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Paleobotanical and palynological evidence for the age of the Matzitzi Formation, Mexico

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Abstract. This study addresses some of the stratigraphical problems of the Matzitzi Formation of Puebla and Oaxaca States in Mexico. The age assignment for this unit is controversial although most researchers today accept a Leonardian age (Kungurian, 279.3–272.3 Ma) based on the presence of the gigantopterid *Lonesomia mexicana* Weber. However, after re-examination of the holotype and two paratypes, the absence of diagnostic taxonomic characters prevents the assignment of this fossil type species to the gigantopterid group. Excluding the presence of gigantopterids in this formation, the macroflora seems to be Permian in age. Samples were collected for palynological analysis to determine the age of the formation. Studied palynological assemblages seem to be reworked and are represented by 18 fossil taxa assigned to the following genera: *Calamospora*, *Deltoidospora*, *Densosporites*, *Granulatisporites*, *Laevigatosporites*, *Latipulvinites*, *Lophotriletes*, *Platysaccus*, *Punctatosporites*, *Raistrickia*, *Schopfipollenites*, *Thymospora*, *Triquitrites*, *Verrucosisporites*, and *Vesicaspora*. Described palynomorphs are likely Late Pennsylvanian according to the presence of *Latipulvinites kosankii* and *Thymospora thiessenii*. The biostratigraphic and geochronologic age disparities should be solved in the future.

Keywords. Paleobotany, Palynology, Matzitzi Formation, *Lonesomia mexicana*, Mexico.

1. Introduction

The Paleozoic Matzitzi Formation is the most important continental unit from Mexico due to its diverse and abundant fossil flora, and because it is a key to understanding the terminal stages of Pangea amalgamation in southern Mexico [Ortega-Gutiérrez, 1992].

Southern Mexico was subjected to large-scale thrusting, reactivation of preexisting structures,

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metamorphism and magmatism that occurred at different depths during burial and exhumation throughout the late Paleozoic and early Mesozoic [Elías-Herrera et al., 2007]. The Matzitzi Formation was affected by the Caltepec fault, a dextral transpressional fault, which is one of the best examples of this main structure with multiple reactivation episodes in Mexico [Ortega-Gutiérrez et al., 2018]. It represents the tectonic contact between the Acatlán crystalline Complex (Cambrian-Ordovician boundary to the latest Devonian) and Mesoproterozoic Oaxacan Complex, delimiting the Mixteco and Zapoteco terranes [Elías-Herrera et al., 2007, Ortega-Gutiérrez et al., 2018]. Whether accretion of the Acatlán and Oaxacan complexes took place during the Devonian or the Cretaceous is still a matter of debate [Elías-Herrera et al., 2007, García-Duarte, 1999, González-Hervert et al., 1984, Ramírez-Espinosa, 1984, Sedlock et al., 1993, Yañez et al., 1991].

The Matzitzi Formation is a post-collisional unit, overlying the amalgamation of the metamorphic Acatlán and Oaxacan complexes, and is also an important lithostratigraphic unit for understanding the western end termination of Pangea amalgamation [Elías-Herrera et al., 2007, 2011, García-Duarte, 1999, Hernández-Láscares, 2000].

The age of the Matzitzi Formation has been variously estimated as Pennsylvanian-Permian based on floral content [Magallón-Puebla, 1991, Silva-Pineda, 1970, Weber, 1997, Weber et al., 1987] to Permian, Triassic and Jurassic based on geological data [Bedoya et al., 2020, Burckhardt, 1930, Calderón-García, 1956, Elías-Herrera et al., 2011, Erben, 1956, Hernández-Láscares, 2000, Mülleried, 1933a,b, 1934]. On the basis of its rich macrofossil plant assemblage, this deposit has been considered as Pennsylvanian [Hernández-Láscares, 2000, Silva-Pineda, 1970] or Permian [Magallón-Puebla, 1991, Velasco-Hernández and Lucero-Arellano, 1996, Weber, 1997, Weber et al., 1987]. However, the Matzitzi Formation is now widely accepted as Leonardian (Kungurian, latest early Permian) [Weber, 1997, Weber and Cevallos-Ferriz, 1994], on the basis of the presence of the gigantopterid *Lonesomia mexicana*. Gigantoperids are believed to have first appeared in North American in the Leonardian (Kungurian, latest early Permian) and this age assignment was based mainly by correlation to their appearance in Texas [Weber, 1997]. Gigantopterids are a poorly defined group of uncertain botanical affinity characterized by their distinctive megaphyll leaves with marked reticular venation [Glasspool et al., 2004], Permian-Triassic in age [Wang, 2010]. According to Weber [1997] Leonardian age was also supported by *Sigillaria ichthyolepis-brardii* group, *Pterophyllum*, *Rhipidopsis* or *Ginkgoites* sp., cf. *Sphenophyllum* ex gr. *thonii*, *Sphenophyllum* sp., *Taeniopteris* cf. *multinervis*, which extend since the Late Carboniferous to the early Permian and *Fascipteris* known in China since the Permian. However, these fossil genera have a wider stratigraphic range.

Assigning a Permian age to the Matzitzi Formation based on the presence of gigantopterids is problematic for two reasons: (1) lack of defining traits, (2) vague stratigraphic range. First, many paleobotanists exclude fossils attributed to gigantopterids from Mexico because of the absence of defining characters (Booi et al., 2009, DiMichele et al., 2011b, among others). Many works on gigantopterids indicate that the venation pattern is an important trait to include a fossil plant within this group [Booi et al., 2009, Koidzumi, 1936, Liu and Yao, 2002, Mamay, 1988, Ricardi-Branco, 2008, Seyfullah et al., 2014]. Weber [1997] created a new genus of gigantopterids, *Lonesomia*, because it was difficult to observe its venation pattern, possibly due to trichomes obscuring the surface. Today the only published gigantopterid from the Matzitzi Formation are three samples of *Lonesomia mexicana* (holotype and two paratypes), which corresponds to a new genus and species within this group by Weber [1997]. Second, the stratigraphic range of gigantopterids in North America is unclear, but it may extend into the middle Permian in the United States of America [DiMichele et al., 2011b]. Moreover, we do not know whether gigantoperid-bearing beds in the United States [DiMichele et al., 2000, 2001, 2004a, 2011b] are synchronous with the Matzitzi Formation.

Palynology is an important biostratigraphic tool for continental deposits. There are no formally published palynological studies from the Matzitzi Formation. There is only one palynological report corresponding to the Matzitzi Formation from an abstract that indicates a Pennsylvanian age in the Río Hondo section [Di Pasquo and Hernández-Láscares, 2013].

To provide a better estimate of the deposition age of this formation, in this study we re-examine the holotype and paratypes of *Lonesomia mexicana*

Weber and discuss the macroflora content and palynological assemblages from the Matzitzi Formation of Puebla and Oaxaca States in Mexico.

2. Geological setting

The Matzitzi Formation crops out in the southern part of Puebla State (Figure 1). The Oaxacan and Acatlán Complexes appear unconformably underlying this unit or in fault contact with the Matzitzi Formation in the Los Reyes Metzontla area, being the crystalline basement of the region [Centeno-García et al., 2009]. The latter is unconformably overlain in Caltepec-Metzontla area by Mesozoic red beds (conglomerates and quartz-feldspathic sandstones) [Centeno-García et al., 2009] informally named as Red Conglomerate Unit [González-Hervert et al., 1984], Caltepec red conglomerate [Hernández-Láscares, 2000] and Metzontla Formation [García-Duarte, 1999] (Figure 2).

Aguilera and Ordoñez [1896] were the first to informally describe the Matzitzi Formation, based on studies of localities between Los Reyes Metzontla and San Luis Atolotitlán. Flores [1909] also studied this formation and collected some fossil plants that were the basis for a comprehensive work of the fossil plants from this formation [Silva-Pineda, 1970]. This formation was informally described in a fieldwork guide by Calderón-García [1956] as a 600 m thick sequence of sandstones intercalated by dark shales with abundant fossil plants and occasionally containing conglomerate and coal seams. Later Centeno-García et al. [2009] described the formation as a clastic succession mainly dominated by sandstones intercalated by shales, carbonaceous mudstone, conglomeratic sandstone, and conglomerate (Figure 3A). They also reported coarse massive conglomerate strata near the locality of Los Reyes Metzontla containing metamorphic clasts from the Oaxacan Complex. This continental deposit has been interpreted as an anastomosing fluvial system with six facies associations described along the road connecting Los Reyes Metzontla and Coatepec localities [Centeno-García et al., 2009]. Described facies by these authors include: (1) alluvial and fluvial channel fill (probably debris flows), (2) probably transverse bedforms, conglomeratic bars and channel fill, (3) sandy channel fill, longitudinal bedforms and/or sandy point bars, with scarce paleosols, (4) mostly sandy channel fill eroded by small currents (scour hollows) which may be the result of crevasse splays in some cases, (5) floodplains and/or crevasse splays, and (6) small swamps associated with the river system or floodplains.

The felsic Atolotitlán Tuff of volcanic-arc origin, exposed in San Luis Atolotitlán, is believed to correspond to the Matzitzi Formation [Centeno-García et al., 2009, Elías-Herrera et al., 2011] (Figure 2). This volcanic unit has been dated by U-Pb method (240 ± 3 Ma) as Middle Triassic [Bedoya, 2018, Elías-Herrera et al., 2011] (Figure 2).

It is important to note that a comprehensive stratotype for the Matzitzi Formation has not been established due to incomplete depositional sequence and tectonically separated deposition from this unit has not been correlated yet. The lack of continuous exposures together with the presence of thrusting and faulting makes it difficult to define a single continuous section of even a composite stratotype, due to difficulty to correlate among sections. The Matzitzi Formation has been dated by its relative stratigraphic position between younger and older deposits (Figure 3A) as formally described by Elías-Herrera et al. [2005, 2011]. This deposit lies in different fault blocks, so the outcrops in many cases appear isolated as it is very difficult to correlate strata. Also, modern vegetation obscures bedrock in the studied area. For this reason, it is difficult to locate the stratigraphic levels of the palynological samples from the nearby areas of Los Reyes Metzontla and San Luis Atolotitlán localities (labelled as MATZ samples) within the synthetic stratigraphic column. Only the Río Hondo section presents a stratigraphic continuity, with some minor faulting, and the palynological samples labelled as MATZ RH could be stratigraphically located (Figure 3B). This latter deposit consists of sandstones and siltstones and shales with floral remains (Figure 3B).

The Matzitzi Formation has been much studied for its rich well-preserved macrofloras [Carrillo and Martínez-Hernández, 1981, Flores-Barragan et al., 2019a,b, Silva-Pineda, 1970, Silva-Pineda et al., 2003, Velasco-Hernández and Lucero-Arellano, 1996, Velasco-de León et al., 2015, Weber, 1997, Weber and Cevallos-Ferriz, 1994, Weber et al., 1989]. Most of the macroflora determinations correspond to professional and Master dissertations [Flores-Barragan, 2018, Galván-Mendoza, 2000, Hernández-Láscares,

