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Jurassic flora in Southeast Mexico: importance and prospects of recent findings in the Mixteco Terrane

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Abstract

Laurasic outcrops with plant fossils from the Jurassic are well known in Europe and Asia, but in North America, toward the Mesoamerican region, floristic Jurassic outcrops are poorly known. This is due to the fact that samples were taken with the goal of geological and/or mining exploration, without a rigorous paleontological approach. This inconsistency in sampling in the region has limited the knowledge of its Jurassic flora. Recently, we initiated a campaign on standardized sampling in the Zorrillo-Taberna Indiferenciadas Formation with the aim of advancing the knowledge of the floristic composition of this formation. The methodology we employ consists of maintaining the stratigraphic control of the fossil origin and sampling in average constant conditions with regard to time and personnel. Taxonomic determination was based on diagnostic characters of each fossil-taxon. The floristic composition is dominated by Bennettitales, but Cycadales, Podozamitales and others are also present. The results show an increase in the floristic diversity of almost 50 % distributed in three stratigraphic zones. It is noteworthy to point out that the floristic association contains one genus and 14 species endemic to the region. In addition, we contribute with new fossil-taxa records of Cycadales, Caytoniales, Podozamitales and some genera of Bennettitales for both formation and region. Thus, we conclude that the application of the sampling method in other localities would consolidate a comprehensive paleofloristic list for the region, and we believe that the paleoflora of the region would set the groundwork for new Jurassic biogeographic analysis.

Keywords: Mesozoic, gymnosperms, fossil plants, Biogeography, North America.

Resumen

En Europa y Asia los afloramientos fosilíferos de plantas jurásicas están bien estudiados, pero en Norteamérica, hacia la región Mesoamericana, los afloramientos de este tipo son poco conocidos. Esta situación se debe a que los muestreos de los afloramientos han sido con énfasis geológico y/o minero, y sin un enfoque paleontológico riguroso. Por lo tanto, esta inconsistencia en el muestreo paleontológico de la región Mesoamericana limita en conocimiento de la composición florística del Jurásico. Recientemente nosotros iniciamos un proyecto para la estandarización del muestreo en la Formación Zorrillo-Taberna Indiferenciadas con el objetivo de consolidar el conocimiento paleoflorístico de dicha formación. La metodología que empleamos consiste en mantener un estricto control estratigráfico sobre el nivel de origen de cada fósil y colectar en condiciones constantes promedio de personal y tiempo. La clasificación taxonómica del material estuvo basada en caracteres diagnósticos de cada fosilitaxon. La flora es dominada por las Bennettitales, pero hay presencia de Cycadales, Podozamitales, entre otros. Los resultados permiten demostrar un incremento en la diversidad florística hasta en un 50 % con los primeros registros de Cycadales, Caytoniales, Podozamitales y algunos géneros de Bennettitales. Identificamos que la flora está distribuida en tres zonas estratigráficas. Dicha diversidad es de notable importancia por la presencia de un género y 14 especies endémicas para la región. Además, contribuimos con nuevos registros paleobotánicos tanto para la formación como para la región. Por lo tanto, concluimos que la aplicación del método de muestreo en otras localidades consolidaría un listado paleoflorístico detallado para la región Mesoamericana, y de este modo consideramos que la paleoflora de la región sentaría las bases para nuevos análisis biogeográficos del Jurásico.

Palabras clave: Mesozoico, gimnospermas, fósiles de plantas, Biogeografía, Norteamérica.

1. Introduction

The Jurassic floristic kingdom of Laurasia is well represented in several outcrops in the northern hemisphere. Outcrops in Europe and Asia are the most well known, with some having been explored for over a hundred years in continued field campaigns. One such outcrop is in the locality of Yorkshire, England, and is the best representative of Jurassic flora in the Euroamerican region (Harris, 1964, 1969; Anderson *et al*., 2007; Taylor *et al*., 2009; Diéguez *et al*., 2010). The paleobotanical discoveries in these outcrops have helped characterize the floristic kingdom of Laurasia. Therefore, we know that Bennettitales, Cycadales, Ginkgoales, Pinales and Cheirolepidiales were widespread, whereas groups like Leptostrobales and Peltaspermales were scarce (Anderson *et al*., 2007). In the North American sector of the Laurasia kingdom, the best explored Jurassic outcrops are in the Morrison Formation (Chure *et al*., 2006). However, the outcrops in the southern portion of North America are poorly known, with some located in Southeast Mexico in the Mixteco Terrane.

The Mixteco tectonostratigraphic terrane is located between the states of Puebla, Guerrero and Oaxaca (Campa and Coney, 1983). The Jurassic outcrops of this terrane were initially explored in the late nineteenth century (Aguilera *et al*., 1896). However, subsequent explorations were intermittent and few, and sometimes tied to geological and/or mining exploration (Wieland, 1914; Silva-Pineda, 1969, 1978a, 1978b). The lack of a paleontological approach on sampling, together with a lack of consistency, has limited the understanding of the floristic composition of the region, as well as the phytogeographic regionalization of southern North America during the Jurassic. Therefore, standard sampling and taxonomic analysis of the paleoflora is necessary, mainly in outcrops of the Mesoamerican region.

Standardization of sampling allows discovering the origin of fossil material collected at any work locality. This information is crucial, since it supports biostratigraphic, paleoecological and taphonomic interpretations, and allows us to correlate between floristic lists of several outcrops, from local to regional and global levels. Thus, we decided that the first place to implement a standardization of sampling and taxonomic analysis in the Jurassic outcrops of the Mixteco Terrane should be the the Zorrillo-Taberna Indiferenciadas Formation (Oaxaca).

Based on our results, we propose that the flora of the Zorrillo-Taberna Indiferenciadas Formation is representative of the Mixteco Terrane. In addition, this flora is diverse, and contributes to an increase in the diversity of this region. It is clear that the Jurassic flora of the Mixteco Terrane is being "rediscovered", and these new findings may very well be the basis for future biostratigraphic, biogeographic and paleoecological interpretations of southern North America.

2. Geological setting

In the Jurassic, all the tectonic processes that occurred during the breakup of Pangea influenced the paleogeography of the Mesoamerican region (Campa and Coney, 1983; Ross and Scotese, 1988; Dickinson and Lawton, 2001). The Mixteco tectonoestratigraphic terrane was located in this region, and the consequence of the breakup in this area was the formation of a horst-and-graben system. These were areas where the main events of weathering, erosion and deposition occurred (Morán-Zenteno *et al*., 1993; Dickinson and Lawton, 2001; Corro-Ortiz and Ruiz-González, 2011). A stratigraphic unit produced by these events is the Tecocoyunca Group.

The Tecocoyunca Group consists of the Zorrillo, Taberna, Simón, Otatera and Yucuñuti formations (Erben, 1956). The rocks of the Zorrillo and Taberna formation outcropping on one side of the Río Ñumí is located 7.3 km northwest of the H. Ciudad de Tlaxiaco and 4.8 km west of Santiago Nundiche. In this area they are grouped in the Zorillo-Taberna Indiferenciadas Formation, and this stratigraphic unit is considered informal because the limit between these units is still undifferentiated (Figure 1). This stratigraphic succession has a thickness of 305 m and is composed of four distinct lithologic facies: shale and coal as the fine portion, and litharenite and greywacke as the sandy portion (Figure 2). The proposed sedimentary environment is a deltaic plain with nearby swamps (Carrasco-Ramírez, 1981; Corro-Ortiz and Ruiz-Gonzales, 2011). The assigned age, according to their stratigraphic position, is Bajocian/Bathonian (Erben, 1956).

