

Articles

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Extinct lineages in a rift landscape: Middle Jurassic Bennettitales from the Otlaltepec Formation

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Abstract

The Bennettitales, a group of extinct gymnosperms, had outstanding species diversity throughout the Mesozoic and were abundant during the Jurassic. They were key components of terrestrial ecosystems, thriving in diverse climates and environmental conditions. However, a deeper understanding of the ecological strategies exhibited by this extinct lineage across time and space within a well-characterized geological context is still lacking for the region. Here, we examine bennettitalean assemblages from the Middle Jurassic Otlaltepec Formation (Otlaltepec Basin) and compare them with floras from two other rift basins (Tlaxiaco and Ayuquila) in low latitudes. Based on morphological features, we propose the new species *Zamites ambigua*, and identify the following additional taxa: *Zamites lucerensis*, *Zamites oaxacensis*, *Zamites tribulosus*, cf. *Zamites diquiyui*, *Zamites* sp. 1, *Zamites* sp. 2, *Bennettitcarpus* sp. 1, *Bennettitcarpus* sp. 2, and cf. *Weltrichia xochitellii*, along with two types of gymnosperm foliage of uncertain affinities.

Our findings on bennettitalean diversity in the Otlaltepec Formation reveal the presence of foliage across all three basins in both time and space, indicating a generalist element among these rift environments. In contrast, other foliage and reproductive structures exhibit two distinct distributional patterns: some are confined to a single basin over time, while others appear only during specific intervals in each basin's history. Our findings highlight that some Bennettitales exhibited ecological resilience, maintaining their morphology and distribution despite the shifting environmental conditions caused by tectonic activity. This suggests that certain generalist taxa persisted across varying moisture regimes and depositional settings, while others displayed more localized or temporally restricted distributions.

Non-technical Summary

The Bennettitales were a group of extinct seed plants that thrived during the age of dinosaurs. These plants looked like modern cycads, and were widespread during the Jurassic period (200 to ca. 145 million years ago), playing an important role in ancient ecosystems. Although scientists have found many Bennettitalean fossils around the world, we still know relatively little about how these plants adapted to different environments. Here, we looked at fossilized Bennettitales from southern Mexico, from Middle Jurassic rocks in the Otlaltepec Formation. We compared these fossils with those from two nearby regions that were all affected by the same large-scale geological event: the rifting of the Earth's crust. We identified several species, including a new one that we named *Zamites ambigua*. By studying the morphology and distribution of these fossils, we discovered that some Bennettitales were found across all three regions and over long periods of time. Meanwhile others were limited to just one region or a specific moment in time, indicating that they were 'specialists' with narrower habitat needs. Our results show bennettitalean resilience, being able to persist through major environmental changes caused by tectonic activity.

Introduction

The fossil record of terrestrial ecosystems provides invaluable insights into how plants modify the environment (Boyce et al., 2010), the early establishment of ecosystems (Edwards et al., 2017), and how plant lineages may compete for ecological dominance under changing climates (Condamine et al., 2020). Based on this record, we can recognize that, as in extant species, some

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extinct species have narrow environmental tolerances, restricting them to specific habitats to which they adapt well (known as 'specialist' species), while others have broader environmental tolerances, allowing them to thrive in a wide variety of habitats (referred to as 'generalist' species) (Büchi and Vuilleumier, 2014). Identifying which plant species fall into each category is valuable for reconstructing past environments, understanding controls on past plant distribution among similar lineages, and identifying factors in speciation processes.

To determine if a species is a generalist or specialist, a comprehensive synthesis of multiple explanatory factors is required, including climate, plate tectonics, and the relative stability of species' niches during environmental changes, both biotic and abiotic (Stigall, 2012). However, finding suitable case studies for such analyses is often challenging due to the spatio-temporal separation of fossil localities. The Jurassic of Mexico presents a unique opportunity, particularly for the Bennettiales (a group of

extinct gymnosperms) because several localities within three coeval rift basins offer a rare instance of spatio-temporal proximity (Fig. 1), providing an opportunity to understand how extinct lineages were affected by or responded to changes caused by the tectonic rifting.

These localities represent the southernmost latitudinal distribution of Jurassic floras from North America. Early paleobotanical studies were documented by Wieland (1914–1916) on the Liassic flora of the Mixteca Alta, Oaxaca. This monograph laid the foundation for over a century of research in the area (e.g., Delevoryas and Gould, 1971, 1973; Silva-Pineda, 1978, 1984; Person and Delevoryas, 1982; Silva-Pineda and González-Gallardo, 1988; Lozano-Carmona and Velasco de León, 2016; Velasco-de León et al., 2019), with most of the work primarily focused on describing fossil plant material, but some also examining the sedimentary environments in which these plants were fossilized. However, an assessment of which species could be considered generalists or specialists remains underexplored.