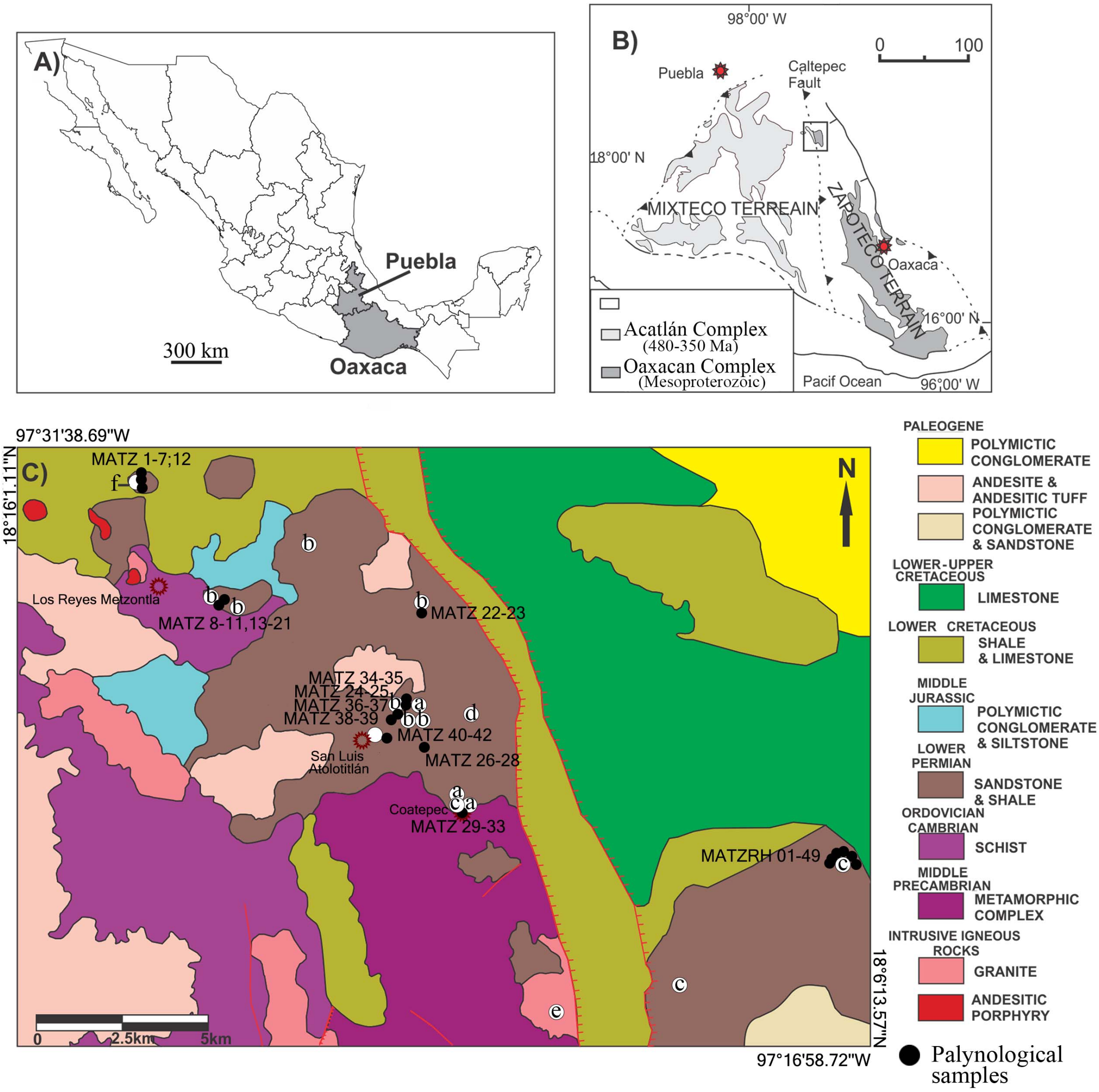

Figure 1. Geographic location, geological setting, and sample location of the studied area. (A) Geographic location of the study area in Mexico. (B) Regional geological setting of the studied area (modified from Elías-Herrera et al., 2005). (C) Detailed geological setting of the studied area. Black circles indicate collected palynological samples (MATZ samples from the nearby areas of Los Reyes Metzontla and San Luis Atolotitlán localities; MATZ RH samples from the Río Hondo section). The location of previously studied biostratigraphic and geochronologic data are indicated by white circles and a letter: fossil plants (a: locations of Weber, 1997; b: Magallón-Puebla, 1991; c: Valdés-Vergara, 2017; Flores-Barragan, 2018); geochronological isotope dating (d: Atolotitlán tuff, Elías-Herrera et al., 2011; e: Cozahuico Granite, Elías-Herrera et al., 2005; f: Bedoya, 2018). *Lonesomia* bearing strata are indicated by the letter a within a white circle, northeast of San Luis Atolotitlán locality.

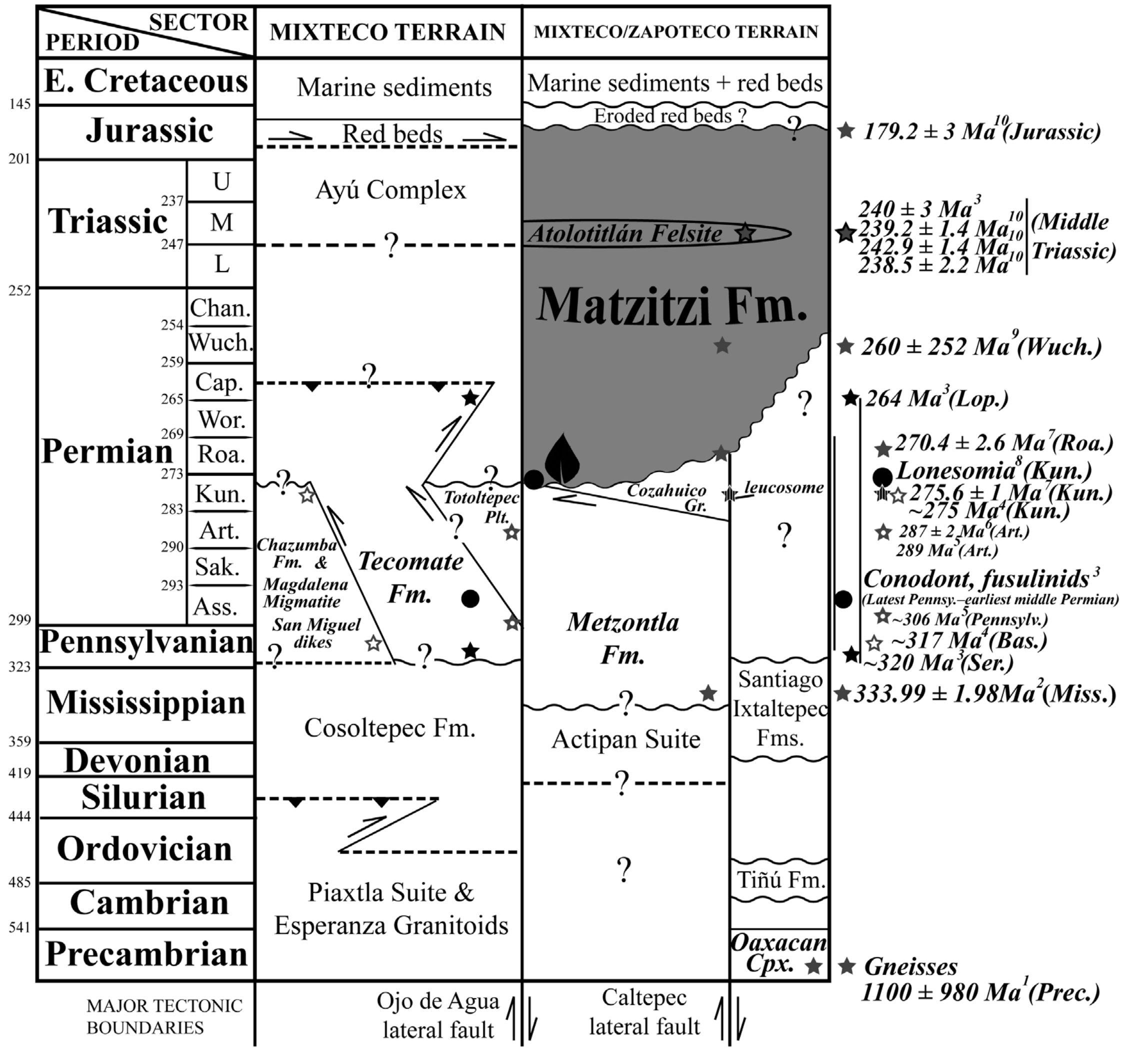

Figure 2. Correlation chart with stratigraphic units present in the studied area and adjacent States. Biostratigraphic and chronostratigraphic data are included. [1]Oaxacan Complex: 1100 ± 980 Ma (Precambrian) [Solari et al., 2003]; [2]Metzontla Formation: 333.99 ± 1.98 Ma (Mississippian) [Elías-Herrera et al., 2011]; [3]Tecomate Formation: Latest Pennsylvanian–earliest Middle Permian (conodont,fusulinids), ~320–264 Ma [Keppie et al., 2004]; [4]Chazumba Suite: ~317–275 Ma [Talavera-Mendoza et al., 2005]; [5]Totoltepec Pluton: ~306–289 Ma [Kirsch et al., 2012]; [6]Totoltepec Pluton: 287 ± 2 Ma (Artinskian) [Yañez et al., 1991]; [7]Anatectic leucosome (275.6 ± 1 Ma); Cozahuico Granite: 270.4 ± 2.6 Ma (Roadian); Matzitzi Formation: 240 ± 3 Ma (Atolotitlán Felsite, Middle Triassic) [Elías-Herrera et al., 2007, 2011]; [8]Matzitzi Formation: Kungurian (Leonardian) on the basis of the presence of the gigantopterid *Lonesomia mexicana* [Weber, 1997]; [9]relative position of the Matzitzi Formation: 260 ± 252 Ma (Wuchiapingian) [Elías-Herrera et al., 2019]; [10]Matzitzi Formation: 238.5 ± 2.2, 239.2 ± 1.4, 242.9 ± 1.4 Ma (Atolotitlán Felsite, Middle Triassic), 179.2 ± 1.98 Ma (Jurassic) [Bedoya et al., 2020]. Cpx.: Complex; Fm.: Formation; Gr.: Granite; Plt.: Pluton; Ass.: Asselian; Sak.: Sakmarian; Art.: Artinskian; Kun.: Kungurian; Roa.: Roadian; Wor.: Wordian; Cap.: Capitanian; Wuch.: Wuchiapingian; Chan.: Changhsingian; L: Lower; M: Middle; U: Upper; E: Early; Prec.: Precambrian; Miss.: Mississippian; Ser.: Serpukhovian; Bas.: Bashkirian; Pennsylv.: Pennsylvanian; Lop.: Lopingian.

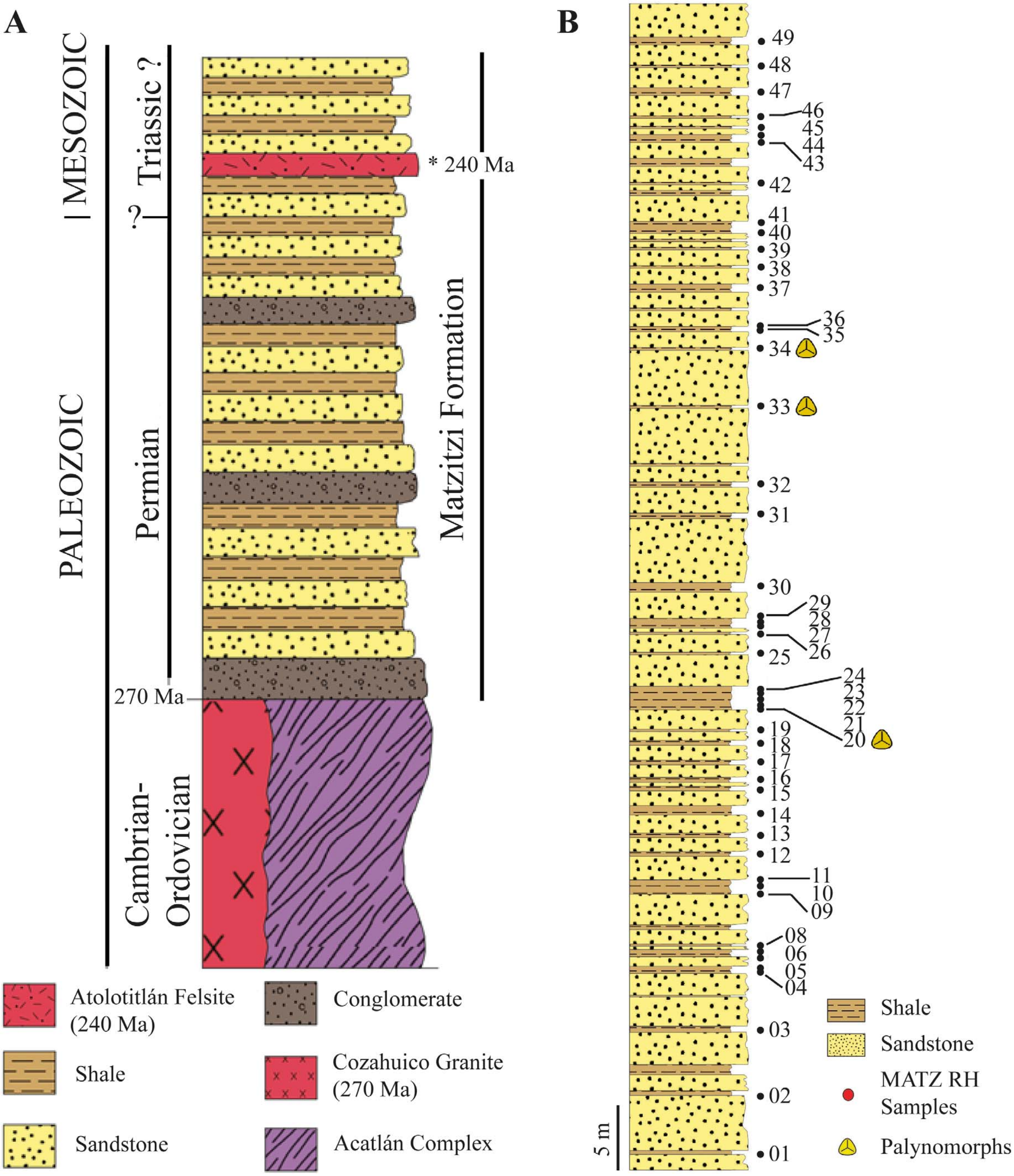

Figure 3. Stratigraphy of the Matzitzi Formation. (A) Synthetic stratigraphic column of the Matzitzi Formation based on Elías-Herrera et al. [2005, 2011]. (B) Stratigraphic column for the Río Hondo Section indicating the stratigraphic position of the 49 collected samples.

2000, Magallón-Puebla, 1991, Rincón-Pérez, 2010, Valdés-Vergara, 2017]. Based on these studies the macroflora is represented by calamitaleans, lepidodendraleans, gigantopterids, ginkgoales, glossopterids and fossil genera including: *Annularia*, *Asolanus*, *Bjuvia*, *Comia*, *Fascipteris*, indeterminate Cycadophyte, *Holcospermum*, *Lesleya*, *Macrotaeniopteris*, *Mexiglossa*, *Neuropteris*, *Pecopteris*, *Plumsteadia*, *Pseudoctenis*, cf. *Psygmophyllum*, *Pterophyllum*, *Schizoneura*, *Sphenophyllum*, *Sphenopteris*, *Taeniopteris*, *Trigonocarpus*, and *Velascoa*.