3. Materials and Methods

To obtain the information needed to strengthen and reinforce the structure of the flora of the Zorrillo-Taberna Indiferenciadas Formation, a standard collection method was used. The following method was applied to achieve the standardization of the sampling: First, any sampling carried out was planned considering the detailed stratigraphic column (Corro-Ortiz and Ruiz-Gonzales, 2011). Next, the sampling was performed by a fixed number of collectors during a set time interval. Every fossil was then registered by its stratum or level of extraction. The collected material was subsequently classified according to key diagnostic characters established in the literature (*e.g.* Silva-Pineda, 1984; Pott and McLoughlin, 2009). Applying this methodology, we were able to obtain important results regarding the floristic composition of the Zorrillo-Taberna Indeferenciadas Formation. This method is similar to that applied by Anderson and Anderson (2003) because they also applied a standard number of collectors during a set time interval. Afterwards, the fossils were cleaned, consolidated, photographed, protected and preserved in

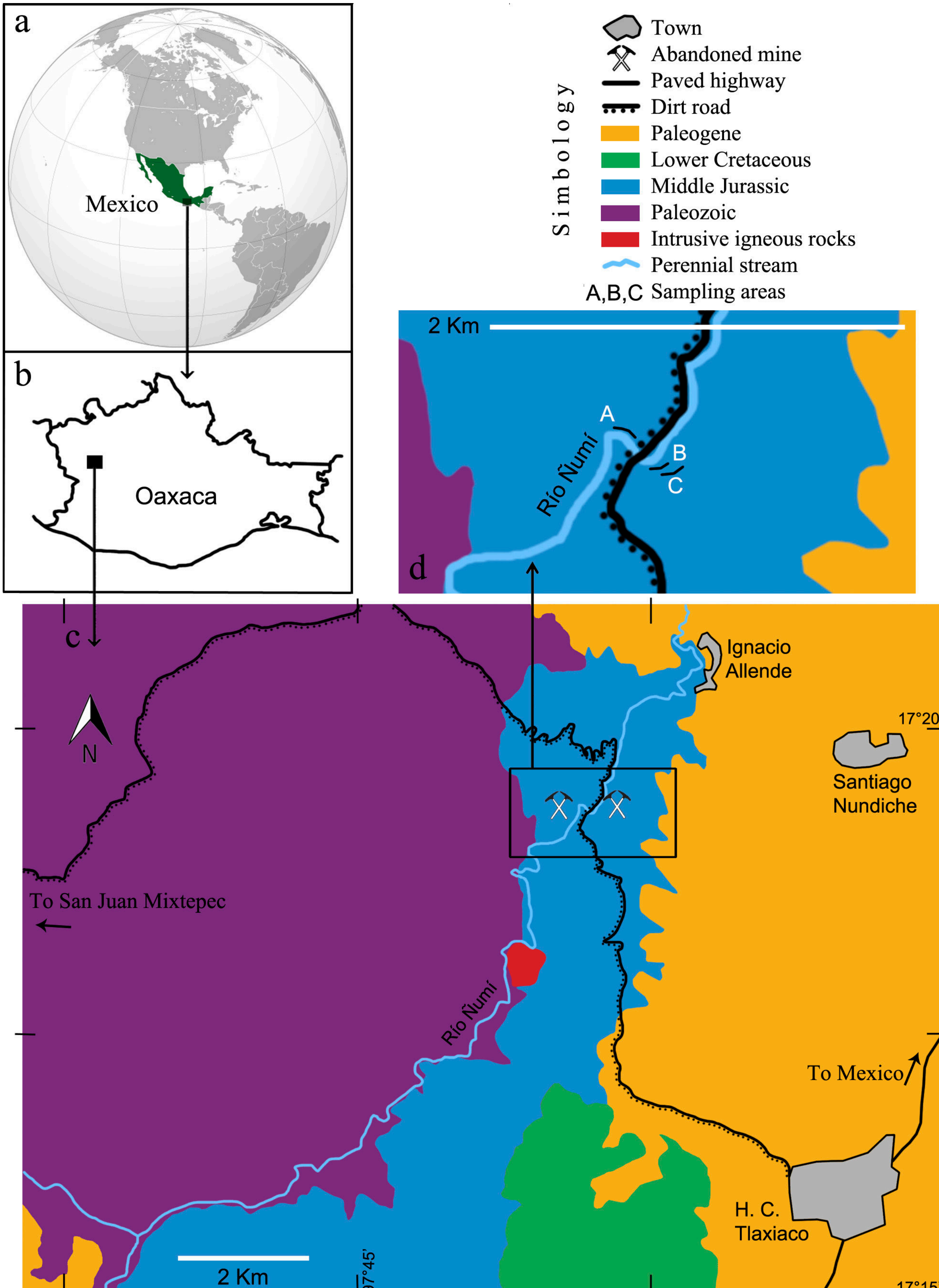

Figure 1. a, Map of the western hemisphere, with Mexico indicated in green. b, State of Oaxaca, with the region of Tlaxiaco highlighted in a black box. c, section of the geological map of the region of Tlaxiaco, Oaxaca, with major access roads and towns; the Rio Ñumi locality is pointed out by the black box. d, close up of the Rio Ñumi locality, with A, B and C signaling sampling areas.

the Collection of Paleontology of the Facultad de Estudios Superiores Zaragoza of Universidad Nacional Autónoma de México. The acronym CFZ-Zt, as well as a number from 1 to 304, was assigned to each rock block. In the case of rock block displays for more than one fossil-taxon, whether the same genus, species or other fossil-taxon, a combination of numbers is applied, *e.g*. CFZ-Zt 297 (8), with 297 representing the rock block and (8) the number of fossil-taxon. With this combination we made sure to maintain control of the abundance in a particular locality. Finally, the taxonomic determination was developed on the basis of unique morphological characters for each fossil-taxon, consulting with the following publications: Wieland (1914); Harris (1964); Bonetti (1968); Silva-Pineda (1969, 1978b, 1984, 1992); Leppe and Moisan (2003); Pott and McLoughlin (2009); Taylor *et al*. (2009); Rojas-Chávez (2010), and Velasco-de León *et al*. (2015). Six paleontological expeditions to the outcrop were conducted between 2008 to 2011, in which an average of eight collectors participated, and in each expedition the stratigraphic origin of the fossils was established.

4. Results

We recognized three fossiliferous zones in the stratigraphic column of Río Ñumi of the Zorrillo-Taberna Indiferenciadas Formation. The first zone was named ZtA and is located between 150 to 190 m; the second zone is ZtB, located between 210 to 240 m; and the third, ZtC, is located from 290 to 305 m (Figure 2). Most of the collected fossil-taxa were preserved as impressions. However, the morphological evidence is clear enough to support taxonomic determinations.

The material used to implement the taxonomic analysis presented here consists of 415 plant fossils included in 304 blocks of rock. The 415 plant fossils were classified into 34 species of 18 genera, belonging to 9 particular orders as well as the *incertae sedis* category. In the systematic description of the flora, only new records of plant fossils collected in the Río Ñumi locality are described. Table 1 presents a comprehensive list of the plant fossils, including previous listings of the locality.

4.1. Systematic Paleontology

Class EQUISETOPSIDA Agardh, 1825
Order EQUISETALES Candolle ex Berchtold et Presl, 1820
Family EQUISETACEAE Michaux ex DeCandolle, 1804
Genus *Equisetites* Sternberg, 1833
Type species. *Equisetites muensteri* Sternberg, 1833.

Equisetites sp.
Figure 3.1

Material studied. CFZ-Zt 7(1), 26, 31(1)(2), 37, 38(5)(7), 39, 124, 170, 205(5), 212, 215(2), 218(1)(2), 222, 287

Description. Stems with internodes, without the presence of preserved nodes or leaves. Internodes are 4.7 to 8.8 cm long and 2 to 8 cm wide. The number of longitudinal grooves is 6 to 23 at 1 cm, with an average of 8 grooves per centimeter.