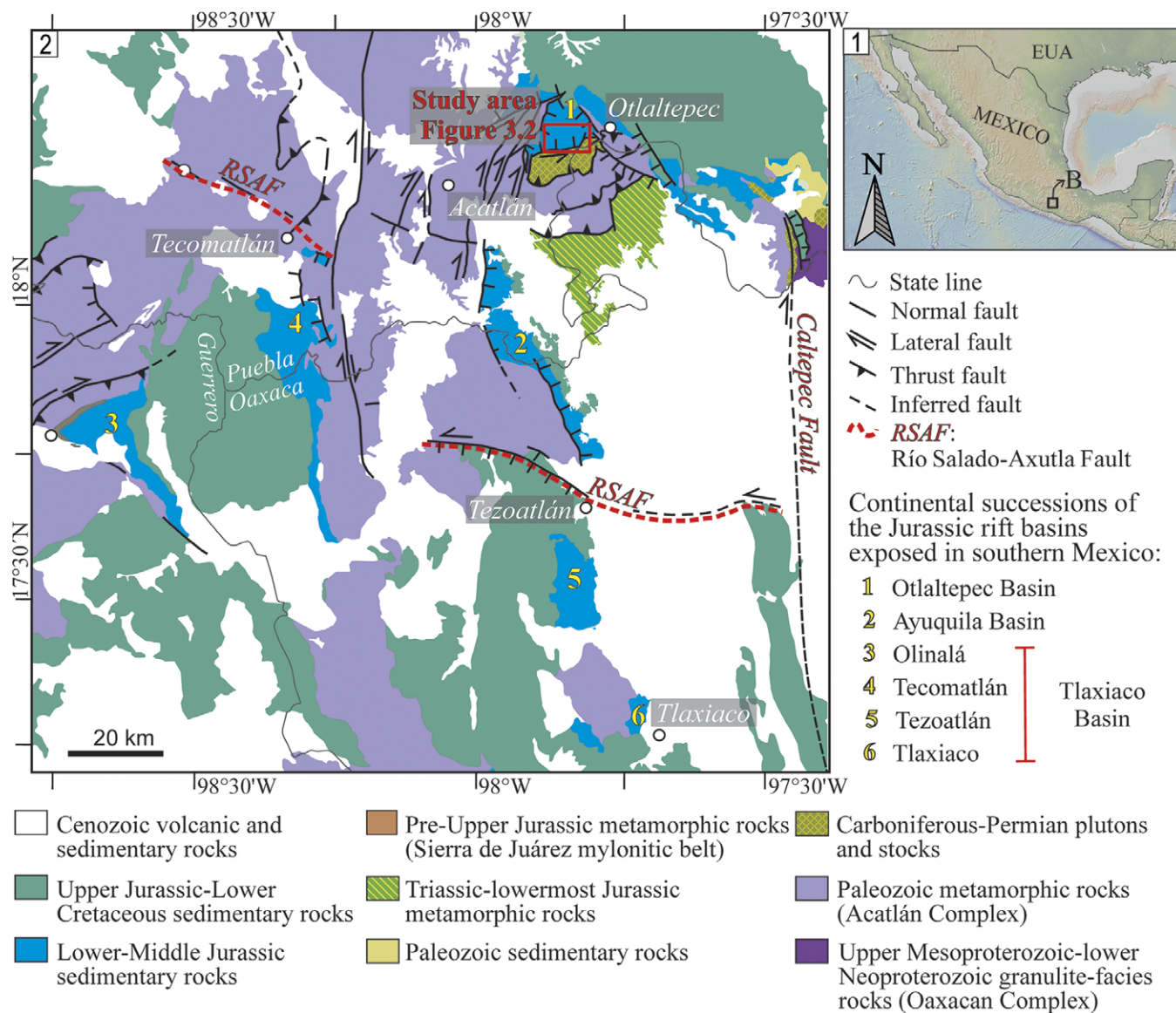


Figure 1. Geographic and geological context of the study area. (1) A map of Mexico showing the geologic map of southern Mexico highlighted in a black square. (2) Geologic map of southern Mexico, showing the extent and location of the Jurassic sedimentary clastic successions and the major metamorphic and plutonic basement complexes. The red rectangle shows the area of the map in Figure 3.2. Modified from Martini et al. (2020) and Zepeda-Martínez et al. (2021).

In southern Mexico, the Lower–Middle Jurassic successions are discontinuously exposed (Morán-Zenteno et al., 1993; Goldhammer, 1999; Martini and Ortega-Gutiérrez, 2018; Fig. 1). These successions are the deposits of the Otlaltepec, