1, scale bar = 2 cm. **C**) Leaf of *Heidiphyllum elongatum* (IANIGLA-PB-716), referred to the mode AZ-2, scale bar = 0.5 cm. **D**) Ovule/seed referred to *Cordaicarpus* sp. (IANIGLA-PB-737), from the mode AZ-2, scale bar = 0.1 cm. **E**) Fragment of *Taeniopteris* sp. leaf, referred to the mode AZ-3. **F**) Fragment of a *Dicroidium* sp. frond, showing the mode AZ-4. **G**) *Rissikia media* shoot (IANIGLA-PB-723) showing the mode AZ-4. **H**) stem of *Neocalamites* sp. (IANIGLA-PB-679), from the mode AZ-4, scale bar = 2 cm.

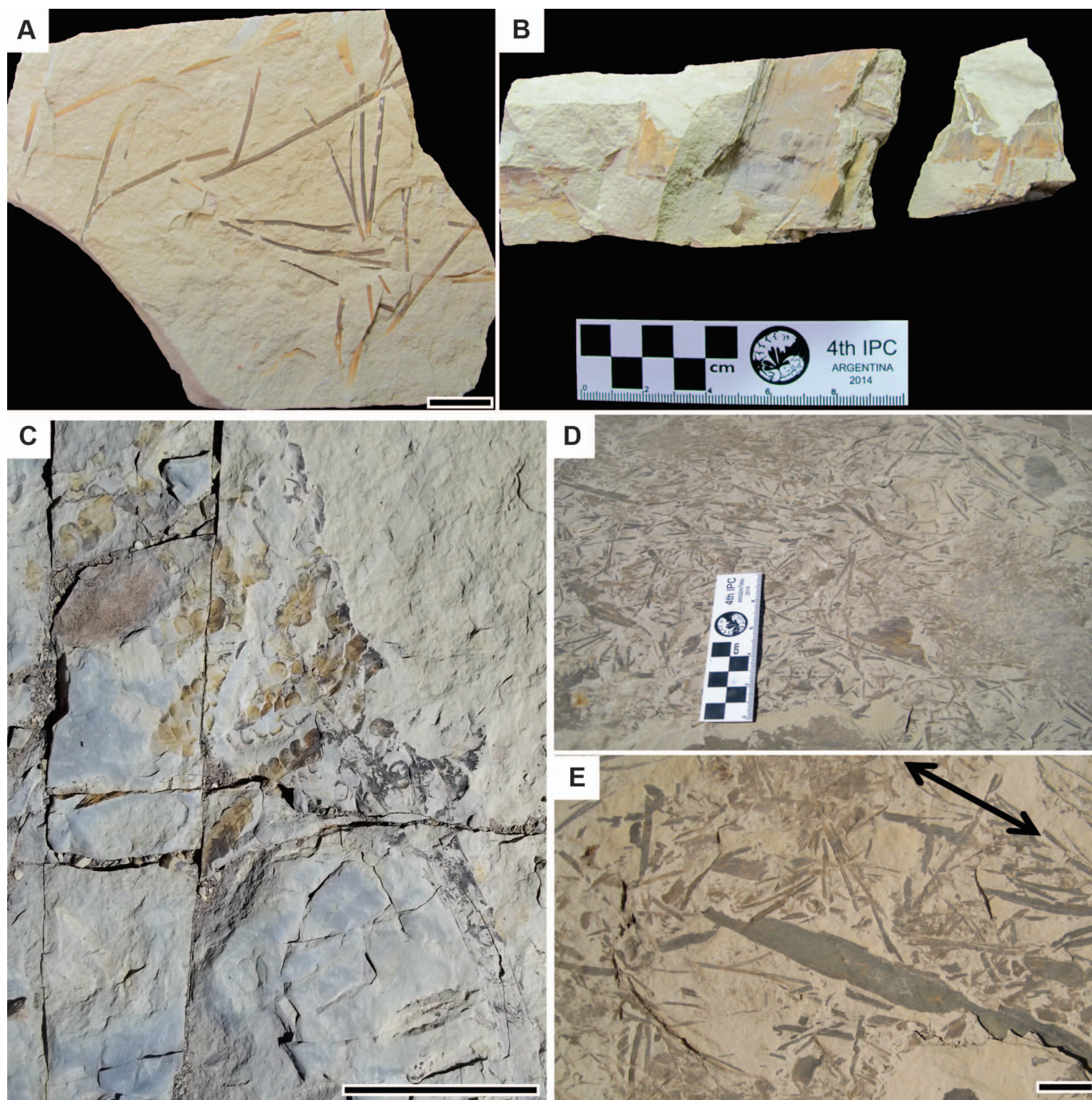


FIG. 5.—Taphonomic modes AZ-5 to AZ-8. **A)** Fronds of *Xylopteris* sp. showing the mode AZ-5, scale bar = 1 cm. **B)** Fragment of *Neocalamites* sp. preserved in three dimensions, from the mode AZ-6, scale bar = 2 cm. **C)** Frond referred to *Zuberia zuberi* (IANIGLA-PB-736) referred to the mode AZ-7, scale bar = 5 cm. **D)** Outcrop photograph showing remains of the mode AZ-8. **E)** Detail of AZ-8 mode, the arrow shows preferential orientation of remains, scale bar = 1 cm.