3. Material and methods

For macroflora studies, images taken by a Nikon D5600 camera were later processed with Photoshop CS6. The re-examined holotype (IGM-PB-1027-1059) and two paratypes (IGM-PB-1027-1058, IGM-PB-1027-1060) of *Lonesomia mexicana* deposited in the National Paleontological Collection at the Instituto de Geología of the Universidad Nacional Autónoma de México (UNAM) were re-studied and re-photographed under a fluorescence stereo microscope (Zeiss AX10 Zoom V16) and were analyzed using Zen Pro software. These three specimens belong to the locality 1027 described by Weber [1997] as Escurridero in the Barranca Xoconoxtitla about 0.5 km northeast of San Luis Atolotitlán in the Puebla State (18° 11′ 36″ N, 97° 24′ 46″ W).

Ninety-one palynological samples were collected from two main areas: nearby Los Reyes Metzontla and San Luis Atolotitlán localities (42 samples) labelled as MATZ located in the state of Puebla and also from the Río Hondo area located in the Mexican Federal Highway 135D connecting Tehuacán and Oaxaca (49 samples) labelled as MATZ RH (Figures 1, 2). None of the palynological sampling localities corresponds to formerly reported macroflora sites except for the Río Hondo section. We also sampled a *Lonesomia mexicana* holotype-containing a piece of rock but lacking palynomorphs. We used standard palynological methods [Batten, 1999, Erdtman, 1960] for palynomorph extraction, using HCl and HF acid digestions followed by Schulze's solution. For palynomorph concentration, we used a 5-micron nylon mesh. Four slides for each stratigraphic level were prepared using Loctite© 349.

We classified and photographed palynomorphs under light microscopy (Olympus BH2, Axio Imager A2m, and Leica DM 2000 LED-equipped by Nikon Coolpix 990, AxioCam Icc5 and Leica ICC50 W cameras respectively). The sample and slide numbers are followed by England Finder© coordinates. All figured specimens are housed at the Paleontology Collection of the Estación Regional del Noroeste (ERNO-UX0016 to ERNO-UX0027), Instituto de Geología, UNAM, in Hermosillo, Sonora, Mexico.

4. Results

4.1. *Macroflora*

The abundant and well-preserved fossil flora from the Matzitzi Formation appears as impression and compression forms. These fossils are autochthonous, parautochthonous, and allochthonous in terms of transportation. Most of the previously studied plant-bearing localities correspond to facies associated with floodplain and/or crevasse splay deposits in anastomosing river system [Centeno-García et al., 2009]. Pieces of evidence supporting the autochthonous nature of fossil plants are the in situ *Calamites* trunks near San Luis Atolotitlán municipality [Carrillo and Martínez-Hernández, 1981] and numerous paleosols associated to these fossiliferous strata from San Francisco Xochiltepec locality [Weber, 2007]. Many paleosols from the Matzitzi Formation and in situ undetermined stumps (possibly of Filicophyta affinity) are also present [Centeno-García et al., 2009, Weber and Cevallos-Ferriz, 1994]. However, most of the flora assemblages are associated to planar or cross-bedding stratification [Centeno-García et al., 2009] corresponding to parautochthonous material. The well-preserved material, the large leaves in connection with the axis, and their disposition parallel to the stratification are an indication of short transport before burial. Lepidodendraleans and calamitalean in most cases are possibly allochthonous (except for in situ autochthonous specimens), and in few cases parautochthonous, as they appear fragmentary associated to channel deposits.

In the Río Hondo section, the plant-bearing strata are scarce and they also present parautochthonous and allochthonous material. Most of the fossil flora from this section is parautochthonous; however, lepidodendraleans and calamitalean appear fragmentary in most cases associated with channel deposits that possibly are parautochthonous–allochthonous (parautochthonous in the case of *Stigmaria*).

We re-examined the holotype and two paratypes of the fossil plant *Lonesomia mexicana* Weber 1997 to determine its affinity to the gigantopterid group. They are poorly preserved as impressions. It is noteworthy that cuticles are not preserved within the flora remains contained in the Matzitzi Formation. As described by Weber [1997] these specimens are characterized by having: "*leaf simple, symmetrical, sessile or with very short petiole, blade elliptic to lanceolate, lamina leathery, arched between midrib and margin, base rounded, tip rounded or retuse, margin entire, lamina reaching about 5 cm in width and over 20 cm in length (length/width ratio about 5). Petiole to 5 mm in width. Midrib straight, to 3 mm wide at lamina base, narrowing to the tip. Venation of at least three orders, secondaries intersected at the midrib at 75°–80°, tertiaries intersected on these at about 45°*".

Only the primary and secondary veins are distinguished in the paratypes (IGM-PB-1027-1058 and IGM-PB-1027-1060) (Figure 4). The tertiary veins only can be observed in the holotype (IGM-PB-1027-1059), and they are not clearly defined (Figure 5A–C). Zen Pro software was used to determine the intersection angles between venation orders in the holotype (Figure 5C). The measured angles differ slightly with Weber's description: secondary veins extend from the midrib at an angle of around 62°–65° (Weber reported 75°–80°) and an angle of 29°–34° at the intersection of the secondaries at the midrib and tertiaries (Weber reported around 45°). The use of a fluorescence stereo zoom microscope (Zeiss Discovery V8) did not help determine third-order or higher venation patterns, which are only visible in a small area of the holotype leaf (Figure 5D). For this reason, until more specimens are found, it will be risky to classify *Lonesomia mexicana* as a gigantopterid.

4.2. *Microflora*

From 91 collected palynological samples of the Matzitzi Formation, only five samples produced scarce and poorly preserved palynomorphs with a total of 18 fossil taxa identified (Figures 6, 7, Tables 1 and 2). Three samples (MATZ 27, MATZ RH 33, and MATZ RH 34) produced less than 10 palynomorphs per stratigraphic level, and only two (MATZ 1 and MATZ RH 20) have more abundance with less than 50 palynomorphs for each stratigraphic level.

Most of the studied palynomorphs from San Luis Atolotitlán, Los Reyes Metzontla (MATZ), and Río Hondo areas (MATZ RH) have a wide stratigraphic range and almost all identified genera indicate a Late Carboniferous–early Permian age. The palynological assemblages correspond to wetland microflora genera as *Calamospora* (Equisetales including calamitaceans, Sphenophyllales and Noeggerathiales), *Deltoidospora*, *Granulatisporites*, *Lophotriletes*, *Triquitrites* and *Raistrickia* (herbaceous fern spores), *Laevigatosporites* (Sphenophyllales and Marattiales), *Punctatosporites* and *Thymospora* (Marattiales), *Schopfipollenites* (Medullosales) and *Vesicaspora* (Peltaspermales). All of the identified spores are typical of Late Pennsylvanian palynofloras elsewhere, but the presence of *Thymospora thiessenii* and *Latipulvinites kosankii* could restrict the age of MATZ RH 20 stratigraphic level of Río Hondo deposit to the Middle-Late Pennsylvanian [e.g. Peppers, 1964, 1985, Ravn, 1979, 1986]. On the one hand, *Latipulvinites kosankii* Peppers 1964 (Figure 6G) is restricted to the Pennsylvanian of Illinois, Kentucky, Texas, and England [Peppers, 1964, Stone, 1969, Ravn, 1979, Turner, 1991]. On the other hand, *Thymospora thiessenii* (Kosanke) Wilson and Venkatachala, 1963 (Figure 6J) known from the Bolsovian–Westphalian boundary (Westphalian C-D) in Europe and the United States of America to the Stephanian C, that is to say, Middle-Late Pennsylvanian [Clendening, 1972, Hower et al., 1983, Jerzykiewicz, 1987, Kosanke, 1984, Lesnikowska and Willard, 1997, Peppers, 1985, Playford and Dino, 2005, Vozárová, 1998, Waters et al., 2011]. This latter fossil species has also been reported from MATZ 27 stratigraphic level from the San Luis Atolotitlán area.

Even though most of the taxa extend into the early Permian, they are gradually supplanted by Permian forms, such as taeniates, which are completely absent in these assemblages. The lack of Permian pollen and spores does not determine that they were not present during the deposition of the Matzitzi Formation because they may not have been preserved or restricted to other paleoenvironmental conditions. So, we could confidently conclude that the palynological assemblages at the Río Hondo section (MATZ RH 20) and MATZ 27 are likely Pennsylvanian, possibly earliest Permian.

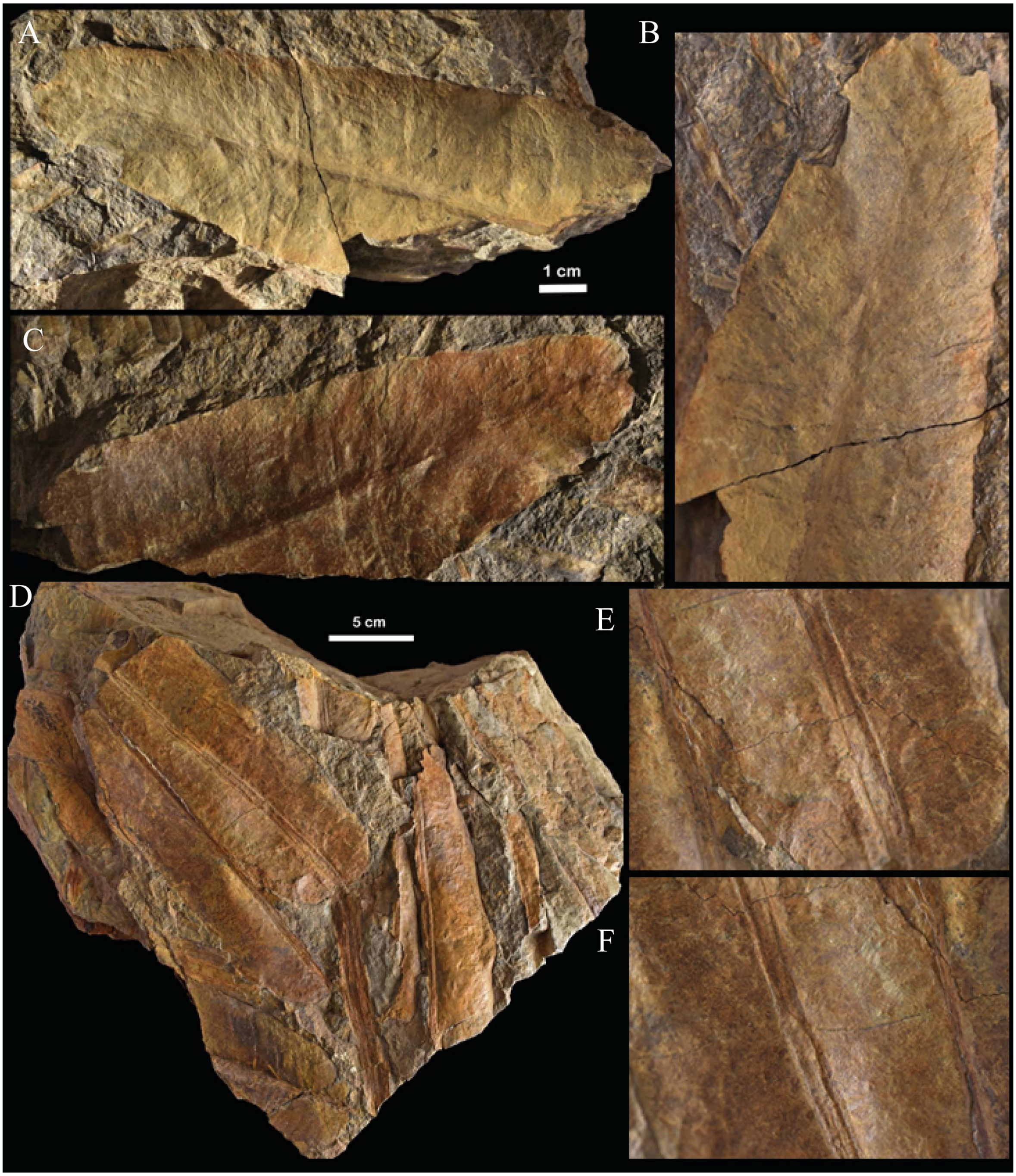

Figure 4. *Lonesomia mexicana* paratypes IGM-PB-1027-1058 and IGM-PB-1027-1060 (A–C). (A) Part and counterpart of the paratype IGM-PB-1027-1060. (B) Detail of the paratype IGM-PB-1027-1060 lacking preserved venation above the second order. (D) Paratype IGM-PB-1027-1058. (E,F) A detail of the leaf belonging to the paratype IGM-PB-1027-1058 which lacks venation above the second order.