Comments. These fossils are found incomplete, lacking the presence of nodes or leaves, and thus the specific assignation is difficult. It is reasonable to consider the genus *Equisetites* due to its fossil condition, as these fossils are very similar to the living genus *Equisetum*.

Class CYCADEOIDOPSIDA Scott, 1923
Order BENNETTITALES Engler, 1892
Family WILLIAMSONIACEAE Carruthers, 1870
Genus *Zamites* Brongniart, 1820
Type species. *Zamites gigas* Lindley and Hutton, 1835.

Zamites oaxacensis (Wieland) Person et Delevoryas, 1982
Figure 3.2

Material studied. CFZ-Zt 11(2), 89(1), 150(2)(3)(4), 184, 194(2), 207 (2), 214(5)(7), 224(2), 228, 232(2), 234(2), 240, 249(2), 260(7), 263(1).

Description. Two incomplete loose leaves, and complete and incomplete leaflets. The leaflets are of ample length, ranging from 1.4 to 12.6 cm long and 1.3 to 2.4 cm wide. The veins are thin and numerous, 17 to 26 per centimeter.

Comments. The classification of this material is mainly based on fragments of leaflets with the basal portion in good condition and two pinnately compound leaves. The morphology and size of the leaflets, as well as the whole leaf, is very distinctive and identifiable, and this facilitates classification. *Zamites gigas* Harris is very similar to *Z. oaxacensis*, but they differ in the number of veins. In *Z. gigas* the number of veins is 13 to 15 per cm, while in *Z. oaxacensis*, it ranges from 15 to 20 per cm. The samples of Río Ñumi display up to 26 veins per cm. *Z. oaxacensis* is comparable with *Z. tribulosus*; however, they differ in the morphology of the leaflets, mainly in length and expansion of the basal auricles, which are more prominent in *Z. oaxacensis*. The number of veins is less in *Z. tribulosus*.

Zamites feneonis Brongniart, 1828
Figure 3.3

Material studied. CFZ-Zt 30(1), 52(8), 206(1), 290(2), 301(2).

Description. Pinnately compound leaf lacking the apical part and incomplete leaflets. The leaf is 7.7 cm long and 6 cm wide, with its leaflets arranged at 60° to 80° angles and a sub-opposite shape 2.8 to 5.9 cm long and 0.8 to 1.4 cm

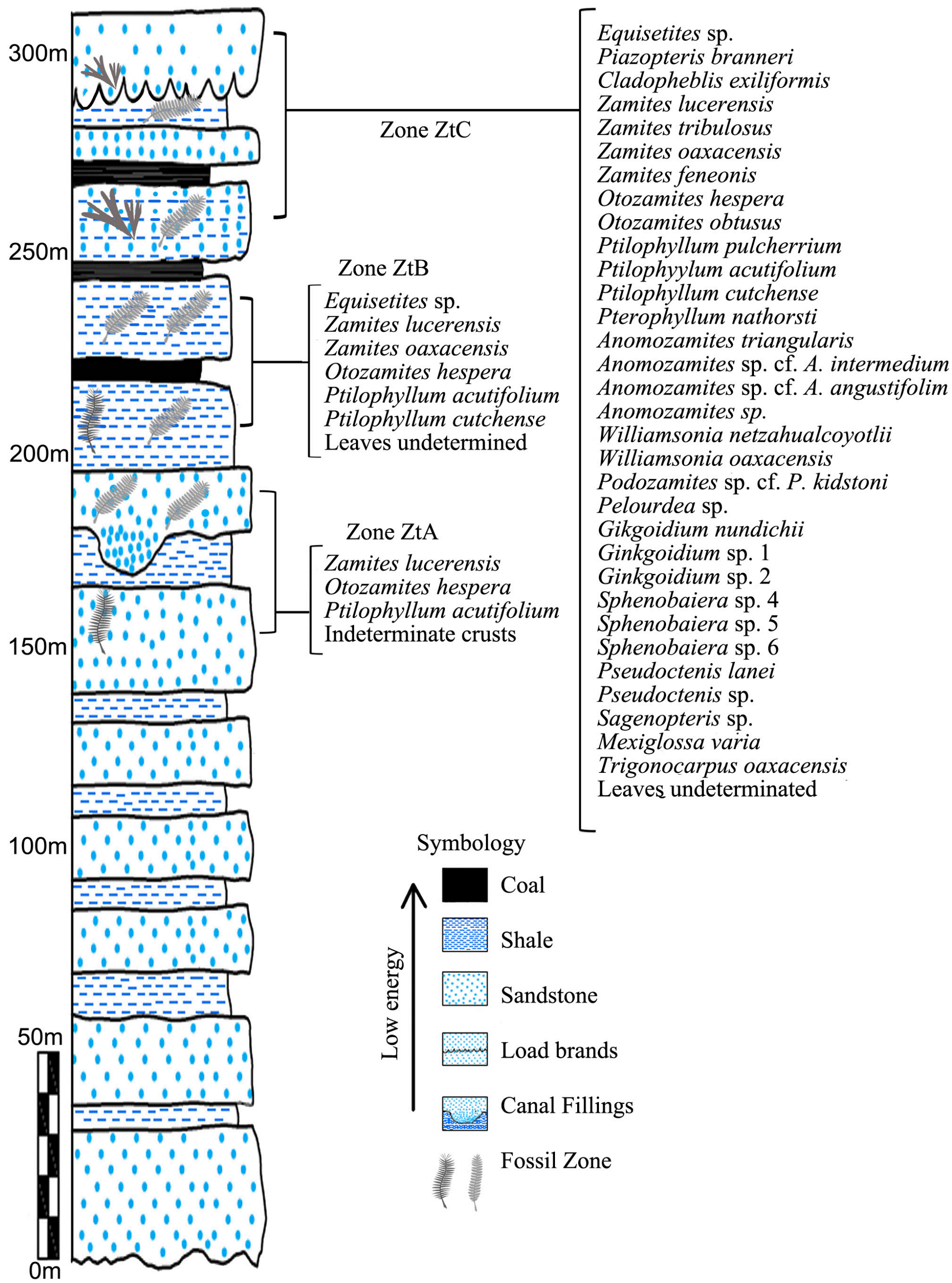

Figure 2. Stratigraphic column of the Zorrillo-Taberna Indiferenciadas Formation with sampling zones ZtA, ZtB and ZtC located in their exact position. Every sampling zone has its paleofloristic richness detailed.

wide. The venation of the leaflets is very fine and numerous. Leaflets are linear and rectangular-shaped, ending with an acute apex.

Comments. The samples match the description reported by Silva-Pineda (1969), which mentions that *Z. feneonis* is a characteristic species of mainly European Jurassic localities. This would be the second report of this species for the Middle Jurassic of Mexico.

Genus *Otozamites* Braun, 1842

Type species. *Filicites bechei* Brongniart or *Filicites bucklandi* Brongniart (see Harris, 1969. p. 11.).

Otozamites hespera Wieland, 1914

Figure 3.4

Material studied. CFZ-Zt 15(1)(2), 25(2), 41(1)(2)(3), 50(1), 51(6)(8)(12), 52(5)(6)(7)(11)(12)(13), 55(1), 61(1),

Table 1. List of plant fossils of the Jurassic Zorrillo-Taberna Indiferenciadas Formation, Oaxaca (Mesoamerican region), North America.

Order or category	Genera	Species	Abundance (specimens)	Stratigraphic Zone (Zt)
Equisetales	*Equisetites*	*E.* sp. *	17	B, C
Filicales	*Cladophlebis*	*C. exiliformis* (rR)	7	C
	Gonatosorus	*G. nathorstii* (rS)	-	-
Gleicheniales	*Piazopteris*	*P. branneri* (rS/R)	30	C
Bennettitales	*Zamites*	*Z. lucerensis* (rC)+	67	A, B, C
		Z. tribulosus (rS)+	20	C
		Z. oaxacensis *+	18	B, C
		Z. feneonis *	5	C
	Otozamites	*O. hespera* *+	59	A, B, C
		O. obtusus (rC)	3	C
		O. paratypus (rC)	-	-
	Anomozamites	*A. triangularis* *	1	C
		A. sp. cf. *angustifolium* *	3	C
		A. sp. cf. *intermedium* *	1	C
		A. sp. *	1	C
	Ptilophyllum	*P. acutifolium* (rS)	6	A, B, C
		P. cutchense *	6	B, C
		P. pulcherrium *+	8	C
	Pterophyllum	*P. nathorsti* (rS)	2	C
	Williamsonia	*W. netzahualcoyotlii* (rS)+	10	C
		W. oaxacensis *+	1	C
Cycadales	*Pseudoctenis*	*P. lanei* *	1	C
		P. sp. *	1	C
Caytoniales	*Sagenopteris*	*S.* sp. *	1	C
Podozamitales	*Podozamites*	*P.* sp. cf. *kidstoni* *	1	C
Coniferales(?) (Pinales)	*Pelourdea*	*P.* sp. (rS)	10	C
Ginkgoales	*Ginkgoidium*	*G. nundichii* (rV)+	3	C
		G. sp1 (rV)+	1	C
		G. sp2 (rV)+	1	C
	Sphenobaiera	*S.* sp4 (rV)+	1	C
		S. sp5 (rV)+	1	C
		S. sp6 (rV)+	1	C
Insertae sedis	*Trigonocarpus* ?	*T. oaxacensis* *+	10	C
	Mexiglossa	*M. varia* *+	21	C
Indeterminados		Flora	27	A, C

Note: * New record; + Endemic species described from Mexican material; r registered by (C: Carrasco-Ramírez, 1981); (R: Rojas-Chávez, 2010); (S: Silva-Pineda *et al*., 2007); (V: Velasco-de León *et al*., 2015).

68(1)(2)(3), 85(2), 87(2), 89(2)(3), 92(2), 144, 145, 150(1), 154, 163(1)(2), 167, 168, 169, 173, 174, 185, 187, 210, 211, 224(1), 233(1), 247, 249(3), 250(2), 253(3), 259(2), 260(3), 274, 279, 283(3), 284 (1)(6), 289(1)(2)(3), 297(2), 302(2).

Description. Fragments of pinnately compound leaves. The leaves are 1.6 to 9.1 cm long and 0.7 to 5.5 cm wide. The length of the leaflets ranges from 1 to 2.7 cm, with 1.9 cm on average. The width of the leaflets varies from 0.1 to 0.4 cm, with an average of 0.3 cm. The attachment to rachis is a small callosity. The attachment angle is 45° to 70° in the middle region, and 20° to 40° in apical and basal regions. However, some samples showed deformed angles up to 90°. The morphology of the apex is varied, ranging from round to acute, but mostly obtuse. The veins are fine and range from 14 to 23 per leaflet.

Comments. *Otozamites hespera* is the second most abundant species in the collection of Río Ñumi. It is noteworthy to point out that the width of the leaflets of Río Ñumi was on average less than 1 mm, according to the reports of Silva-Pineda (1984). Also, the size of the leaves

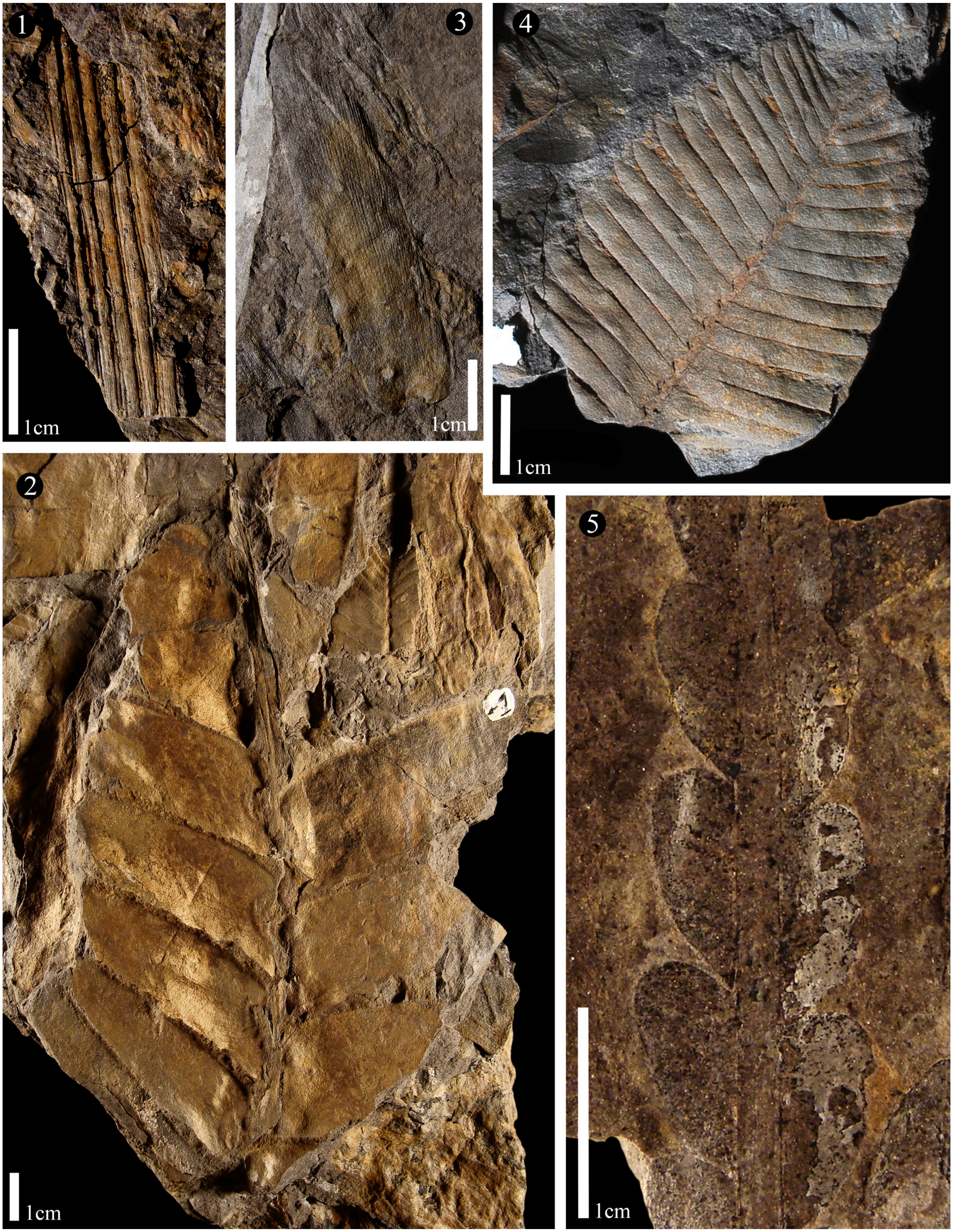

Figure 3. 1, *Equisetites* sp., showing an internode sample. 2, *Zamites oaxacensis*, pinnately compound leaf. 3, *Zamites feneonis* leaflet showing the fine venation of the species. 4, *Otozamites hespera*, pinnately compound leaf showing the characteristic base type of leaflets. 5, *Anomozamites triangularis*, pinnately compound leaf showing triangular type leaflets.

was small in some cases, which might suggest that these samples were juvenile. In the determination process, it is very important to perform a detailed observation of the union of the leaflets to the rachis, because sometimes this species can be easily confused with the genus *Ptilophyllum*.