DISCUSSION

Taphonomic Model

The most frequent taphonomic mode was the AZ-1, with 46% of occurrences, followed by the AZ-4 and AZ-5 modes, with 26% and 11%, respectively. The rest of the modes are represented by percentages that vary between 7% and 1% (Fig. 7). A taphonomic pathway model for the Agua de la Zorra Formation plant fossils is proposed (Fig. 8).

The plant fossils recovered from the Agua de la Zorra Formation were interpreted as allochthonous and parautochthonous elements. Transport in tractive water flow was the primary transport process, characteristic for seven of eight taphonomic modes (AZ-1, AZ-3 through AZ-8). Only the elements included in mode AZ-2 were transported by aerial dispersion. The *post mortem* and biofabric attributes of the water-transported modes suggest that each mode represents transport over different distances from the production site to the lake. The longest transport distance was inferred for mode AZ-1, whereas material in mode AZ-8 was the least transported.

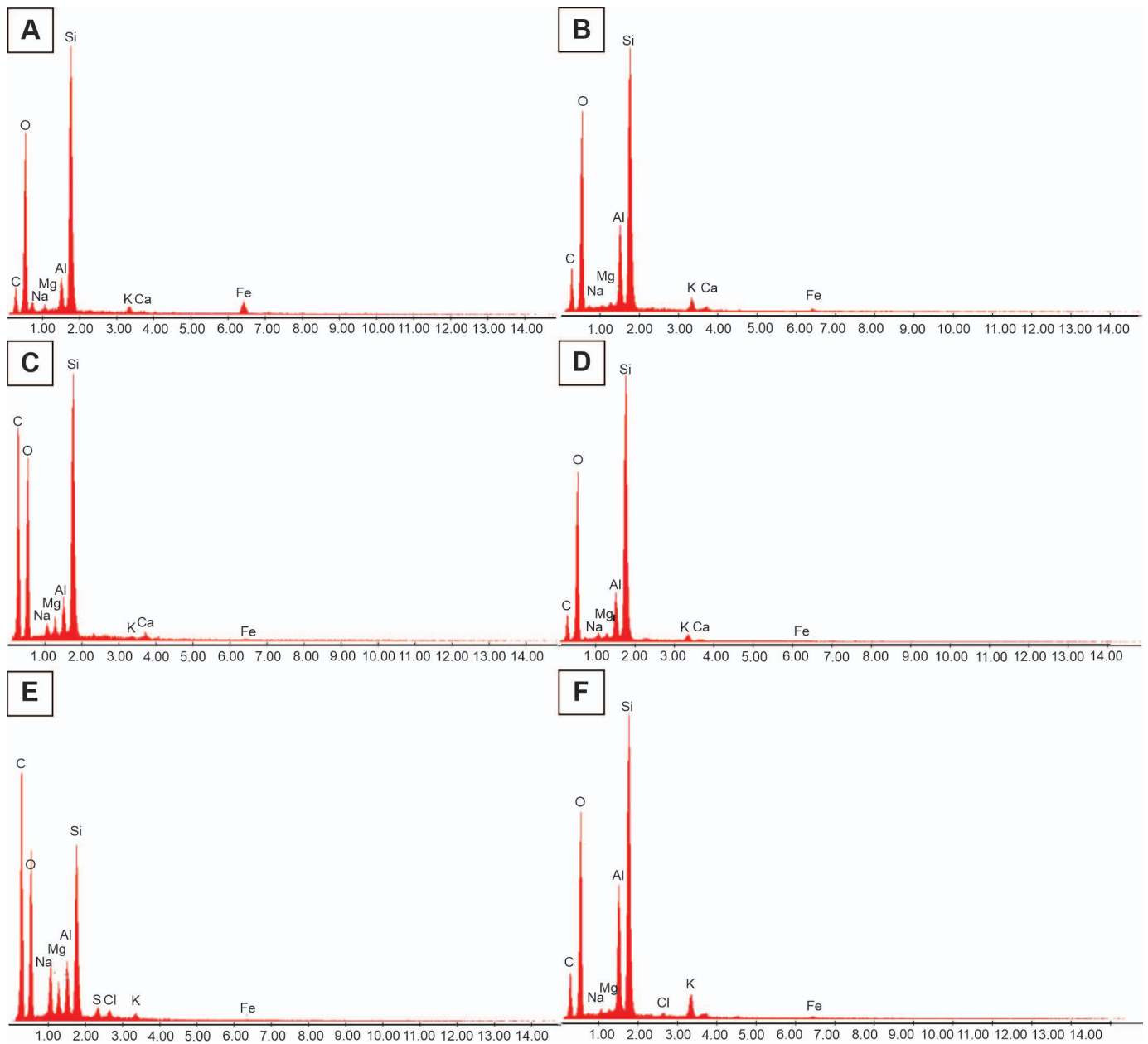


FIG. 6.—EDX-SEM spectra from matrix rock and fossil samples. **A**) G1 Fossil (S7). **B**) G1 matrix (S7). The spectra of this group are similar for the fossil and the host rock areas. **C**). G2 Fossil (S3). **D**) G2 Matrix (S3). The fossil EDX spectra show similar high-intensity peaks of the C and O, host rock spectra show a significant difference between C and O peaks; the peak intensity of Si is similar between the fossil and host rock spectra. **E**) G3 Fossil (S6). **F**) G3 Matrix (S6). The fossil spectra, show a high-intensity peak of C with a lower intensity peak of O and Si. The host rock spectra show a high-intensity peak of Si, with lower O.

Five of the taphonomic modes (AZ-1, AZ-2, AZ-3, AZ-4, AZ-7) were recorded in the lacustrine offshore environment, which is typified by a low sedimentation rate. Thus, plant fossil preservation, in this subenvironment, is enhanced mainly by the development of anoxic bottom water. Modes AZ-5, AZ-6, and AZ-8 are associated with proximal facies of the prodelta. In this subenvironment, preservation has been enhanced by a high sedimentation rate despite higher levels of oxygen and thus elevated rates of decay.

Spicer (1981, 1989, 1991) describes two different depositional models for leaf remains in lakes; the low energy system, and the high energy system. The low energy lacustrine system is characterized by two distinct plant horizons, one restricted to the bottom set and other recorded in the top of the foreset. Remains recovered from the high energy system are not

distributed precisely by level. The Agua de la Zorra Formation is characterized by successive levels that include plant remains in both proximal and offshore facies, suggesting a high energy system according to the models by Spicer. Moreover, the forest floor litter remains evidence rapid transport and burial (AZ-1, AZ-5, AZ-6). The evidence of preferential orientation (AZ-8), and plant parts produced by traumatic events (AZ-7), are also all associated with high-energy hydraulic conditions. High-energy flows are commonly caused by storms (Spicer 1989, 1991). Summarizing, the plant remains recovered from the Agua de la Zorra Formation show taphonomic attributes that suggest they were deposited in a high energy system, with high-energy episodic discharges resulting from storms.