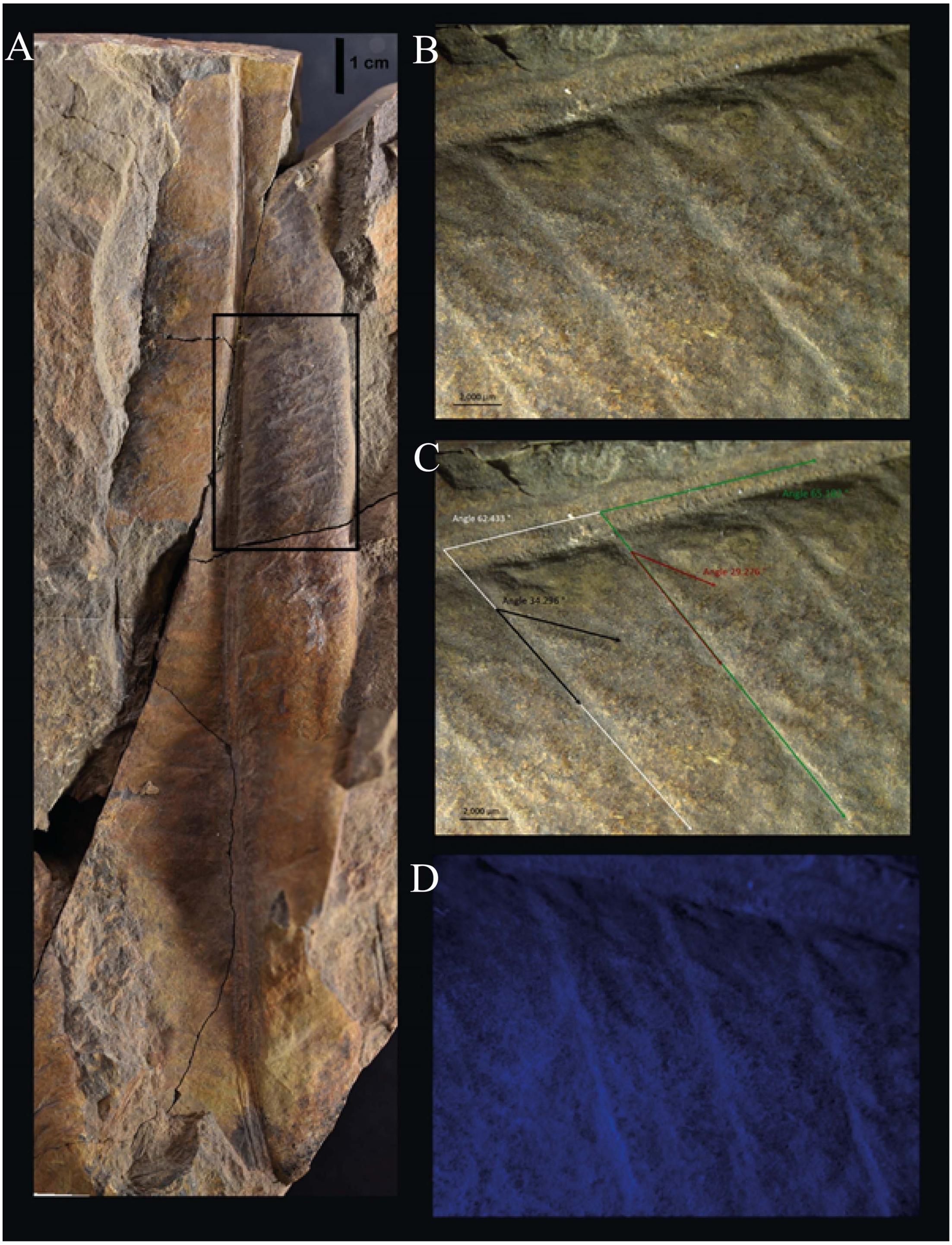

Figure 5. (A) *Lonesomia mexicana* IGM-PB-1027-1059 holotype. (B) Detail of an area of the leaf (indicated by a black square) used for the character description under white light. (C) Image taken using the Zen Pro programme indicating the second and third order venation angles. (D) Image under ultraviolet light that demonstrates the difficulty for determining third order venation pattern.

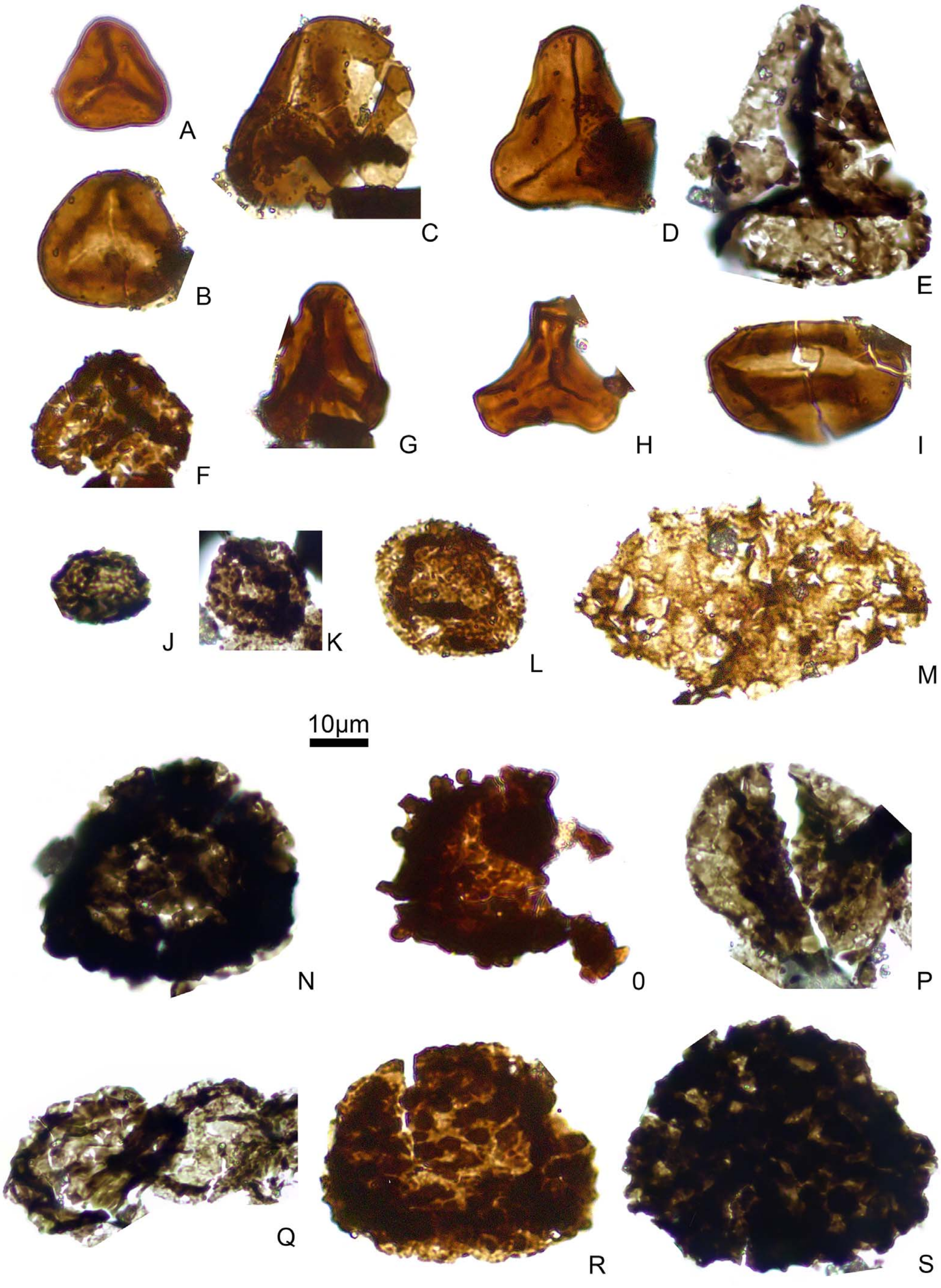

Figure 6. Palynomorphs from the Matzitzi Formation from San Francisco Xochiltepec, Santiago Coatepec, San Luis Atolotitlán, Los Reyes Metzontla and Río Hondo areas, Mexico. (A) *Deltoidospora gracilis* (Imgrund) Ravn, 1986, EF: MATZ 1_4_4_U322. (B) *Deltoidospora levis* (Kosanke) Ravn, 1986 EF: MATZ 1_2_4_S520. (C) *Deltoidospora priddyi* (Berry) McGregor, 1973, EF: MATZ 1_3_4 D464. (D) *Deltoidospora adnata* (Kosanke) McLean, 1993, EF: MATZ 1_3_4 U301. (E) *Deltoidospora sphaerotriangula* (Loose) Ravn, 1986, EF: MATZ RH 20_2_4_T431. (F) *Granulatisporites* sp., EF: MATZ RH 34_3_4_V321.

Figure 6 (cont.). (G) *Latipulvinites kosankii* Peppers, 1964, EF: MATZ 1_4_4_C432. (H) *Triquitrites* sp., EF: MATZ 1_4_4_S310. (I) *Laevigatosporites medius* Kosanke, 1950, EF: MATZ 1_2_4_X681. (J) *Thymospora thiessenii* (Kosanke) Wilson and Venkatachala, 1963, EF: MATZ RH 20_2_4_S384. (K) *Punctatosporites minutus* (Ibrahim) Alpern and Doubinger, 1973, EF: MATZ RH 20_2_4_X430. (L) *Punctatosporites punctatus* Ibrahim, 1933, EF: MATZ RH 34_2_4_Q474. (M) *Laevigatosporites minor* Loose, 1934, EF: MATZ RH 20_2_4_P551. (N) *Densosporites* sp., EF: MATZ RH 20_4_4_R324 (O) *Raistrickia saetosa* (Loose) Schopf et al., 1944, EF: MATZ RH 34_4_4_O574. (P) *Vesicaspora* cf. *wilsonii* (Schemel) Wilson and Venkatachala, 1963, EF: MATZ RH 20_4_4_M394. (Q) *Platysaccus* sp., EF: MATZ RH 20_2_4_P352. (R) *Verrucosisporites* sp. Type 1, EF: MATZ RH 20_3_4_C490. (S) *Verrucosisporites* sp. Type 2, EF: MATZ RH 20_1_4_Q290. EF: England Finder® coordinates. Scale bar: 10 µm.

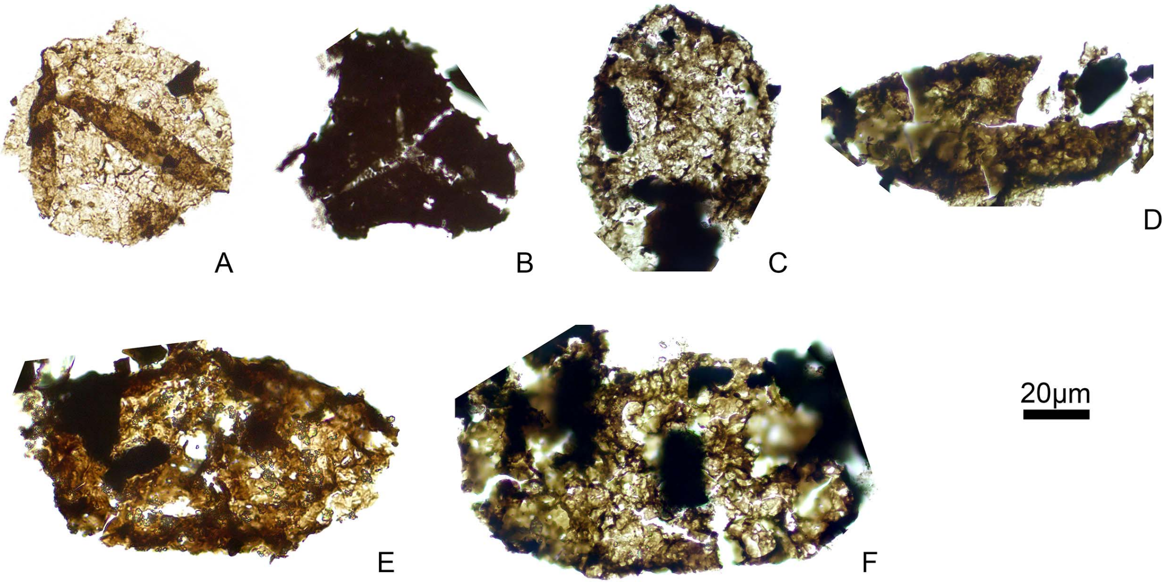

Figure 7. Palynomorphs from the Matzitzi Formation from San Francisco Xochiltepec, Santiago Coatepec, San Luis Atolotitlán, Los Reyes Metzontla, and Río Hondo areas, Mexico. (A) *Calamospora* sp., EF: MATZ RH 20_1_4_N353. (B) *Lophotriletes* sp., EF: MATZ 27_1_4_Y560. (C) *Schopfipollenites ellipsoides* (Ibrahim) Potonié and Kremp, 1954, EF: MATZ RH 20_2_4_Y380. (D) *Laevigatosporites vulgaris* (Ibrahim) Ibrahim, 1933, EF: MATZ RH 20_4_4_O340. (E) *Laevigatosporites maximus* (Loose) Potonié and Kremp, 1956, EF: MATZ RH 33_2_4 S522. (F) *Laevigatosporites maximus* (Loose) Potonié and Kremp, 1956, EF: MATZ RH 20_2_4_W312. EF: England Finder® coordinates. Scale bar: 20 µm.

5. Discussion

The palynomorphs seem to be reworked, especially given the poor condition of the preservation and the very low amount of grains, contrary to the parautochthonous fossil plants. Hence, it is impossible to correlate micro and macroflora. As stated by Silva-Pineda [1970] and Weber [1997] it seems that the Matzitzi Formation contains typical Late Pennsylvanian and early Permian macroflora.

In Euramerican areas, based on macroflora and palynological studies, it has been observed that the initial flora adapted to humid conditions in the tropics during the Late Mississippian (Namurian) was replaced by the Pennsylvanian wetland flora dominated by lycopsids, ferns, and primitive seed plants [DiMichele et al., 2006, Pfefferkorn et al., 2000]. During the Late Pennsylvanian, when aridity increased but alternated with wetter periods, floras rich in conifers, peltasperms, and other seed plants began

Table 1. Observed pollen and spores from studied palynomorph-containing samples

Genera/Levels	MATZ 1	MATZ 27	MATZ RH 20	MATZ RH 33	MATZ RH 34
Calamospora sp.			1		
Deltoidospora gracilis	1				
Deltoidospora levis	3				
Deltoidospora priddyi	7				
Deltoidospora adnata	16	1			
Deltoidospora sphaerotriangula			2		
Deltoidospora sp.		2	2		
Densosporites sp.			1		
Granulatisporites sp.			1		1
Laevigatosporites medius	7	1	1		3
Laevigatosporites minor			2		
Laevigatosporites maximus			1	1	
Laevigatosporites vulgaris			1		
Latipulvinites kosankii			2		1
Lophotriletes sp.		1		1	
Platysaccus sp.			1		
Punctatosporites minutus		4	2		
Punctatosporites punctatus					4
Raistrickia saetosa					1
Schopfipollenites ellipsoides			1		
Thymospora thiessenii		1	1		
Triquitrites sp.	3				
Verrucosisporites sp. Type 1			2		1
Verrucosisporites sp. Type 2			1		1
Vesicaspora cf. *wilsonii*			1		
Total	37	10	23	2	12

to appear while the species that dominated the Pennsylvanian wetlands declined [DiMichele et al., 2004b]. In the Euramerican Province, the transition from the Pennsylvanian to the Permian encompassed a gradual global environmental change from ever-wet during the Pennsylvanian to a drier Permian [e.g. DiMichele et al., 2004a, 2008, Michel et al., 2015, Tabor and Poulsen, 2008]. During this change, considerable tectonic activity in the tropics is recorded. These phenomena, may have combined to affect both local and regional microclimates and depositional environments [DiMichele et al., 2004a]. A replacement of hygrophytic by mesophytic and meso-xerophytic flora that tolerate seasonally dry climate is observed. Also, xeric floras can be found intercalated with vegetation typical of very wet conditions, even at the scale of individual outcrops [Broutin et al., 1990, DiMichele and Aronson, 1992, DiMichele et al., 2004b, 2019, Kerp and Fichter, 1985]. It seems that climatic conditions maintained along wetland corridors since Middle Pennsylvanian to Artinskian, possibly fringing the channels surrounded by plants adapted to a drier condition under a seasonal climate as reported for the Appalachians, New Mexico, Texas and Utah [DiMichele et al., 2011a]. It is also significant that the transition from wetter-to-drier climates during Pennsylvanian–Cisuralian range is different depending on the paleogeographic location; being earlier in New Mexico (Middle Pennsylvanian), and later in Texas–Appalachians (Late Pennsylvanian) and Utah (Permian) [DiMichele et al., 2011a] so it is worth expecting a diachronic disappearance of typically Carboniferous flora adapted to wetlands in drier conditions in Euramerica.

In the Euramerican Province (including Mexico and the U.S.A.), the more common small spores

Table 2. Collected samples and their coordinates. Outlined in grey colour indicate palynomorph-containing stratigraphic levels

Samples	Coordinates	Samples	Coordinates
MATZ		MATZ RH	
MATZ 1	18° 15′ 11.8″ N, 97° 29′ 42.6″ W	MATZ RH 1	18° 09′ 09.3″ N, 97° 18′ 2.8″ W
MATZ 2	18° 15′ 11.6″ N, 97° 29′ 42.7″ W	MATZ RH 2	18° 09′ 09.4″ N, 97° 18′ 3.0″ W
MATZ 3	18° 15′ 11.3″ N, 97° 29′ 42.5″ W	MATZ RH 3	18° 09′ 09.5″ N, 97° 18′ 3.2″ W
MATZ 4	18° 15′ 11.3″ N, 97° 29′ 42.5″ W	MATZ RH 4	18° 09′ 09.7″ N, 97° 18′ 4.0″ W
MATZ 5	18° 15′ 11.3″ N, 97° 29′ 42.5″ W	MATZ RH 5	18° 09′ 09.7″ N, 97° 18′ 4.0″ W
MATZ 6	18° 15′ 11.3″ N, 97° 29′ 42.6″ W	MATZ RH 6	18° 09′ 09.8″ N, 97° 18′ 4.3″ W
MATZ 7	18° 15′ 11.3″ N, 97° 29′ 42.6″ W	MATZ RH 7	18° 09′ 09.8″ N, 97° 18′ 4.3″ W
MATZ 8	18° 13′ 20.4″ N, 97° 28′ 22.5″ W	MATZ RH 8	18° 09′ 09.8″ N, 97° 18′ 4.3″ W
MATZ 9	18° 13′ 21.0″ N, 97° 28′ 22.3″ W	MATZ RH 9	18° 09′ 10.1″ N, 97° 18′ 4.9″ W
MATZ 10	18° 13′ 21.0″ N, 97° 28′ 22.3″ W	MATZ RH 10	18° 09′ 10.1″ N, 97° 18′ 4.9″ W
MATZ 11	18° 13′ 21.0″ N, 97° 28′ 22.3″ W	MATZ RH 11	18° 09′ 10.4″ N, 97° 18′ 5.2″ W
MATZ 12	18° 15′ 11.3″ N, 97° 29′ 42.6″ W	MATZ RH 12	18° 09′ 10.9″ N, 97° 18′ 5.8″ W
MATZ 13	18° 13′ 16.1″ N, 97° 28′ 13.1″ W	MATZ RH 13	18° 09′ 11.0″ N, 97° 18′ 6.1″ W
MATZ 14	18° 13′ 16.1″ N, 97° 28′ 13.1″ W	MATZ RH 14	18° 09′ 11.2″ N, 97° 18′ 6.3″ W
MATZ 15	18° 13′ 16.1″ N, 97° 28′ 13.1″ W	MATZ RH 15	18° 09′ 11.5″ N, 97° 18′ 6.8″ W
MATZ 16	18° 13′ 16.1″ N, 97° 28′ 13.1″ W	MATZ RH 16	18° 09′ 11.5″ N, 97° 18′ 6.8″ W
MATZ 17	18° 13′ 16.0″ N, 97° 28′ 12.6″ W	MATZ RH 17	18° 09′ 11.7″ N, 97° 18′ 7.3″ W
MATZ 18	18° 13′ 16.0″ N, 97° 28′ 12.6″ W	MATZ RH 18	18° 09′ 12.1″ N, 97° 18′ 8.2″ W
MATZ 19	18° 13′ 24.1″ N, 97° 28′ 09.4″ W	MATZ RH 19	18° 09′ 12.4″ N, 97° 18′ 8.8″ W
MATZ 20	18° 13′ 24.1″ N, 97° 28′ 09.4″ W	MATZ RH 20	18° 09′ 12.6″ N, 97° 18′ 9.2″ W
MATZ 21	18° 13′ 24.1″ N, 97° 28′ 09.4″ W	MATZ RH 21	18° 09′ 12.6″ N, 97° 18′ 9.2″ W
MATZ 22	18° 13′ 04.3″ N, 97° 24′ 53.4″ W	MATZ RH 22	18° 09′ 12.6″ N, 97° 18′ 9.2″ W
MATZ 23	18° 13′ 04.3″ N, 97° 24′ 53.4″ W	MATZ RH 23	18° 09′ 12.6″ N, 97° 18′ 9.2″ W
MATZ 24	18° 11′ 39.0″ N, 97° 25′ 00.2″ W	MATZ RH 24	18° 09′ 12.6″ N, 97° 18′ 9.2″ W
MATZ 25	18° 11′ 39.0″ N, 97° 25′ 00.2″ W	MATZ RH 25	18° 09′ 12.8″ N, 97° 18′ 9.6″ W
MATZ 26	18° 11′ 07.8″ N, 97° 24′ 38.9″ W	MATZ RH 26	18° 09′ 12.9″ N, 97° 18′ 9.9″ W
MATZ 27	18° 11′ 07.8″ N, 97° 24′ 38.9″ W	MATZ RH 27	18° 09′ 13.1″ N, 97° 18′ 10.1″ W
MATZ 28	18° 11′ 07.8″ N, 97° 24′ 38.9″ W	MATZ RH 28	18° 09′ 13.1″ N, 97° 18′ 10.1″ W
MATZ 29	18° 09′ 59.5″ N, 97° 23′ 53.6″ W	MATZ RH 29	18° 09′ 13.1″ N, 97° 18′ 10.1″ W
MATZ 30	18° 09′ 59.5″ N, 97° 23′ 53.6″ W	MATZ RH 30	18° 09′ 13.4″ N, 97° 18′ 10.7″ W
MATZ 31	18° 09′ 59.5″ N, 97° 23′ 53.6″ W	MATZ RH 31	18° 09′ 13.8″ N, 97° 18′ 11.9″ W
MATZ 32	18° 09′ 59.5″ N, 97° 23′ 53.6″ W	MATZ RH 32	18° 09′ 14.0″ N, 97° 18′ 12.3″ W
MATZ 33	18° 09′ 59.5″ N, 97° 23′ 53.6″ W	MATZ RH 33	18° 09′ 14.3″ N, 97° 18′ 13.6″ W
MATZ 34	18° 11′ 41.7″ N, 97° 24′ 59.2″ W	MATZ RH 34	18° 09′ 14.3″ N, 97° 18′ 14.3″ W
MATZ 35	18° 11′ 41.7″ N, 97° 24′ 59.2″ W	MATZ RH 35	18° 09′ 14.0″ N, 97° 18′ 14.6″ W
MATZ 36	18° 11′ 36.2″ N, 97° 25′ 03.1″ W	MATZ RH 36	18° 09′ 14.0″ N, 97° 18′ 14.6″ W
MATZ 37	18° 11′ 36.2″ N, 97° 25′ 03.1″ W	MATZ RH 37	18° 09′ 13.6″ N, 97° 18′ 15.0″ W
MATZ 38	18° 11′ 33.1″ N, 97° 25′ 08.6″ W	MATZ RH 38	18° 09′ 13.7″ N, 97° 18′ 15.4″ W
MATZ 39	18° 11′ 33.1″ N, 97° 25′ 08.6″ W	MATZ RH 39	18° 09′ 13.4″ N, 97° 18′ 16.1″ W
MATZ 40	18° 11′ 14.5″ N, 97° 25′ 18.2″ W	MATZ RH 40	18° 09′ 13.4″ N, 97° 18′ 16.3″ W
MATZ 41	18° 11′ 14.5″ N, 97° 25′ 18.2″ W	MATZ RH 41	18° 09′ 13.2″ N, 97° 18′ 16.5″ W
MATZ 42	18° 11′ 14.5″ N, 97° 25′ 18.2″ W	MATZ RH 42	18° 09′ 12.7″ N, 97° 18′ 17.5″ W

(continued on next page)

Table 2. (continued)

Samples	Coordinates
MATZ RH	
MATZ RH 43	18° 09′ 11.9″ N, 97° 18′ 18.6″ W
MATZ RH 44	18° 09′ 11.9″ N, 97° 18′ 18.6″ W
MATZ RH 45	18° 09′ 11.7″ N, 97° 18′ 18.8″ W
MATZ RH 46	18° 09′ 11.5″ N, 97° 18′ 18.9″ W
MATZ RH 47	18° 09′ 10.6″ N, 97° 18′ 19.4″ W
MATZ RH 48	18° 09′ 09.9″ N, 97° 18′ 19.8″ W
MATZ RH 49	18° 09′ 09.3″ N, 97° 18′ 20.0″ W

found in Late Pennsylvanian coals include Marattialean spores (*Thymospora* spp., *Punctatisporites minutus*, *Punctatosporites* spp., *Cyclogranisporites* spp., *Laevigatosporites minimus*, *Laevigatosporites medius*, *Laevigatosporites ovatus*), as well as such herbaceous fern taxa as *Lophotriletes*, *Raistrickia*, *Triquitrites* and *Deltoidospora* [DiMichele et al., 2018, Eble et al., 2013]. *Verrucosisporites* also occur, but much less frequently [Eble et al., 2013]. These taxa are typical of the uppermost Pennsylvanian coal from the Bursum Formation, New Mexico, including significant amounts of *Vesicaspora* [DiMichele et al., 2016] and coal of similar age described from north-central Texas [Looy and Hotton, 2014].

There is also evidence of calamitaleans, reported from macrofossil remains [DiMichele et al., 2016] in the Bursum Formation (Carrizo Arroyo, New Mexico, U.S.A.). Therefore, Marattialeans and calamitaleans were the most important wetland plant groups throughout western Pangea during the Late Pennsylvanian and well into the early Permian, reflecting their tolerance of soil moisture fluctuation and also their dispersal capacities [DiMichele et al., 2016].

In the eastern part of Euramerican Province (Western Europe), palynological assemblages display a broadly similar pattern [e.g. Clayton et al., 1977, Juncal et al., 2019]. The wetland microflora (marattialean spores and herbaceous fern taxa) and pollen of *Calamites* and *Cordaites* are dominant.

The only two studies [Rincón-Pérez, 2010, Valdés-Vergara, 2017] based on macrofloral content from the Río Hondo section, representing the most complete and continuous stratigraphic section for the Matzitzi Formation, show different abundance data due to methodological procedure: the first author without considering their stratigraphic level and the second author indicating it. The main flora representatives in this locality seem to be Filicophyta, Lycophyta and Spermatophyta and less abundant is Equisetophyta (calamitalean). The macroflora composition changes depending on its stratigraphic range [Valdés-Vergara, 2017] due to differences in the depositional environment. Both studies agree that Marattiales (*Pecopteris* spp.) and lepidodendrales (*Sigillaria*) are well-represented in the macroflora assemblage. Based on macroflora remains from the Río Hondo section [Rincón-Pérez, 2010, Valdés-Vergara, 2017] an early Permian age is suggested for the Matzitzi Formation. Four key taxa ranging from late Carboniferous to early Permian age have been described. *Sigillaria brardii-ichthyolepis* group is present in the Río Hondo section [Valdés-Vergara, 2017, Weber, 1997], which is also common in the Matzitzi Formation [Weber, 1997], and it ranges from the Late Pennsylvanian [Remy and Remy, 1977] to early Permian in USA [Blake and Gillespie, 2011]. *Taeniopteris multinervis* is known from the Late Pennsylvanian-early Permian in the USA [Remy and Remy, 1975] and medullosalean seed *Trigonocarpus* extend from Late Mississippian to early Permian [Cleal and Thomas, 2019]. *Holcospermum* is a common element from the Carboniferous but some reports have described it from the early Permian in Germany [Barthel, 2016] and Kansas [McKinley, 1966]. Moreover, the fossil genus *Comia* is known since the Permian [Mamay et al., 2009, Weber, 1997] and it occurs in North America (Texas and Oklahoma) in the early Permian (Artinskian, Cisuralian) [Mamay et al., 2009], restricting the age of the Matzitzi Formation in this locality to a probable age not older than the Artinskian. In consequence, the macroflora from the Río Hondo section would likely correspond to the Artinskian–Kungurian. This would support the idea of reworked palynomorphs. Reports of *Pseudoctenis* from the Matzitzi Formation at Río Hondo and Camino sites [Valdés-Vergara, 2017] remain inconclusive due to the poor preservation of described specimens and lack of cuticle information. *Pseudoctenis* is known since the late Permian [Blomenkemper et al., 2018, Schweitzer, 1986] and it is an important component during the Mesozoic, especially in the uppermost Triassic and Jurassic [Taylor et al., 2009]. This fossil genus has been described from early and middle Permian deposits in India [Maheshwari and Bajpai, 2001], however, it has not been figured. If confirmed the occurrence of *Pseudoctenis* in the Matzitzi Formation, this fossil genus would extend its stratigraphic range up to the lower Permian.

Other fossil flora genera from the Matzitzi Formation known since the early Permian from other localities are *Fascipteris* [Magallón-Puebla, 1991] and *Bjuvia* [Velasco-de León et al., 2015]. Magallón-Puebla [1991], also noted that although a new species of *Pecopteris* might be present in this formation, it should have more Permian than Carboniferous affinities. Likewise, using the macroflora, a Permian age seems more likely for the Matzitzi Formation.

The fossil plants exhibit fragmentary preservation, breakup during collection, and obscured plant characters, that make much of the material unidentifiable. This is the case of *Lonesomia mexicana* that does not allow the identification of the venation pattern above the second order. In the long run, the identification of plant fossils of the Matzitzi Formation is greatly reduced due to the poor preservation of key diagnostic characters, their fragmented nature, and in some cases their very low abundance in the fossil record. This is especially problematic for specimens with glossopterid affinity. For example, a specimen initially described as *Glossopteris* was finally identified as *Sphenophyllum* ex gr. *thonii* [Weber, 1997]. There are also examples of misidentified specimens such as *Fascipteris* sp. cf. *F. hallei* [Magallón-Puebla, 1991] which was initially described as *Neuropteris jugosa* by Silva-Pineda [1970] and *Schizoneura gondwanensis* [Flores-Barragan, 2018] that was initially described as *Annularia* sp. by Velasco-de León et al. [2015]. These complications indicate that more studies are required for a comprehensive determination of the macroflora remains from the Matzitzi Formation, including consideration of their stratigraphic level and locality.

The available geochronological data for the Matzitzi Formation differs from our results (Figure 2). On the one hand, the Oaxacan Complex exposed southeast of San Luis Atolotitlán consists of quartz-feldspathic and garnet gneisses in granulite facies that are Grenvillian in age (1.1–0.98 Ga) [Keppie and Ortega-Gutiérrez, 1999, Solari et al., 2003]. On the other hand, the Acatlán Complex appears as highly deformed and metamorphosed green schists to the west of Los Reyes Metzontla and southeast of La Compañía (Puebla) whose age is poorly understood [Keppie et al., 2004]. The youngest units belonging to the Acatlán Complex (in chronological order: Tecomate Formation, Totoltepec stock, and San Miguel intrusions) are less deformed and metamorphosed compared to the oldest units of this complex [Yañez et al., 1991]. The Tecomate Formation has been considered the Latest Pennsylvanian–earliest middle Permian in age based on U–Pb SHRIMP dating (~320–264 Ma) and conodont and fusulinid content [Keppie et al., 2004]. One of the youngest units of the Acatlán Complex is the Chazumba Suite: the maximum depositional age of the Magdalena Formation is ~317 Ma, and the maximum depositional age of the overlying Chazumba Formation is ~275 Ma [Talavera-Mendoza et al., 2005]. The youngest unit of the Acatlán Complex, the San Miguel intrusive has interpreted with two distinct emplacement ages based on Rb–Sb dating indicating two thermal events in the Late Triassic–Early Jurassic (Rhaetian–Hettangian; 207 ± 9 Ma) and Middle Jurassic (Aalenian; 173 ± 0.3 Ma) [Ruiz-Castellanos, 1979]. The Magdalena migmatite also corresponding to one of the youngest units of the Acatlán Complex, is concordant with this Middle Jurassic age (Aalenian–Bajocian; 170 ± 2 Ma) by U–Pb method [Powell et al., 1999]. The amalgamation of the Acatlán and Oaxacan complexes apparently took place in the early Permian represented by the foliated Totoltepec pluton (287 ± 2 Ma; ~306–289 Ma) dated by U–Pb method in zircons [Kirsch et al., 2012, Yañez et al., 1991] and the anatectic leucosome (275.6 ± 1 Ma) and the syntectonic milonitized intrusive Cozahuico Granite (Kungurian–Roadian, 270.4 ± 2.6 Ma) dated by SHRIMP method [Elías-Herrera et al., 2007]. The Cozahuico Granite has been interpreted as one of the oldest and deepest tectono-magmatic-metamorphic activity in the fault zone related to the oblique collision between Oaxacan and Acatlán complexes [Elías-Herrera and Ortega-Gutiérrez, 2002, Elías-Herrera et al., 2007]. In an abstract, Elías-Herrera et al. [2019] indicates an age not older than the Lopingian (260–252 Ma) for the Matzitzi Formation based on its relative stratigraphic position over deposits affected by the Caltepense Orogeny. However, it is unclear whether deposition of the Matzitzi Formation and this latter orogeny is contemporaneous or post-depositional. The Atolotitlán Tuff corresponding to this formation is reported as Middle Triassic (240 ± 3 Ma: Elías-Herrera et al., 2011; 239.2 ± 1.4/242.9 ± 1.4/238.5 ± 2.2 Ma: Bedoya, 2018). However, the geochronology of the Caltepense Orogeny and the Atolotitlán Tuff awaits formal publication. Moreover, the age of the Matzitzi Formation is a vexing matter by the Middle Jurassic maximum depositional age (177 Ma) for a sampled sandstone [Bedoya, 2018].

In summary, based on its relative stratigraphic position, the non-metamorphosed Matzitzi Formation has been placed overlying the metamorphosed units such as the Cozahuico Granite and the Acatlán Complex. Geochronological data indicate that the depositional age of the Matzitzi Formation should be not older than 270 Ma (earliest Roadian, middle Permian) corresponding to the underlying Cozahuico Granite and not older than Latest Pennsylvanian–earliest middle Permian (Tecomate Formation, Acatlán Complex), leading some geologists to think that the Matzitzi Formation is younger than the Roadian. Nevertheless, the Tecomate Formation has not been reported in direct contact with the Matzitzi Formation. Moreover, the macroflora remains indicate an Artinskian–Kungurian maximum age (e.g. Río Hondo section), so the deposition of the Matzitzi Formation was possibly contemporaneous, at least in part, to the Caltepense Orogeny and the emplacement of the Cozahuico Granite. The Atolotitlán Tuff corresponding to the Matzitzi Formation has been reported as Middle Triassic, and this formation also contains Jurassic deposits. Besides, the depositional setting and controls of deposition of the Matzitzi Formation and its geologic contacts with other metamorphosed rocks are still poorly understood. There is a great need for work to do to understand the geological contact between different geological units and also to disentangle the geological setting and evolution of the area.

Three important aspects should be clarified. First, the possibility that the Matzitzi Formation may include different chronostratigraphic units from the early Permian (or from the early middle Permian in the case of palynomorph reworking) to at least Middle Triassic or even younger (Jurassic) that may all record the same sedimentary environment must be considered. Also, a more comprehensive stratigraphic and sedimentologic work should be done. To achieve it, a re-examination of the already studied fossil flora controlling its stratigraphic level and geographical location is required. Besides, it is important to understand the evolution from Late Carboniferous wet conditions to drier conditions during the early Permian in Mexico. It has been proved a diachronous climatic change in the USA depending the locality so it is not worth expecting a diachronous appearance of certain macroflora and microflora key taxa. Second, it is important to control the correlation of the strata of the Matzitzi Formation, and third, a more comprehensive study of the geologic contact with underlying metamorphosed rocks is needed.

6. Conclusion

A more comprehensive study of the Matzitzi Formation is necessary to define its stratotype; not yet formally defined. Also, the biostratigraphic and geochronologic age disparities need to be resolved to improve stratigraphic correlation among disparate outcrops of the Matzitzi Formation. From those outcrops, it seems that the most continuous and complete stratigraphic section of this formation corresponds to the Río Hondo section. The fundamental problem of the Matzitzi Formation is that it may represent more than a single package of rocks with a similar depositional environment. The palynological assemblages presented in this study indicate most likely Late Pennsylvanian in the Río Hondo section. However, palynomorphs were possibly reworked and re-deposited in rock along with the Permian parautochthonous macroflora from this formation. If palynomorphs are reworked, their source would correspond to the erosion of Middle-Upper Pennsylvanian continental deposits. The re-study of the holotype and paratypes of the gigantopterid fossil plant species *Lonesomia mexicana*, a key specimen for Kungurian age assignment, showed the lack of diagnostic characters to place them within the gigantopterids. Although these fossil plant specimens have a huge lamina, they do not have the reticulate venation that characterizes gigantopterids. The paratypes only showed primary and secondary veins whilst the holotype also presents a tertiary vein in a small area of the lamina due to the poor preservation of these specimens. Macroflora described from the early Permian Matzitzi Formation suggests wetland corridors possibly fringing the channels associated with anastomosing river systems related to a gradual global environmental change from everwet during the Late Pennsylvanian to a drier early Permian. This study suggests that maybe the deposition of the Matzitzi Formation possibly was contemporaneous, at least in part, to the Caltepense Orogeny and the emplacement of the Cozahuico Granite.

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References

Aguilera, J. G. and Ordoñez, E. (1896). Bosquejo geológico de México. *Bol. Inst. Geol. Mex.*, 4–6:1–262.

Alpern, B. and Doubinger, J. (1973). *Microfossiles organiques du Paléozoïque. 6, Les spores : les miospores monolètes du paléozoïque*. Centre National de la Recherche Scientifique, Paris, France.

Barthel, M. (2016). The Lower Permian (Rotliegend) flora of the Döhlen Formation. *Geol. Saxonica*, 61(2):105–238.

Batten, D. J. (1999). Small palynomorphs. In Jones, T. P. and Rowe, N. P., editors, *Fossil Plants and Spores: Modern Techniques*, pages 15–19. Geological Society, London, UK.

Bedoya, A. (2018). Análisis de procedencia y termocronología detrítica de las Formaciones Matzitzi y Tianguistengo: Implicaciones tectónicas en la evolución Paleozoica–Mesozoica del sur de México. Master Thesis, Centro de Geociencias UNAM, Juriquilla, Mexico, 221 p.

Bedoya, A., Anaya-Guarneros, J. A., Abdullin, F., Martini, M., and Solari, L. (2020). Provenance analysis of the Matzitzi and Agua de Mezquite formations, southern Mexico: Different fluvial successions formed during late Paleozoic and post-Middle Jurassic time along the southernmost North America Pacific margin. *J. South Am. Earth Sci.* in press.

Blake, B. M. and Gillespie, W. H. (2011). The Enigmatic Dunkard Macroflora. In Harper, J. A., editor, *Geology of the Pennsylvanian–Permian in the Dunkard Basin: Guidebook*, 76th Annual Field Conference of Pennsylvania Geologists, Washington, pages 103–143. Field Conference of Pennsylvania Geologists, Washington.

Blomenkemper, P., Kerp, H., Hamad, A. A., DiMichele, W. A., and Bomfleur, B. (2018). A hidden cradle of plant evolution in Permian tropical lowlands. *Science*, 362:1414–1416.

Booi, M., Van Waveren, I. M., and Van Konijnenburg-Van Cittert, J. H. (2009). The Jambi gigantopterids and their place in gigantopterid classification. *Bot. J. Linn. Soc.*, 161(3):302–328.

Broutin, J., Doubinger, J., El Hamet, M. O., and Lang, J. (1990). Palynologie comparée du Permien nigérien (Afrique occidentale) et péritéthysien. Implications stratigraphiques et phytogéographiques. *Rev. Palaeobot. Palynol.*, 66:243–

261.

Burckhardt, C. (1930). Étude synthetique sur le Mesozoique mexicain. *Mem. S. Paleont. Suisse*, 49–50:1–280.

Calderón-García, A. (1956). Bosquejo geológico de la región de San Juan Raya, Puebla. In García-Rojas, A., editor, *XX Congreso Geológico Internacional, Libreto guía Excursión A-11*, pages 9–27. Instituto de Geología UNAM, Ciudad de México, Mexico.

Carrillo, M. and Martínez-Hernández, E. (1981). Evidencias de Facies Continentales en la Formación Matzitzi, Estado de Puebla. *Rev. Inst. Geol. UNAM*, 5:117–118.

Centeno-García, E., Mendoza-Rosales, C. C., and Silva-Romo, G. (2009). Sedimentología de la Formación Matzitzi (Paleozoico superior) y significado de sus componentes volcánicos, región de Los Reyes Metzontla-San Luis Atolotitlán, Estado de Puebla. *Rev. Mex. Cienc. Geol.*, 26(1):18–36.

Clayton, G., Coquel, R., Doubinger, J., Gueinn, K. J., Loboziak, S., Owens, B., and Streel, M. (1977). Carboniferous miospores of western Europe: illustration and zonation. *Meded. Rijks Geol. Dienst*, 29:1–71.

Cleal, C. J. and Thomas, B. (2019). *Introduction to Plant Fossils*. Cambridge University Press, New York.

Clendening, J. A. (1972). Stratigraphic placement of the Dunkard according to palynological assemblages. *Castanea*, 37(4):258–287.

Di Pasquo, M. M. and Hernández-Láscares, D. (2013). Primeros registros palinológicos de las formaciones Matzitzi y Zapotitlán, regiones de Coatepec y Teotitlán, Estados de Oaxaca y Puebla, México. In Reynoso, V. H., editor, *VIII Congreso Latinoamericano de Paleontología y XIII Congreso Nacional de Paleontología (Guanajuato 2013), Abstracts, Guanajuato, Mexico*, page 45. Universidad de Guanajuato, Guanajuato (Mexico).

DiMichele, W. A. and Aronson, R. B. (1992). The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. *Evolution*, 46:807–824.

DiMichele, W. A., Cecil, C. B., Chaney, D. S., Elrich, S. D., Lucas, S. G., Lupia, R., Nelson, W. J., and Tabor, N. J. (2011a). Pennsylvanian-Permian vegetational changes in tropical Euramerica. In Harper, J. A., editor, *Geology of the Pennsylvanian-Permian in the Dunkard basin: Guidebook. 76th Annual Field Conference of Pennsylvania Geologists, Washington, PA*, pages 60–102. Field Conference of Pennsylvania Geologists, Washington.

DiMichele, W. A., Chaney, D. S., Dixon, W. H., Nelson, W., and Hook, R. W. (2000). An Early Permian coastal flora from the central basin platform of Gaines County, West Texas. *Palaios*, 15(6):524–534.

DiMichele, W. A., Hook, R. W., Kerp, H., Hotton, C. L., Looy, C. V., and Chaney, D. S. (2018). Lower Permian flora of the Sanzenbacher Ranch, Clay County, Texas. In Krings, M., Harper, C. J., Cuneo, N. R., and Rothwell, G. W., editors, *Transformative Paleobotany*, pages 95–126. Academic Press, London (United Kingdom).

DiMichele, W. A., Hook, R. W., Nelson, W. J., and Chaney, D. S. (2004a). An unusual Middle Permian flora from the Blaine Formation (Pease River Group: Leonardian-Guadalupian Series) of King County, West Texas. *J. Paleontol.*, 78(4):765–782.

DiMichele, W. A., Hotton, C. L., Looy, C. V., and Hook, R. W. (2019). Paleoecological and paleoenvironmental interpretation of three successive macrofloras and palynofloras from the Kola Switch locality, Lower Permian (Archer City Formation, Bowie Group) of Clay County, Texas, USA. *Paläontol. Z.*, 93:423–451.

DiMichele, W. A., Kerp, H., and Chaney, D. S. (2004b). Tropical floras of the Late Pennsylvanian-Early Permian transition: Carrizo Arroyo in context. *Bull. N. M. Mus. Nat. Hist. Sci.*, 25:105–109.

DiMichele, W. A., Kerp, H., Tabor, N. J., and Looy, C. V. (2008). The so-called "Paleophytic–Mesophytic" transition in equatorial Pangea—Multiple biomes and vegetational tracking of climate change through geological time. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 268:152–163.

DiMichele, W. A., Looy, C. V., and Chaney, D. S. (2011b). A new genus of gigantopterid from the Middle Permian of the United States and China and its relevance to the gigantopterid concept. *Int. J. Plant Sci.*, 172(1):107–119.

DiMichele, W. A., Mamay, S. H., Chaney, D. S., Hook, R. W., and Nelson, W. J. (2001). An Early Permian flora with Late Permian and Mesozoic affinities from North-central Texas. *J. Paleontol.*, 75(2):449–460.

DiMichele, W. A., Schneider, J. W., Lucas, S. G., Eble, C. F., Falcon-Lang, H. J., Looy, C. V., Nelson, W. J., Elrick, S. D., and Chaney, D. (2016). Megaflora and palynoflora associated with a Late Pennsylvanian coal bed (Bursum formation, Carrizo Arroyo, New Mexico, USA) and paleoenvironmental significance. *New Mexico Geol. Soc. Annual Field Conf. Guidebook*, 67:351–368.

DiMichele, W. A., Tabor, N. J., Chaney, D. S., and Nelson, W. J. (2006). From wetlands to wet spots: environmental tracking and the fate of Carboniferous elements in Early Permian tropical floras. *Geol. Soc. Am. Spec. Pap.*, 399:223–248.

Eble, C. F., Grady, W. C., and Blake, B. M. (2013). Dunkard Group coal beds: Palynology, coal petrography and geochemistry. *Int. J. Coal Geol.*, 119:32–40.

Elías-Herrera, M., Macías-Romo, C., Sánchez-Zavala, J. L., Jaramillo-Méndez, C., Ortega-Gutiérrez, F., and Solari, L. (2019). Evento orogénico Cisuraliano-Guadalupiano ("Orogenia Caltepense") relacionado a la consolidación de pangea occidental: Nuevas evidencias tectono-estratigráficas y geocronológicas en el sur de México. *Bol. Inst. Geol. UNAM*, 122:6–7.

Elías-Herrera, M. and Ortega-Gutiérrez, F. (2002). Caltepec fault zone: an early Permian dextral transpressional boundary between the Proterozoic Oaxacan and Paleozoic Acatlán complexes, southern Mexico, and regional tectonic implications. *Tectonics*, 21(3):1013.

Elías-Herrera, M., Ortega-Gutiérrez, F., Macías-Romo, C., Sánchez-Zavala, J. L., and Solari, L. A. (2011). Colisión oblicua del Cisuraliano-Guadalupiano entre bloques continentales en el sur de México. Evidencias estratigráfico-estructurales y geocronológicas. In Ortega, F., Ferrusquía, I., Molina-Garza, R. S., and Centeno-García, E., editors, *Simposio en Honor del Dr. Zoltan de Cserna, Abstracts, Instituto de Geología UNAM, Ciudad de México, Mexico*, pages 159–164.

Elías-Herrera, M., Ortega-Gutiérrez, F., Sánchez-Zavala, J. L., Macías-Romo, C., Ortega-Rivera, A., and Iriondo, A. (2005). La falla de Caltepec: raíces expuestas de una frontera tectónica de larga vida entre dos terrenos continentales del sur de México. *Bol. Soc. Geol. Mex.*, 42(1):83–109.

Elías-Herrera, M., Ortega-Gutiérrez, F., Sánchez-Zavala, J. L., Macías-Romo, C., Ortega-Rivera, A., and Iriondo, A. (2007). The Caltepec fault zone: exposed roots of a long-lived tectonic boundary between two continental terranes of southern Mexico. *Geol. Soc. Am. Spec. Pap.*, 422:317–342.

Erben, H. K. (1956). El Jurásico Medio y Calloviano de México. In García-Rojas, A., editor, *XX Congreso Geológico Internacional, Instituto de Geología UNAM, Ciudad de México, Mexico*, pages 1–140. Instituto de Geología UNAM, Ciudad de México (Mexico).

Erdtman, G. (1960). The acetolisis method. *Svensk Botanisk Tidskrift*, 54(4):561–564.

Flores, T. (1909). Datos para la geología del Estado de Oaxaca. *Bol. Soc. Geol. Mex.*, 5:107–128.

Flores-Barragan, M. A. (2018). Las Ginkgophytas de la Formación Matzitzi, implicaciones taxonómicas y ecológicas. Master Thesis, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Ciudad de México, Mexico, 83 p.

Flores-Barragan, M. A., Velasco-de León, M. P., Lozano-Carmona, D. E., and Ortega-Chavez, E. (2019a). Avance en el conocimiento de la paleoflora de la Formación Matzitzi y sus implicaciones temporales. *Bol. Inst. Geol. UNAM*, 122:21–22.

Flores-Barragan, M. A., Velasco-de León, M. P., Valdés-Vergara, N. A., and Fernández Barajas, M. R. (2019b). Avance en el conocimiento de la paleoflora de la Formación Matzitzi, implicaciones ecológicas y temporales (Localidad Carretera). *Paleontol. Mex. Spc. Num.*, 5:132.

Galván-Mendoza, E. (2000). Contribución al Conocimiento Paleoecológico de la Tafoflora Matzitzi, Paleozoico Tardío, sur del estado de Puebla. Master Thesis, Facultad de Ciencias UNAM, Ciudad de México, Mexico, 77 p.

García-Duarte, R. (1999). Evidencias de la naturaleza estructural y relaciones estratigráficas de la Formación Matzitzi en el sur de Puebla, México. Bachelor Thesis, Centro de Estudios Superiores del Estado de Sonora, Hermosillo, Mexico, 90 p.

Glasspool, I. J., Hilton, J., Collinson, M. E., Wang, S. J., and Li, C. S. (2004). Foliar physiognomy in Cathaysian gigantopterids and the potential to track Palaeozoic climates using an extinct plant group. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 205:69–110.

González-Hervert, M. G. G., Martínez, P. R. G., Martínez, J. A. G., and Rojas-Rosas, R. (1984). Características estratigráficas y estructurales del límite de los terrenos Mixteco y Oaxaca, en la región de

Los Reyes Metzontla, Pue. *Bol. Soc. Geol. Mex.*, 45(1/2):21–33.

Hernández-Láscares, D. (2000). Contribución al conocimiento de la estratigrafía de la Formación Matzitzi, área Los Reyes Metzontla-Santiago Coatepec, extremo suroriental del estado de Puebla. Master Thesis, Colegio de Ciencias y Humanidades UNAM, Ciudad de México, Mexico, 117 p.

Hower, J. C., Fiene, F. L., Wild, G. D., and Helfrich, C. T. (1983). Coal metamorphism in the upper portion of the Pennsylvanian Sturgis Formation in western Kentucky. *Geol. Soc. Am. Bull.*, 94(12):1475–1481.

Ibrahim, A. C. (1933). *Sporenformen des Aegirhorizonts des Ruhr-Reviers*. PhD thesis, University of Berlin, Wurzburg, Germany. 47 p.

Jerzykiewicz, J. (1987). Latest Carboniferous (Stephanian) and Early Permian (Autunian) palynological assemblages from the intrasudetic basin, southwestern Poland. *Palynology*, 11(1):117–131.

Juncal, M. A., Lloret, J., Diez, J. B., López-Gómez, J., Ronchi, A., de la Horra, R., Barrenechea, J. F., and Arche, A. (2019). New Upper Carboniferous palynofloras from southern Pyrenees (NE Spain): Implications for palynological zonation of Western Europe. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 516:307–321.

Keppie, J. D. and Ortega-Gutiérrez, F. (1999). Middle American Precambrian basement: A missing piece of reconstructed 1-Ga Origen. *Geol. Soc. Am. Spec. Pap.*, 336:199–210.

Keppie, J. D., Sandberg, C. A., Miller, B. V., Nance, R. D., and Poole, F. G. (2004). Implications of latest Pennsylvanian to Middle Permian paleontological and U–Pb SHRIMP data from the Tecomate Formation to re-dating tectonothermal events in the Acatlán Complex, southern Mexico. *Int. Geol. Rev.*, 46(8):745–753.

Kerp, H. and Fichter, J. (1985). Die Makrofloren des saarpfälzischen Rotliegenden (? Ober-Karbon-Unter-Perm; SW-Deutschland). *Mainzer Geowis. Mitteil.*, 14:159–286.

Kirsch, M., Keppie, J. D., Murphy, J. B., and Solari, L. (2012). Permian–Carboniferous arc magmatism and basin evolution along the western margin of Pangea: Geochemical and geochronological evidence from the eastern Acatlán Complex, southern Mexico. *Geol. Soc. Am. Bull.*, 124(9–10):1607–1628.

Koidzumi, G. (1936). Gigantopteris. *Acta Phytotax. Geobot.*, 5:130–144.

Kosanke, R. M. (1950). Pennsylvanian spores of Illinois and their use in correlation. *Illinois State Geol. Surv. Bull.*, 74:1–128.

Kosanke, R. M. (1984). Palynology of selected coal beds in the proposed Pennsylvanian System stratotype in West Virginia (No. USGS-PP-1318). *U.S. Geol. Surv. Prof. Pap.*, 1318:1–44.