Genus *Anomozamites* Schimper, (1870) emend. Pott et McLoughlin, 2009

Type species. *Anomozamites nilssonii* (Phillips) Harris, 1969.

Anomozamites triangularis (Nathorst) Pott et McLoughlin, 2009
Figure 3.5

Material studied. CFZ-Zt 8.

Description. Pinnately compound leaf, with small triangular leaflets sub-opposed and attached to rachis at an angle of 45°. The basiscopic and acroscopic angles of each leaflet are 45° and 90° respectively. The apex is rounded to slightly obtuse. Leaf size is 5.7 cm long and 1.8 cm wide. Leaflets are 0.8 cm long and 0.8 cm wide, with a 1:1 length/width ratio, and have 7 to 9 veins in each leaflet with dichotomies in the base. The rachis has a longitudinal groove.

Comments. The leaflets of *Anomozamites triangularis* of Río Ñumi decrease in size toward one end, suggesting that it is the apex of the leaf. Pott and McLoughlin (2009) made the proposal of this species, and mentioned that its distinctive characters were the basiscopic and acroscopic angles of leaflets, characters observed in the samples of Río Ñumi.

Anomozamites sp. cf. *angustifolium* Pott et McLoughlin, 2009
Figure 4.1

Material studied. CFZ-Zt 59, 82(1) (2).

Description. Pinnately compound leaves 3.3 to 5.5 cm long and 1.1 to 2.5 cm wide, with slightly falcate leaflets 0.8 to 1.2 long, and 0.8 to 0.9 cm wide, with a 1:1 length/width ratio. Leaflets alternate to sub-opposites with an acroscopic angle of 90° and 70° basiscopic. They display a rounded apex, a straight base, a longitudinally corrugated rachis, and veins ranging from 9 to 15 per leaflet, parallel and perpendicular to the rachis, with bifurcations near the base.

Comments. The plant fossils of Río Ñumi are morphologically consistent with the description given by Pott and McLoughlin (2009), except for the apex morphology. In Pott and McLoughlin (2009), they have a semi-square morphology, whereas the samples of Río Ñumi have a rounded apex. In addition, the lack of cuticle and well-preserved samples limit a certain determination.

Anomozamites sp. cf. *intermedium* Antevs, 1919
Figure 4.2

Material studied. CFZ-Zt 20(1).

Description. Basal portion of a pinnately compound leaf, 9.8 cm long including the petiole, and 2.2 cm wide. The leaflets are trapezoidal with a length of 1 cm and width of 0.6 cm, and are attached over the entire width of the base. The basiscopic and acroscopic angles are 65° and 90° respectively. They are arranged in a sub-opposite shape, have a rounded apex, and the number of veins is 9 per leaflet. The rachis has two longitudinal striations.

Comments. In the rachis of the *Anomozamites* sp. cf. *intermedium* of Río Ñumi, two longitudinal striations are observed. In the description of Pott and McLoughlin (2009), the rachis of *A. intermedium* has a series of transverse striations, which does not match the material of Río Ñumí.

Anomozamites sp.
Figure 4.3-3a

Material studied. CFZ-Zt 6(1).

Description. Pinnately compound leaf, 5.7 cm long by 1.8 cm wide. Leaflets are rounded, 0.8 cm long and 0.8 cm wide, with a 1:1 length/width ratio, attached to the rachis throughout the base with a 90° angle, round apex, arranged oppositely and alternately. The vein density is 11 per leaflet. The rachis has a robust longitudinal striation.

Comments. This sample is very similar to that reported by Silva-Pineda (1984). However, the species has not been determined at a specific level. In this case, we consider that additional and better samples are needed in order to define a new species. Because, the mentioned specimen they have characters that distinguished of the others, like morphology, the attached to the rachis, and vein density of the leaflets.

Genus *Ptilophyllum* Morris en Grant, 1840

Type species. *Ptilophyllum acutifolium* Morris en Grant, 1840.

Ptilophyllum cutchense Bose et Kasat, 1972
Figure 4.4

Material studied. CFZ-Zt 52(4), 87(1) (3), 161, 176(2), 284(4).

Description. Pinnately compound leaves are 3.1 to 7 cm long and 2 to 4 cm wide. The leaflets are 0.8 to 2.6 cm long and 0.2 to 0.6 cm wide, attached to the rachis at angles ranging from 45° to 70°, showing an obtuse apex, and they are arranged sub-opposite or alternate, without venation.

Comments. Generally, these leaves are similar to *Ptilophyllum acutifolium* and *P. pecten* (Phillips) Harris. In the first case, *P. cutchense* differs from *P. acutifolium* in the length and shape of the apex. In the second case, the

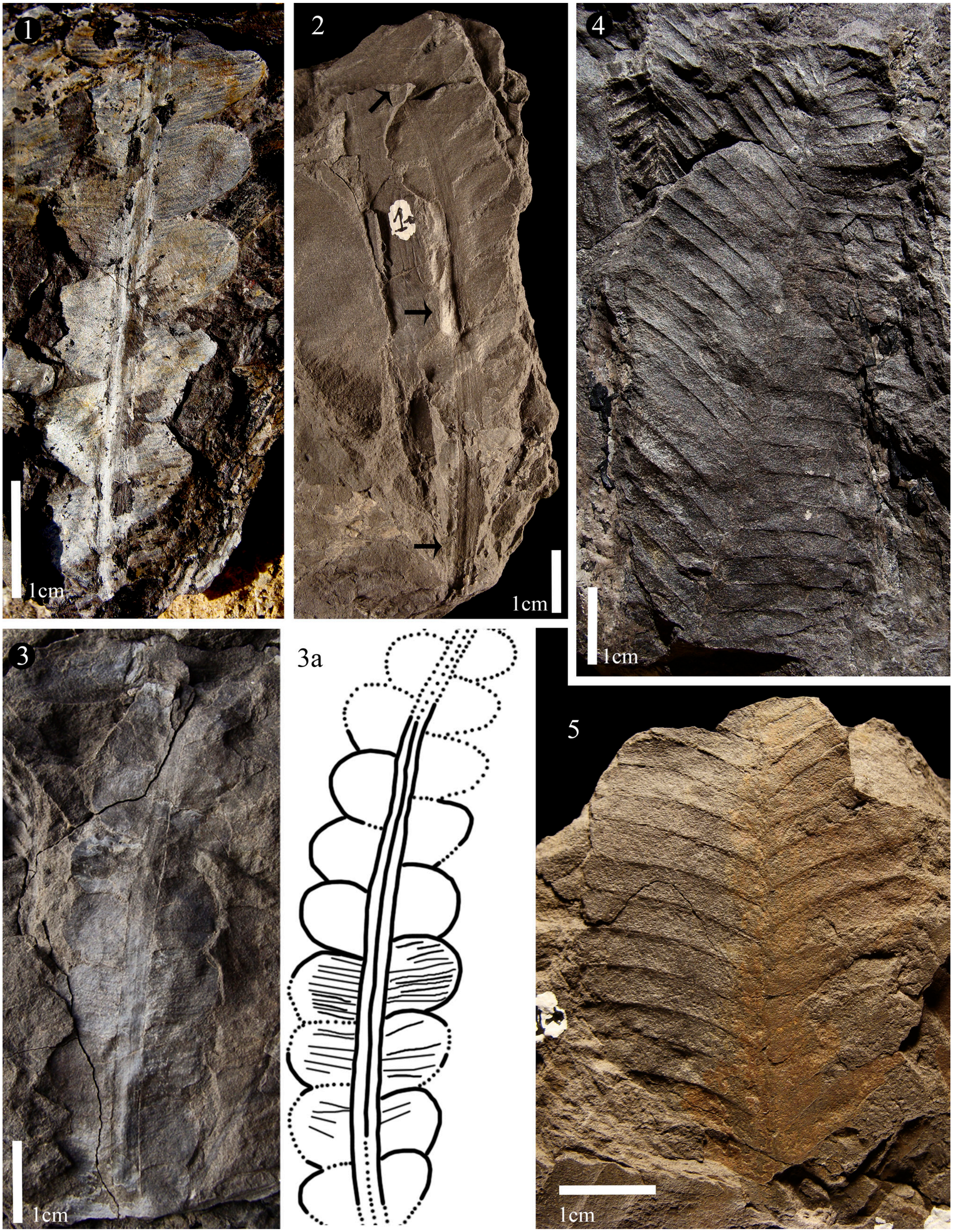

Figure 4. 1, *Anomozamites* sp. cf. *angustifolium*, pinnately compound leaf showing venation type and longitudinally corrugated rachis. 2, *Anomozamites* sp. cf. *intermedium*, with black arrows indicating the pinnately compound leaf. 3, *Anomozamites* sp., pinnately compound leaf showing venation type (3a, sketch of 3 *A.* sp.). 4, *Ptilophyllum cutchense*, pinnately compound leaf showing the base type of leaflets. 5, *Ptilophyllum pulcherrium*, pinnately compound leaf showing its characteristic falcate shape.

similarities with *P. pecten* are in the apical and basal part of leaf. The samples of Río Ñumi were impressions in fine sandstone, which complicated the observation of the veins in the samples. However, enough characters were preserved for a fairly good determination, based on the work of Silva-Pineda (1969).

Ptilophyllum pulcherrium Wieland, 1914
Figure 4.5

Material studied. CFZ-Zt 85(3), 155, 193(1), 199, 260(2) (4)(5), 284(5).

Description. Pinnately compound leaves between 1.7 and 8.4 cm in length, and 1.1 to 5.2 cm wide. The leaflets have a full length of 0.5 to 2.6 cm, between 0.1 and 0.3 cm wide, and have a smaller apex, round and slightly obtuse, without venation. They are attached to the rachis at angles ranging from 49° to 90°. The rachis is 0.5 cm wide.

Comments. This was the most abundant species of the genus *Ptilophyllum*. *P. pulcherrium* is morphologically very similar to *P. acutifolium*. However, they are distinguishable by the width, apex and shape of the leaflets, and the rachis, which is more robust in *P. pulcherrium*.

Genus *Williamsonia* Carruthers, 1870

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

Williamsonia oaxacensis Delevoryas et Gould, 1973
Figure 5.1

Material studied. CFZ-Zt 252.

Description. The samples of this species consist of receptacle with interseminal polygonal scales with individual diameters of 0.1 to 0.2 cm, and ovule micropyles less than 0.1 cm in diameter. The diameter of the preserved fossil is 2 cm, and the mark of attachment to the pedicel is 0.2 cm, without receptacle.

Comments. The interseminal scales are the main characteristic that differentiates *W. oaxacensis* from other species in this genus, because this species has a polygonal arrangement and a smaller diameter.

Class CYCADOPSIDA Brongniart, 1843
Order CYCADALES Dumortier, 1892
Family CYCADACEAE Persoon, 1807
Genus *Pseudoctenis* Seward, 1911

Type species. *Pseudoctenis eathiensis* Seward, 1911.

Pseudoctenis lanei Thomas, 1913
Figure 5.2

Material studied. CFZ-Zt 35.

Description. Pinnately compound leaf, 12 cm long and 8 cm wide, with a 0.4 cm wide rachis, tapering to the apex. The leaflets are incomplete and disposed at an angle of 55°, 8 cm long by 0.7 cm wide, without apex, alternate, and they have 13 veins in 0.5 cm. The veins are parallel throughout the leaflet. The base of the leaflets is separated by a distance of 0.3 cm, and is of an expanded type.

Comments. The sample of *Pseudoctenis lanei* in Río Ñumi shows both deformation and fragmentation in the leaflets, probably due to transport before burial. However, the diagnostic characters of the species are sufficiently clear to support its classification.

Pseudoctenis sp.
Figure 5.3-3.a

Material studied. CFZ-Zt 63.

Description. Pinnately compound leaf, 38 cm long by 15.9 cm wide. The leaflets are 7.4 cm long and 0.6 to 0.8 cm wide. They are alternate with a separating distance of 0.2 to 0.3 cm. The venations are very fine, consisting of 25 veins per leaflet. The rachis is 0.5 cm wide.

Comments. This particular sample presented very different characteristics when compared to the type species of this genus (Harris, 1964; Bonetti, 1968). Therefore, it has no assigned species, and more samples are needed to contemplate the possibility that it might represent a new species. The type and number of veins, and size of leaflets and rachis are the main characters that distinguish it from other species.

Class CONIFEROPSIDA Meyen, 1984
Order PODOZAMITALES Nêmejc, 1968
Family PODOZAMITACEAE Nêmejc, 1950
Genus *Podozamites* Braun 1843

Type species. *Podozamites distans* (Presl) Braun, 1843.

Podozamites sp. cf. *kidstoni* Etheridge, in Jack et Etheridge, 1982
Figure 5.4-4.a

Material studied. CFZ-Zt 238.

Description. Oval leaf with obtuse apex, 1.6 cm long and 0.9 cm wide in the middle region of the leaf. It displays 16 leaf veins, parallel and converging toward the ends.

Comments. This leaf is 0.3 cm wider than the specimen reported by Silva-Pineda (1992) for the Upper Jurassic of Mexico. The same author mentioned *Podozamites kidstoni* Etheridge from Afghanistan, slightly wider than the Mexican specimen. Therefore, measures would be in the same range as the specimen from Río Ñumi. This species differs from other species of the same genus mainly in its length. Unfortunately, we only have one sample, and this makes it difficult to make a strong specific determination. However, their characteristics are clearly distinguishable from the Bennettitales leaflets.

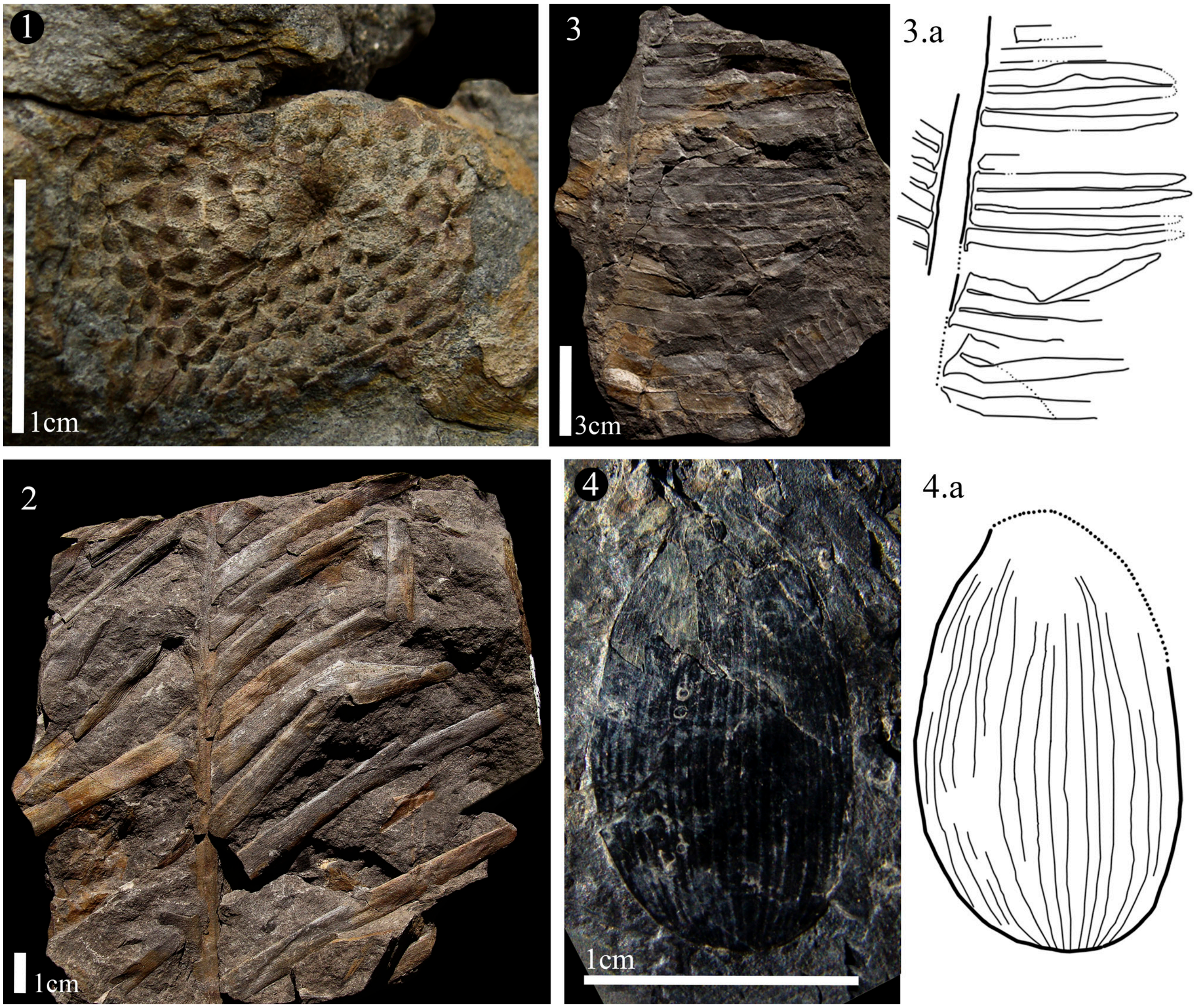

Figure 5. 1, *Williamsonia oaxacensis*, female reproductive organ showing the interseminal scales. 2, *Pseudoctenis lanei*, pinnately compound leaf showing venation, base type of the leaflets, and the deformation occurred during the taphonomic process. 3, *Pseudoctenis* sp., pinnately compound leaf, 3a sketch shows the base type and deformation suffered by the leaflets. 4, *Podozamites* sp. cf. *kidstoni*, simple leaf with parallel type venation.

Class GINKGOOPSIDA Engler, 1897
Order CAYTONIALES Harris, 1964
Genus *Sagenopteris* Presl, 1838 emend. Harris, 1964

Type species. *Sagenopteris acuminata* Presl in Stemberg, 1838, designated by Cleal and Rees, 2003; original designation. Early Jurassic of Strullendorf, Germany.

Sagenopteris colpodes Harris, 1940 emend. Harris, 1964
Figure 6.1-1.a

Material studied. CFZ-Zt 25(1).

Description. Palmately compound leaves on a petiole. Two incomplete leaflets associated with the same specimen. The leaflets have a well-marked median vein extending from the base toward the apex. Anastomosing secondary venation (slightly marked), apex not preserved and a thin rachis lightly striated lengthwise. The length of the compound leaf is 9.3 cm with petiole; the width is 8 cm; basal leaves angle at the junction where the petiole is 150°, 7 to 8 veins per centimeter. The leaflets are between 4.6 and 6.4 cm long, and 1.4 to 1.7 cm wide, with an average of 1:5 length/width ratio.

Comments. This fossil is compatible with the description of *Sagenopteris colpodes* in its size, number of veins and form of the leaflet (Harris, 1964; Cleal and Rees, 2003). *S. colpodes* differs from other species mainly in the shape of the apex and cuticle. Species such as *S. nilssoniana* (Brongniart) Ward have lanceolate leaflets with pointed ends. *S. pualensis* Barbacka presents round leaflets with a broader apex. *S. phillipsi* has longer than wide leaflets with a length/width ratio of up to 1:10 (Harris, 1964; Barbacka *et al*., 2006).

INCERTAE SEDIS

Genus *Trigonocarpus* Brongniart, 1828

Type species. *Trigonocarpus parkinsonii* Brongniart, 1828.

Trigonocarpus? *oaxacensis* Wieland, 1914

Figure 6.2

Material studied. CFZ-Zt 4, 66, 81, 113(2), 255, 256(1), 259 (1), 260(6), 261, 303.

Description. Small obovate seeds with a sharp apex. Most of the specimens have a slight degree of deformation. They are 1.2 to 1.9 cm long and 0.7 to 1.3 cm wide.

Comments. Wieland (1914) mentioned that it would be necessary to make a longitudinal cut to strengthen the description of this species. However, no permineralized material has been recovered to date.