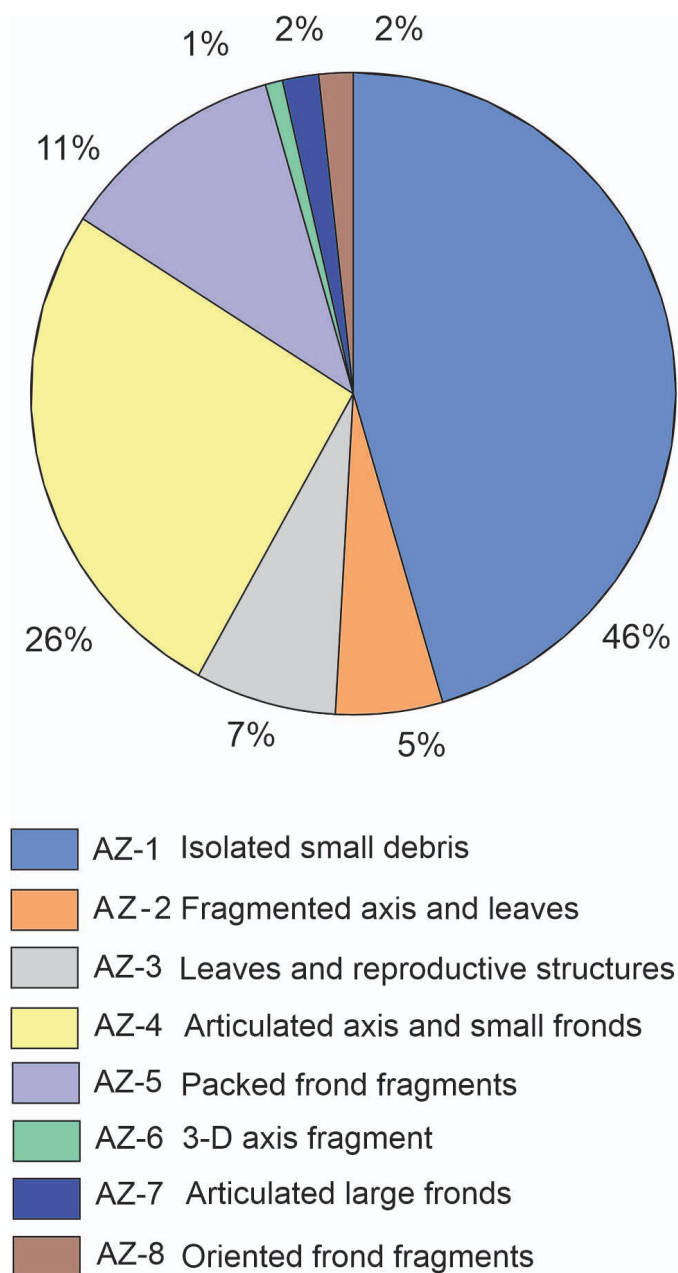


FIG. 7.—Percentages of the taphonomic modes recorded in the Agua de la Zorra Formation.

Paleoecological Reconstruction

The plant fossils recorded in the lacustrine-deltaic system of the Agua de la Zorra Formation serve as an indicator of the diversity of the paleocommunities that developed at the margins of the system; 69% of the encountered taxa can be assigned to the Umkomasiaceae family, Gymnosperms of uncertain affinity represent 10%, the Equisetaceae 7%, the Voltziales and the Cycadales 5% and 4% of the samples respectively, and remains referred to Osmundales Coniferales each account for 2%; finally, the Ginkgoales were the least abundant elements (1%) (Fig. 9).

Spicer (1991) note that high-energy systems are good at preserving spatial patterns of plant associations. Considering that no significant changes are recorded in the taxonomic composition of the plant

assemblages throughout the stratigraphic section, we suggest that differences between fossiliferous horizons of the Agua de la Zorra Formation could reflect the spatial pattern of the plant communities more than a temporal pattern.

According to studies of the paleoecology and diversity of Triassic Gondwana floristic associations by Anderson and Anderson (1983, 1989, 2003, 2018) and Anderson et al. (1998, 2008), along with associated palynoflora, and taphonomic analysis presented herein, we propose a reconstruction of possible original communities from this part of Gondwana during the Upper Triassic (Fig. 10).

The Agua de la Zorra lake margins were characterized by an Umkomasiales forest dominated by *Xylopteris*, shrubs of Osmundales, such as *Cladophlebis* spp. and Cycadales referred to the genus *Taeniopteris* with Equisetales such as *Neocalamites* in the palustrine area. The Sphenophytes are also the dominant floral component along the river margins. In the woodland, within the floodplains of active fluvial system, upstream paleocommunities would have formed a forest dominated by Umkomasiales, particularly the genera *Dicroidium*, *Johnstonia*, *Zuberia*, and in lower proportional abundance, *Xylopteris*, with emergent of *Linguifolium* (Gymnosperms of uncertain affinity), *Heidiphyllum* (Voltziales), *Rissikia* (Coniferales) and *Sphenobaiera* (Ginkgoales) forming a minor component.