Lesnikowska, A. D. and Willard, D. A. (1997). Two new species of *Scolecopteris* (Marattiales), sources of *Torispora securis* Balme and *Thymospora thiessenii* (Kosanke) Wilson et Venkatachala. *Rev. Palaeobot. Palyno.*, 95(1–4):211–225.

Liu, L. and Yao, Z. (2002). Comparison in leaf architecture between Chinese and American species of *Gigantopteridium*. *Acta Palaeontol. Sin.*, 41(3):322–333.

Loose, F. (1934). Sporenformen aus dem Floz Bismarck des Ruhrgebeites. *Arbeiten aus dem Institut Palaeobotanik und Petrographie der Brennsteine*, 4:128–164.

Looy, C. V. and Hotton, C. L. (2014). Spatiotemporal relationships among late Pennsylvanian plant assemblages: Palynological evidence from the Markley formation, West Texas, USA. *Rev. Palaeobot. Palyno.*, 211:10–27.

Magallón-Puebla, S. A. (1991). Estudio sistemático y biométrico de helechos del tipo Pecopteris (Marattiales; Pteridophyta) de la Formación Matzitzi (Permo-Carbonífero), estado de Puebla. Undergraduate Thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, Mexico, 110 p.

Maheshwari, H. and Bajpai, U. (2001). Phytostratigraphical succession in the *Glossopteris* flora of India. *Revista UNG Geociências*, VI(6):22–34.

Mamay, S. H. (1988). *Gigantonoclea* from the Lower Permian of Texas. *Phytologia*, 64:330–332.

Mamay, S. H., Chaney, D. S., and DiMichele, W. A. (2009). *Comia*, a seed plant possibly of peltaspermous affinity: A brief review of the genus and description of two new species from the Early Permian (Artinskian) of Texas, *C. greggii* sp. nov. and *C. craddockii* sp. nov. *Int. J. Plant Sci.*, 170(2):267–282.

McGregor, D. C. (1973). Lower and Middle Devonian spores of Eastern Gaspé, Canada. I. *Systematics*. *Palaeontographica Abt. B*, 142:1–77.

McKinley, K. (1966). The Mill Creek flora, Roca Shale, Wabaunsee County, Kansas. Ms Thesis, Kansas State University, 54 p.

McLean, D. (1993). *A palynostratigraphic classification of the Westphalian of the southern North Sea carboniferous basin.* PhD thesis, University of Sheffield, Sheffield, Great Britain. 251 p.

Michel, L. A., Tabor, N. J., Montañez, I. P., Schmitz, M. D., and Davydov, V. I. (2015). Chronostratigraphy and Paleoclimatology of the Lodève Basin, France: Evidence for a pan-tropical aridification event across the Carboniferous-Permian boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 430:118–131.

Mülleried, F. (1933a). Estudios Paleontológicos y estratigráficos en la región de Tehuacán, Pue., Primera Parte. *An. Inst. Biol. UNAM*, 4(1):33–46.

Mülleried, F. K. G. (1933b). Estudios Paleontológicos y estratigráficos en la región de Tehuacán, Pue., Segunda Parte. *An. Inst. Biol. UNAM*, 4(2):79–93.

Mülleried, F. K. G. (1934). Estudios Paleontológicos y Estratigráficos de Tehuacán Pue., Conclusión. *An. Inst. Biol. UNAM*, 5(1):75–80.

Ortega-Gutiérrez, F. (1992). Tectonostratigraphic analysis and significance of the Paleozoic Acatlán Complex of southern Mexico. In Ortega-Gutiérrez, F., Centeno-García, E., Morán-Zenteno, D. J., and Gómez-Caballero, A., editors, *First Circum - Pacific and Circum-Atlantic Terrane Conference, Terrane geology of southern Mexico. Guidebook of field trip B*, pages 54–60. Instituto de Geología UNAM, Guanajuato, Mexico.

Ortega-Gutiérrez, F., Elías-Herrera, M., Morán-Zenteno, D. J., Solari, L., Weber, B., and Luna-Gutiérrez, L. (2018). The pre-Mesozoic metamorphic basement of Mexico, 1.5 billion years of crustal evolution. *Earth Sci. Rev.*, 183:2–37.

Peppers, R. A. (1964). Spores in strata of Late Pennsylvanian cyclothems in the Illinois Basin. *Ill. State Geol. Survey Bull.*, 90:1–72.

Peppers, R. A. (1985). Comparison of miospore assemblages in the Pennsylvanian System of the Illinois basin with those in the Upper Carboniferous of Western Europe. In Sutherland, P. K. and Manger, W. L., editors, *Biostratigraphy. Proc. Ninth International Congress for Carboniferous Stratigraphy and Geology, Southern Illinois University Press 2, Carbondale, United States*, pages 483–502.

Pfefferkorn, H. W., Gastaldo, R. A., and DiMichele, W. A. (2000). Ecological stability during the Late Paleozoic cold interval. *Paleontol. Soc. Spec. Pap.*, 6:63–78.

Playford, G. and Dino, R. (2005). Carboniferous and Permian palynostratigraphy. In Koutsoukos, E. A. M., editor, *Applied Stratigraphy*, pages 101–121. Springer, Dordrecht, Netherlands. Chapter 5.

Potonié, R. and Kremp, G. O. W. (1954). Die Gattungen der palaozoischen Sporae dispersae und ihre Stratigraphie. *Geol. Jb.*, 69:111–194.

Potonié, R. and Kremp, G. O. W. (1956). Die sporae dispersae des Ruhrkarbons. Teil II. *Palaeontographica Abt. B*, 99:85–191.

Powell, J. T., Nance, R. D., Keppie, J. D., and Ortega-Gutiérrez, F. (1999). Tectonic significance of the Magdalena Migmatite, Acatlán Complex, Mexico. *Geol. Soc. Am. Abstracts with Programs*, 31(7):A–294.

Ramírez-Espinosa, J. R. (1984). La acreción de los terrenos Mixteco y Oaxaca durante el Cretácico inferior. Sierra Madre del sur de México. *Bol. Soc. Geol. Mex.*, 45(1–2):7–19.

Ravn, R. L. (1979). An introduction to the stratigraphic palynology of the Cherokee Group (Pennsylvnian) coals of Iowa. *Iowa Geol. Surv. Tech. Pap.*, 6:1–117.

Ravn, R. L. (1986). Palynostratigraphy of the Lower and Middle Pennsylvanian coal of Iowa. *Iowa Geol. Surv. Tech. Pap.*, 7:1–245.

Remy, W. and Remy, R. (1975). Beiträge zur Kenntnis des Morpho-Genus *Taeniopteris* Brongniart. *Argumenta Palaeobot.*, 4:31–37.

Remy, W. and Remy, R. (1977). *Die Floren des Erdaltertums.* Glückauf Verlag, Essen, Germany.

Ricardi-Branco, F. (2008). Venezuelan paleoflora of the Pennsylvanian-Early Permian: Paleobiogeographical relationships to central and western equatorial Pangea. *Gondwana Res.*, 14(3):297–305.

Rincón-Pérez, A. (2010). Listado paleoflorístico de las plantas fósiles del Pérmico, pertenecientes a la Formación Matzitzi, ubicadas entre los kms. 90 a 95 de la carretera Cuacnopalan-Oaxaca. Bachelor Thesis, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico, 213 p.

Ruiz-Castellanos, M. (1979). *Rubidium-strontium geochronology of the Oaxaca and Acatlán metamorphic areas of southern Mexico.* PhD thesis, University of Texas, Dallas, United States. 178 p.

Schopf, J. M., Wilson, L. R., and Bentall, R. (1944). An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Illinois State Geol. Surv. Rep. Investigations*, 91:1–73.

Schweitzer, H. J. (1986). The land flora of the English and German Zechstein sequences. In Harwood, G. M. and Smith, D. B., editors, *The English Zechstein and Related Topics*, volume 22 of *Geological Society Special Publication*, pages 31–54. The Geological Society, London.

Sedlock, R. L., Ortega-Gutiérrez, F., and Speed, R. C. (1993). Tectonostratigraphic terranes and tectonic evolution of Mexico. *Boulder, Geol. Soc. Am. Spec. Pap.*, 278:1–153.

Seyfullah, L. J., Glasspool, I. J., and Hilton, J. (2014). Hooked: habits of the Chinese Permian gigantopterid *Gigantonoclea*. *J. Asian Earth Sci.*, 83:80–90.

Silva-Pineda, A. (1970). Plantas del Pensilvánico de la región de Tehuacán. *Paleontol. Mex.*, 29:1–108.

Silva-Pineda, A., Buitrón-Sánchez, B., Arellano-Gil, J., Vachard, D., and Ramírez, J. (2003). Permian continental and Marine Biota of South-central Mexico: a synthesis. *Am. Assoc. Petr. Geol. Mem.*, 79:462–475.

Solari, L. A., Keppie, J. D., Ortega-Gutierrez, F., Cameron, K. L., Lopez, R., and Hames, W. E. (2003). 990 and 1100 Ma Grenvillian tectonothermal events in the northern Oaxacan Complex, southern Mexico; roots of an orogeny. *Tectonophysics*, 365(1–4):257–282.

Stone, J. F. (1969). Palynology of the Eddleman Coal (Pennsylvanian) of North-central Texas. In *The University of Texas at Austin, Bureau of Economic Geology, Report of Investigations 64, Austin, United States*, page 55. The University of Texas, Austin (United States of America).

Tabor, N. J. and Poulsen, C. J. (2008). Palaeoclimate across the Late Pennsylvanian–Early Permian tropical palaeolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 268:293–310.

Talavera-Mendoza, O., Ruiz, J., Gehrels, G. E., Meza-Figueroa, D., Vega-Granillo, R., and Campa-Uranga, M. F. (2005). U–Pb geochronology of the Acatlán Complex and implications for the Paleozoic paleogeography and tectonic evolution of southern Mexico. *Earth Planet. Sci. Lett.*, 235:682–699.

Taylor, E. L., Taylor, T. N., and Krings, M. (2009). *Paleobotany: The Biology and Evolution of Fossil Plants*. Academic Press.

Turner, N. (1991). The occurrence of *Elaterites triferens* Wilson 1943 in miospore assemblages from Coal Measures of Westphalian D age, North Staffordshire, England. *Palynology*, 15(1):35–46.

Valdés-Vergara, N. A. (2017). Contribución al conocimiento de la flora fósil de la Formación Matzitzi. Bachelor Thesis, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Ciudad de México, Mexico, 56 p.

Velasco-de León, M. P., Flores-Barragan, M. A., and Lozano-Carmona, D. E. (2015). An analysis of a new foliar architecture of the Permian period in Mexico and its ecological interactions. *Am. J. Plant Sci.*, 6(05):612–619.

Velasco-Hernández, M. and Lucero-Arellano, M. R. (1996). Una localidad nueva de la Formación Matzitzi en el Río Calapa, límite estatal de Oaxaca y Puebla, México. *Rev. Cienc. Geol. Mex.*, 13(1):123–127.

Vozárová, A. (1998). Late Carboniferous to Early Permian time interval in the western Carpathians: Northern Tethys margin. *Geodiversitas*, 20(4):621–641.

Wang, X. (2010). *The Dawn Angiosperms*. Springer, Heidelberg, Germany.

Waters, C. N., Somerville, I. D., Stephenson, M. H., Cleal, C. J., and Long, S. L. (2011). Biostratigraphy. In Waters, C. N., Somerville, I. D., Jones, N. S., Cleal, C. J., Collinson, J. D., Waters, R. A., Besly, B. M., Dean, M. T., Stephenson, M. H., Davies, J. R., Freshney, E. C., Jackson, D. I., Mitchell, W. I., Powell, J. H., Barclay, W. J., Browne, M. A. E., Leveridge, B. E., Long, S. L., and McLean, D., editors, *A Revised Correlation of Carboniferous Rocks in the British Isles. London*, volume 26 of *The Geological Society London Special Report*, pages 11–22. Geological Society of London, Bath (United Kingdom).

Weber, R. (1997). How old is the Triassic flora of Sonora and Tamaulipas, and news on Leonardian floras in Puebla and Hidalgo, México. *Rev. Mex. Cienc. Geol.*, 14(2):225–243.

Weber, R. (2007). Virutas Paleobotánicas Pérmico de México.

Weber, R., Centeno-García, E., and Magallón-Puebla, S. A. (1987). La Formación Matzitzi tiene edad permocarbonífera. In Alcayde, M., editor, *II Simposio* *sobre la Geología Regional de México, Instituto de Geología UNAM, Ciudad de México, Mexico*, pages 57–59.

Weber, R. and Cevallos-Ferriz, S. R. S. (1994). Perfil actual y perspectivas de la paleobotánica en México. *Bol. Soc. Bot. Mex.*, 55:141–148.

Weber, R., Magallón-Puebla, S. A., and Sour-Tovar, S. (1989). La flora paleozoica de Puebla. *ICYT*, 11:19–26.

Wilson, L. R. and Venkatachala, B. S. (1963). Thymospora, a new name for Verrucososporites. *Oklahoma Geol. Notes*, 23:75–79.

Yañez, P., Ruiz, J., Patchett, P. J., Ortega-Gutiérrez, and Gehrels, G. E. (1991). Isotopic studies of the Acatlán Complex, southern Mexico: implications for Paleozoic North American tectonics. *Geol. Soc. Am. Bull.*, 10:817–828.