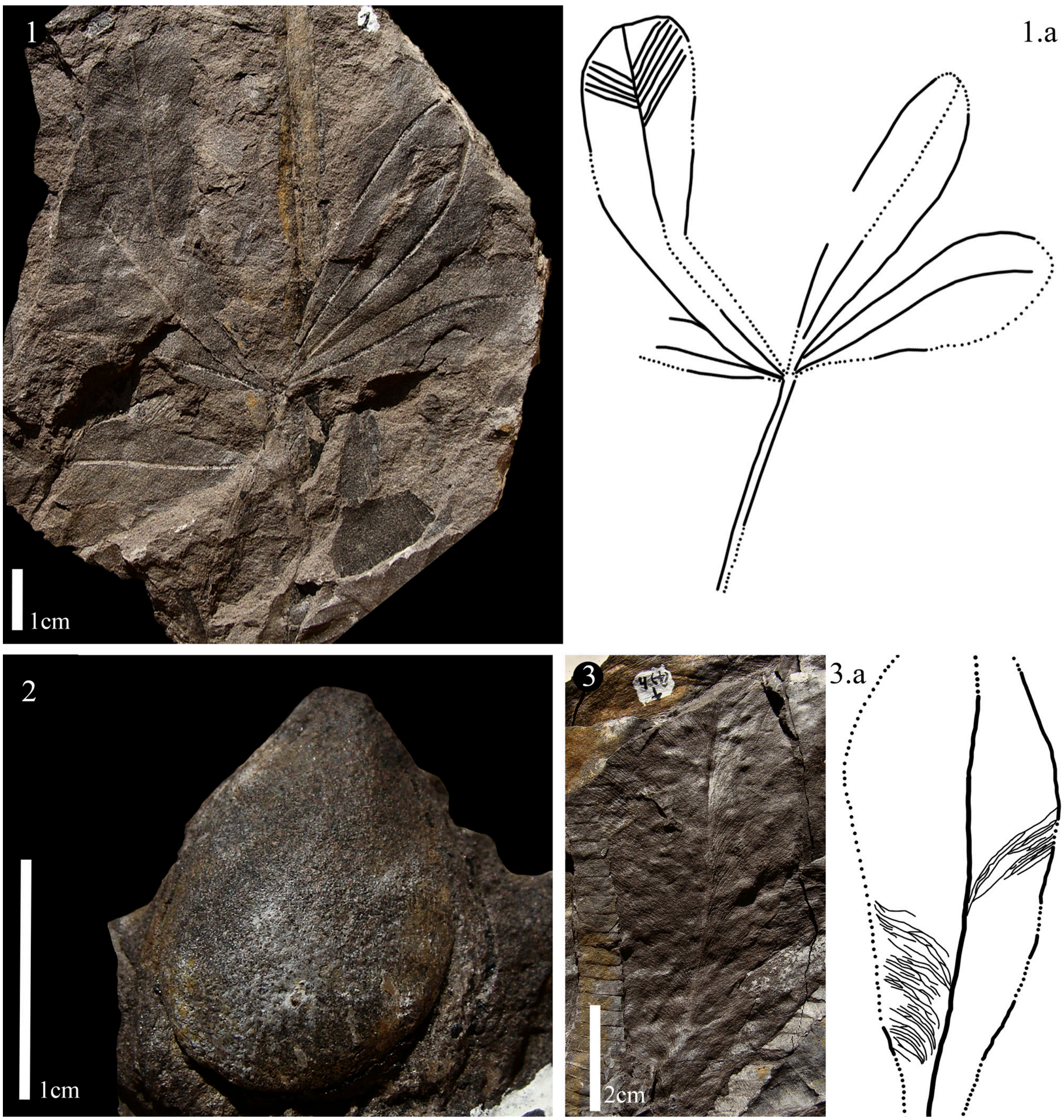

Figure 6. 1, *Sagenopteris colpodes*, palmately compound leaves on a petiole, 1a sketch of *S. colpodes* showing the venation type. 2, *Trigonocarpus*? *oaxacensis*, small obovate seed. 3, *Mexiglossa varia*, simple leaf showing the primary and secondary venation; 3a, sketch of *M. varia* showing the anastomosed venation

Genus *Mexiglossa* Delevoryas et Person, 1975
Type species. *Mexiglossa varia* Delevoryas et Person, 1975.

Mexiglossa varia Delevoryas et Person, 1975
Figure: 6.3-3.a

Material studied. CFZ-Zt 42(3), 51(1)(9), 56, 68(4), 90, 141(2), 186, 201(2), 209(1), 214(4)(6), 231(1), 232(1), 233(2), 234(1)(4), 254, 257(1), 264(1), 298.

Description. Simple leaves with an acute apex, most with secondary anastomosing venation and a large midrib that does not reach the apex. The length of the leaves ranges from 2.5 to 14.2 cm, and its width varies between 1.5 and 4.8 cm, and has 11 to 17 veins per centimeter.

Comments. This species was described by Delevoryas and Person (1975), based on hundreds of very similar leaves of Late Paleozoic Glossopteris. However, the Jurassic material has no reproductive structures or cuticles, and thus it is difficult to assert that they are related to the Glossopteridales which, incidentally, did not reach the Jurassic.

5. Discussion

In the last 100 years, there have been great advances in the knowledge of the Jurassic flora of the Mesoamerican region. The best information generated to date comes from the Mixteco Terrane. These advances were the consequence of studies carried out by several and different generations of paleobotanists. However, the samplings have been intermittent (Aguilera *et al*., 1896; Wieland, 1914; Person and Delevoryas, 1982; Silva-Pineda, 1984; Anderson *et al*., 2007; Pérez-Crespo, 2011), and as such the paleofloristic knowledge is biased. Recently, paleobotanic research has resumed in the Mixteco Terrane (Lozano-Carmona, 2012; Ortiz-Martínez *et al*., 2013; Lozano-Carmona and Velasco-de León, 2014, 2015; Velasco-de León *et al*., 2015) Our results are part of this new wave of paleobotanic work aimed at standardizing research methods, and whose findings are considered significant to the Jurassic flora of the Mixteco Terrane field of knowledge.

The Jurassic flora of the Mixteco Terrane has been collected in several outcrops, distributed in the states of Puebla, Guerrero and Oaxaca (Silva-Pineda, 1984; Ortega-Chávez, 2013; Guerrero-Arévalo, 2014; Martínez-Martínez, 2015; Martínez, 2015). Among these, the Río Ñumi locality of the Zorrillo-Taberna Indiferenciadas Formation (Oaxaca) is outstanding. In the present study we report an increase of almost 50% in the paleofloristic richness (Table 1) as well as new paleofloristic elements. These elements are species belonging to the Equisetales, Bennettitales, Cycadales, Podozamitales, Caytoniales and *Incertae Sedis* (Table 1 and Systematic Paleontology in this work). The Bennettitales are the most diverse group in the paleofloristic association. Also, the presence of the genus *Podozamites*, recorded for the first time in the Mixteco Terrane, is highlighted. Now we can state that the most complete listings of the Mixteco Terrane, produced by Person and Delevoryas (1982) and Silva-Pineda (1984), are easily surpassed by the findings in Río Ñumi. This floristic diversity was collected from three fossiliferous zones of the stratigraphic column.

These zones are located in the stratigraphic column of the Zorrillo-Taberna Indiferenciadas Formation as ZtA (first), ZtB (second) and ZtC (third). Fossiliferous associations differ in every zone. The ZtA association is composed exclusively of Bennettitales, whereas in zones ZtB and ZtC there is more diversity. In ZtB the floristic association is composed of Bennettitales and Equisetales, while in zone ZtC the diversity doubles that of the lower regions (ZtA y ZtB). The diversity of the ZtC zone is increased by seven orders (Table 1; Figure 2).

Overall, it is possible that the floristic diversity of the Zorrillo-Taberna Indiferenciadas Formation was favored by environmental conditions, mainly by an increase in humidity, since in the ZtC zone the increasing diversity is related to the increased availability of water (Lozano-Carmona, 2012). This favourable condition is inferred from the presence of seasonal swamps, this is deduced by the presence of lenticular coal strata in the locality. (Corro-Ortiz and Ruiz-Gonzáles, 2011; Lozano-Carmona, 2012). Then, due to the stability and abundance of resources during the time of deposit of the ZtC zone of the Zorrillo-Taberna Indiferenciadas Formation, a diverse floristic community was established. Furthermore, the presence of endemic genus and species of flora make the Río Ñumi locality representative of the Mixteco Terrane.

The taxonomic composition of the Zorrillo-Taberna Indiferenciadas Formation is the most outstanding among the fossiliferous localities of the Mixteco Terrane, mainly because endemic taxa are registered, and the total number of species exceeds the previous listings for other localities (Person and Delevoryas, 1982; Silva-Pineda, 1984; Pérez-Crespo, 2011; Ortega-Chávez, 2013; Flores-Barragan, 2014; Guerrero-Arévalo, 2014; Martínez-Martínez, 2015; Martínez, 2015). For example, the genus and species *Mexiglossa varia* is an endemic fossil-taxon of the Mixteco Terrane. In addition, there are 13 endemic species belonging to Bennettitales and Ginkgoales: seven species from four genera in the case of Bennettitales, and six species of two genera for Ginkgoales (Table 1) (Wieland, 1914; Delevoryas and Person, 1975; Silva-Pineda, 1984; Velasco-de León *et al*., 2015).

Therefore, the taxonomic composition reported here shows that in the Jurassic outcrops of the Mixteco Terrane, there are still unknown taxa for the Mexican paleobotany. Citing an example, Lozano-Carmona *et al*. (2015) recently reported the first record for the Mixteco Terrane of *Williamsoniella* Thomas. This means that knowledge of the Jurassic flora of the Mixteco Terrane still has a long way to go.

6. Conclusions

In this work we introduce new findings of Jurassic plant fossils for the Zorrillo-Taberna Indiferenciadas Formation, collected using a standardized method. This procedure has led us to propose that this method should be applied to other fossiliferous localities, as it facilitates gathering paleobotanic information, allowing for the consolidation of a paleofloristic list of the Mesoamerican region. With regard to our results, we consider that the floristic association of the studied formation is representative of the Mixteco Terrane, and might constitute the basis for future biostratigraphic, biogeographic and paleoecological interpretations, not only for the Mixteco Terrane, but for the southern portion of North America as well.

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