Volcanic Disruption/Effect

Volcanic eruptions have negative consequences on biodiversity, and disturb fluvial and lacustrine dynamics producing changes in the physicochemical characteristics of sedimentary environments (Spicer 1991; Behrensmeyer and Hook 1992; Burnham 1993; Dale et al. 2005; Payne and Egan 2019). Although tephra and fine ash layers best represent volcanic events in lake and river deposits, basalts and pyroclastic flows are commonly found in these environments. Volcanic processes can capture and preserve an entire community with little or no alteration. However, changes in the physicochemical characteristics of sedimentary environments influence the preservation of plant remains, and are especially important in determining diagenetic processes (e.g., Lafuente Díaz et al. 2018).

Burnham (1993) describes and compares plant deposition in different modern volcanic environments, and discusses the potential for preservation of plants in them (see Burnham 1993 and references therein). Burnham (1993) observed that thicker ash layers decrease mechanical and bacterial degradation, enhancing the potential for preservation of leaf remains in terrestrial depositional settings.

The fact that the plant taxa recorded (with the exception of *Neocalamites* and *Cladophlebis*) are considered to have been deciduous plants (Pigg 1990; Axsmith et al. 1998; Cúneo et al. 2003; Bomfleur and Kerp 2010; Bomfleur et al. 2011, 2013; Escapa et al. 2011; Mays and Mcloughlin 2019), and the features observed in most of the taphonomic modes, suggest that abscission was by physiologic or natural processes. However, mode AZ-7 features taphonomic evidence (high articulation) that suggests that this kind of plant remains was produced by traumatic abscission. The remains of the AZ-7 mode would have been produced by storms. Furthermore, the taphonomic attributes are compatible with transport by water flow, except for mode AZ-2, in which materials were transported by aerial dispersion (wind). There is no evidence that indicates volcanism influenced the production of remains in the Agua de la Zorra taphoflora, and a cause-effect relationship between volcanic events and ecological processes in the geological record is complicated (Payne and Egan 2019).

As mentioned before, the spectra for sample G1 are similar for the fossil and the host rock areas. The spectra show a high dominance of Na, Mg, Al, and Si, which suggests a silicate composition, and complete oxidation of organic matter, thus, the fossil remains could be interpreted as impressions.

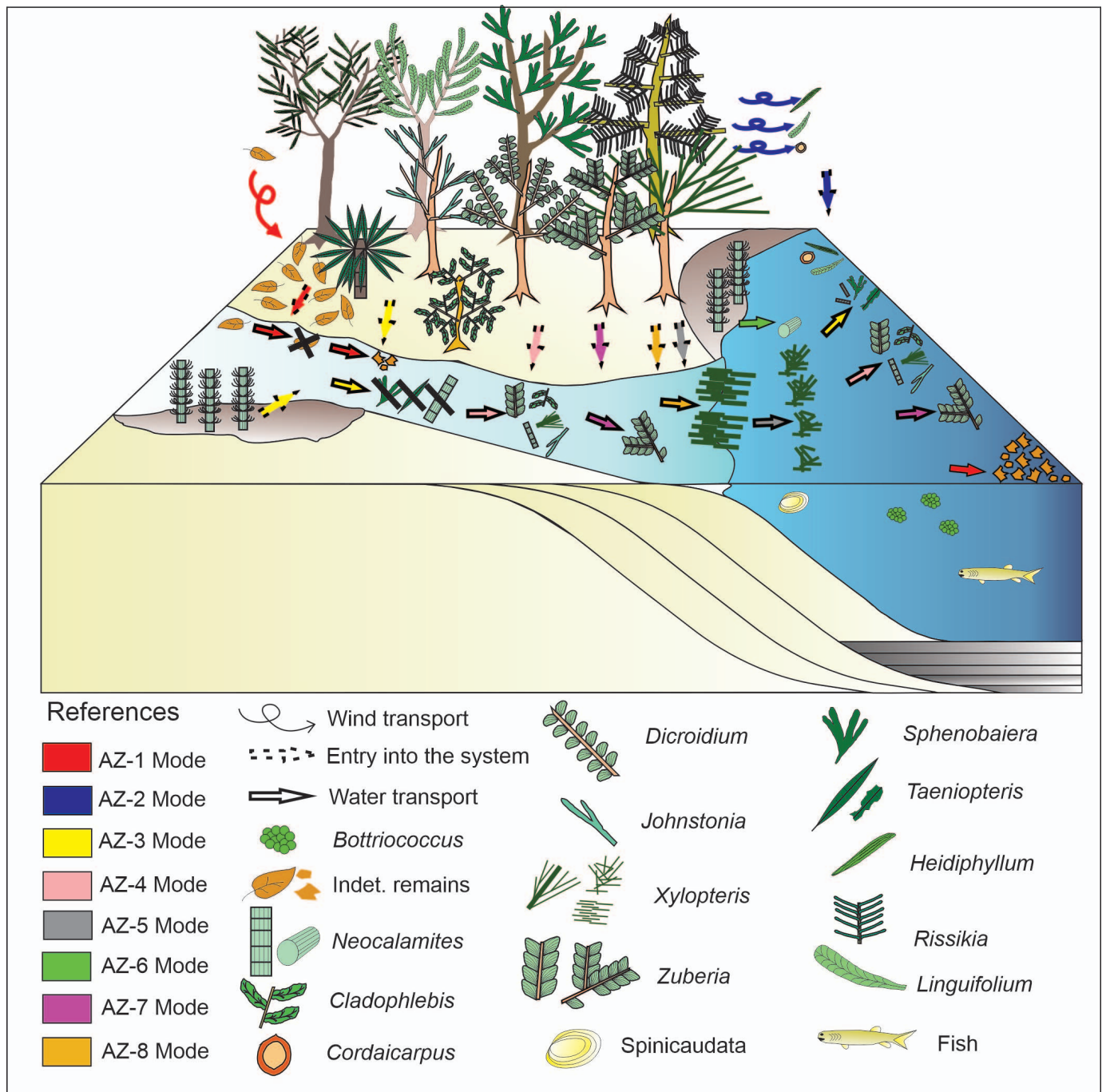


FIG. 8.—Taphonomic pathway reconstructions of each taphonomic mode described for the Agua de la Zorra Formation. AZ-1 Isolate small plant fragments. AZ-2, includes simple leaves and ovules/seeds. AZ-3, includes simple leaves and axis fragments. AZ-4 is characterized by articulated axis and fronds. AZ-5, loosely to densely packed fronds fragments. AZ-6, axis fragment preserved as mold-cast in three dimensions. AZ-7, articulate large frond fragments. AZ-8, loosely to densely packed fronds fragments with preferential orientation.

The silica detected in the fossil impression corresponds to the sediment in which remains were deposited. Lack of organic matter is due to modern weathering. The samples were assigned to taphonomic modes AZ-1 and AZ-4 and were collected from F1 levels not related to tuffs or basalts.

The fossil G2 samples that show the higher peaks of C and O suggest a higher concentration of organic matter. However, the Si peaks in fossil and host rock are similar, which could be interpreted as an indicator of the preservation of some original material in the fossil remains. In these cases,

the samples were recovered from F1 facies just below sandstone levels (Sm of the facies association AZ-A, and Sh from facies association AZ-B). The rapid sedimentation of the sands could have helped remove the plant remains from the TAZ.

Lastly, G3 encompasses samples with a greater quantity of preserved C in the fossils and a lower concentration of Si. This is interpreted as indicative of a higher organic content. The samples were associated with taphonomic modes AZ-1 and AZ-2 and were found in levels just below

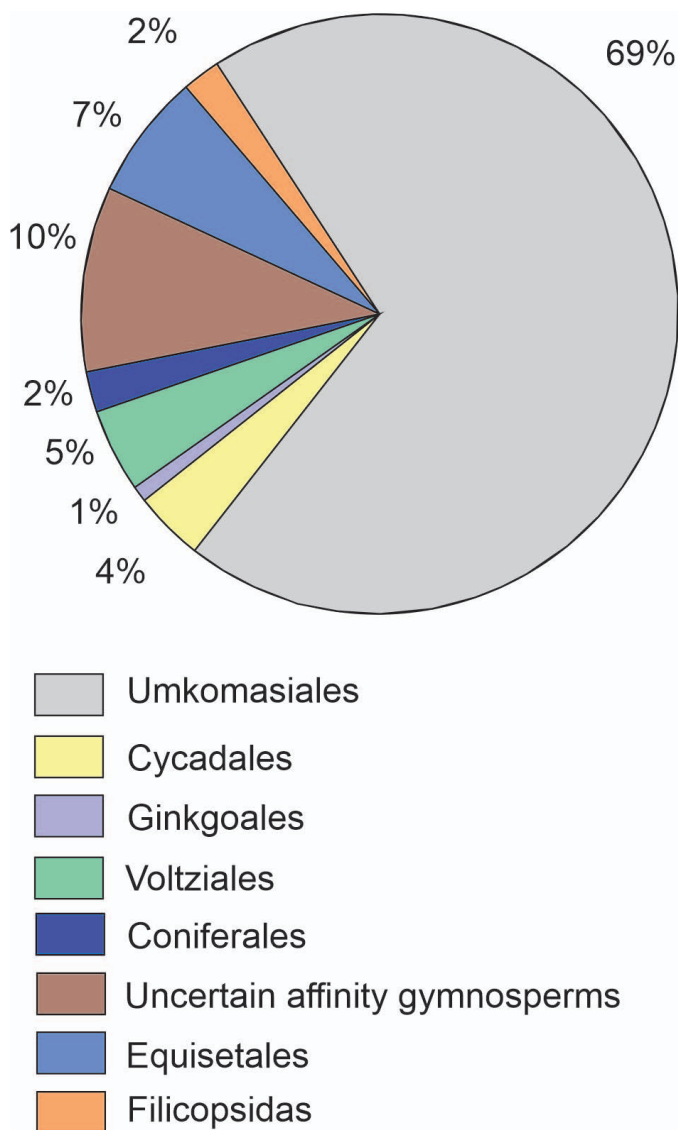


FIG. 9.—The plant fossils recorded in the lacustrine-deltaic system of the Agua de la Zorra Formation serve as an indicator of the diversity of the paleocommunities that would have developed at the margins of the system. The plot shows percentage of the different taxonomic groups identified in the Agua de la Zorra Formation succession.

volcanic horizons. The S2 sample comes from F1 facies associated with basalt levels, whereas the S6 sample was found in F1 facies, associated with an air-fall tuff. The significant organic matter content related to the basalt and tuff levels might be acting as the sandstone levels mentioned above, rapidly burying the plant remains and removing them from the TAZ, but also as a protection of the remains from the normal diagenetic pathways.

The three groups recognized from SEM-EDX analysis are not equivalent to the taphonomic modes described previously from the taphonomic attributes related to biostratinomic processes. Therefore, the characteristics observed in the three groups are a product of diagenetic processes and not related to the taphonomic pathways interpreted previously.

In comparison with other Triassic paleolakes with volcanic activity, such as the Cerro Puntudo Formation, where the predominant remains are leaves registered in the margins of the lake and foliar materials were interpreted as autochthonous elements, and their preservation, despite aerobic conditions, was attributed to deposition of pyroclastic material that improved conservation (Mancuso et al. 2009). However, in the Agua de la Zorra

Formation, the remains identified are interpreted as allochthonous and parautochthonous elements. In both formations, preservation was improved by pyroclastic materials; however, the abundant remains, different organs and diverse taxa found in the Agua de la Zorra system were mainly enhanced by the lake bottom anoxia conditions and high storm generated flows in proximal areas.

Another lacustrine Triassic sequence with evidence of volcanism is the Cacheuta Formation. The Agua de la Zorra and Cacheuta taphofloras show similar taxonomic diversity, but some of the differences between them were interpreted as an effect of original ecological variation (Pedernera et al. 2019). In the Hilario-Sorocayense sub-basin, the Agua de los Pajaritos-El Alcázar records continuous input of tuff and pyroclastic materials (Drovandi et al. 2016), which enhanced the plant preservation, as in the Agua de la Zorra Formation. Also, the taphoflora preserved in the Agua de los Pajaritos-El Alcázar succession shows evidence, in the form of charcoalfication and oriented logs, that suggests the succession was more proximal to the volcanic source, and the production of the remains was by volcanic trauma (Drovandi et al. 2016). In the Agua de la Zorra Formation there are materials interpreted as elements produced by trauma but the production is attributed to storms. Furthermore, there is no evidence of charcoalfication or other signs of volcanic trauma in the Agua de la Zorra Formation as documented in the Agua de los Pajaritos-El Alcázar succession (Drovandi et al. 2016).

According to Ottone et al. (2011), the episodic entrance of basaltic lava and ashfalls into the freshwater body might have occurred during the burial of fossil remains. These authors also indicated that plant remains of the Agua de la Zorra Formation were not affected thermally by the lava flow incursions into the paleolake (Ottone et al. 2011).

In the Agua de la Zorra Formation, basalt and tuff increased the potential for the preservation of plant remains. On the one hand, they increase the sedimentation supply, and remove remains from the active taphonomic zone, similar to the sandstone supply effect. And, on the other hand, volcanism affects plant preservation by modifying the microenvironmental conditions thus altering the normal diagenetic processes. Recent contributions have explored the influence of volcanic activity on the diagenetic processes involved in plant fossilization (e.g., Matysová et al. 2010; Lafuente-Díaz et al. 2018). Lafuente-Díaz et al. (2018) emphasized that the acidic conditions generated by volcanic activity in the Anfiteatro de Ticó (Baquero Group, Santa Cruz Province, Argentina), increased the preservation potential of plant debris, even improving the preservation of the cuticle. In accordance with this, the present contribution, despite the plant remains being preserved without cuticle, demonstrates a higher preservation of organic matter in remains from the group G3, recorded in F1 facies associated with basaltic flows and pyroclastic sediments. Although the Lafuente-Díaz et al. (2018) model was proposed for fluvial environments, and the Agua de la Zorra succession represents a paleolake, there are similarities between them. The rapid burial favored by the input of siliciclastics, pyroclastics and basalts inhibited the decay process enhancing the retention of C and O (G2 and G3 in the Agua de la Zorra); but also, the volcanic input in the system modified the chemical microenvironment, increasing plant preservation potential.

As mentioned before, the Agua de la Zorra taphoflora is represented, as known to date, by plant remains without cuticle preserved (Ottone et al. 2011; Pedernera et al. 2019). Perhaps the lack of cuticle preserved in the Agua de la Zorra could be due to the fact that basaltic lavas recorded in this unit are classified as alkaline lavas (Ramos and Kay 1991; Ottone et al. 2011; Orellano et al. 2019). Cuticle preservation has been observed in other depocenters of the Cuyana Basin with volcanic influence such as the Potrerillos and Cacheuta formations, and their chemical structure has been analyzed (D'Angelo et al. 2011; D'Angelo and Zodrow 2018; D'Angelo 2019). D'Angelo (2019) proposed that cuticle preservation in these cases could be enhanced by thermal maturity and geochemical factors. However, D'Angelo (2019) does not investigate how volcanic activity influences

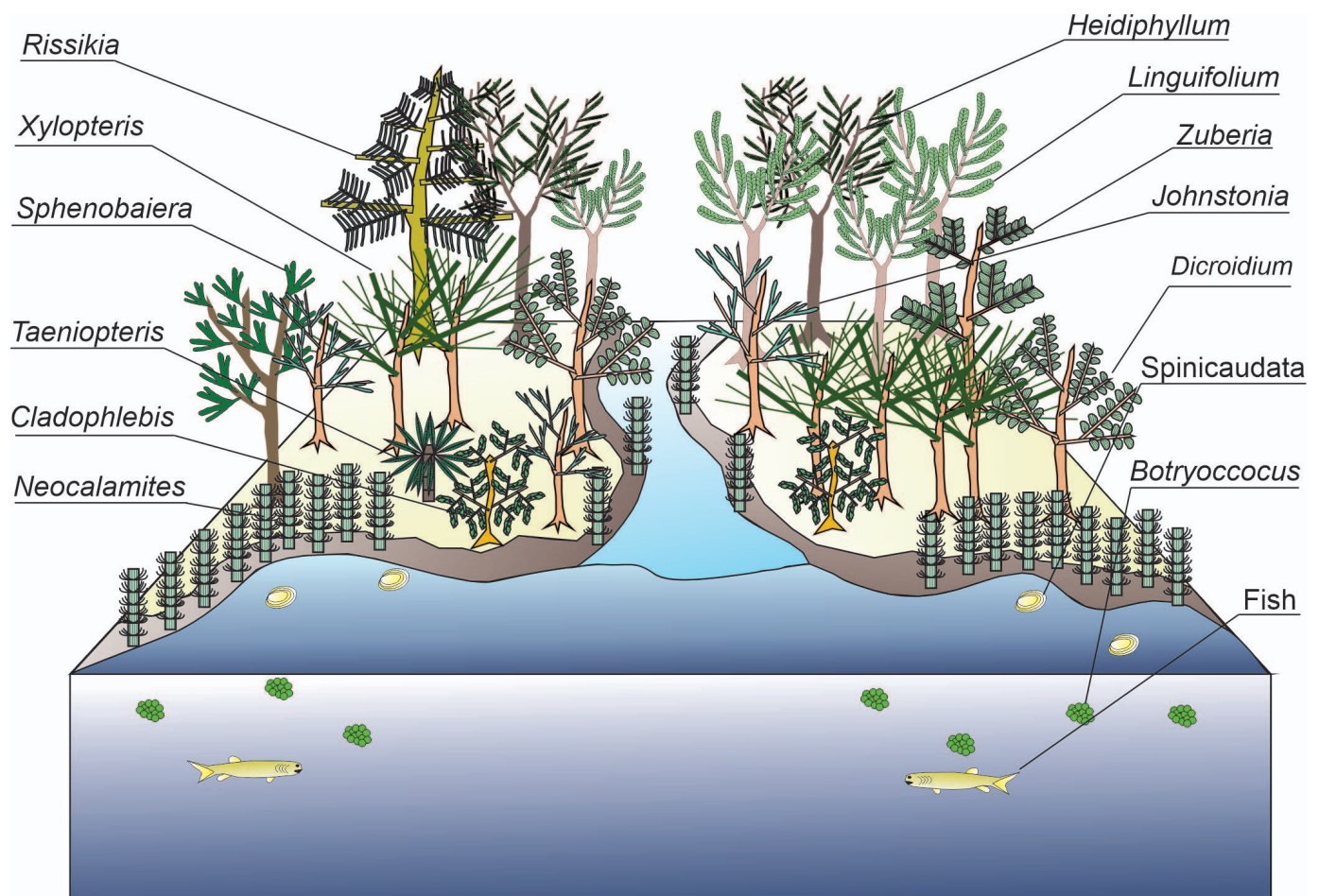


FIG. 10.—Reconstruction of the vegetal paleocommunities of the Upper Triassic of the Agua de la Zorra Formation.

plant preservation. Exploring other paleofloras from lacustrine-deltaic systems with evidence of volcanic activity is required for a better understanding of the implications of volcanic activity on the preservation of plant remains.

CONCLUSIONS

The Agua de la Zorra paleolake preserved allochthonous and parautochthonous material associated with anoxic conditions in the offshore lacustrine area, and in areas with high sedimentation rates, associated with flows in the prodelta area. The taphonomic features observed in the plant fossils found in this succession suggest that the remains were deposited in a high-energy system. The high-energy episodic discharge was most likely generated by storms. The different levels bearing fossils of the Agua de la Zorra Formation broadly reflect the spatial pattern of the plant communities rather than any vegetation changes through time, and represent the taxonomic composition of the paleocommunities developed in the margins of the Agua de la Zorra paleolake. There are no signs or evidence that the plant remains recorded in the Agua de la Zorra Formation were produced by volcanic trauma. Elements produced by trauma recorded in the Agua de la Zorra Formation were interpreted as having been produced by storms.

Despite eight taphonomic modes described from evaluation of biostratigraphic features, only three different diagenetic types of plant preservation were recognized based on the SEM-EDX analysis. The three groups are not equivalent to the taphonomic modes based on biostratigraphic features, and are more likely linked to diagenesis. The results

indicate that plant remains were not uniformly preserved throughout the section of the Agua de la Zorra Formation. The volcanic activity modified microenvironmental physicochemical conditions and diagenetic processes, enhancing organic matter preservation. The higher preservation of organic matter in remains recorded in facies associated with basaltic flows and pyroclastic sediments suggests that the effects of volcanic activity were largely post-entombment of the plant remains.

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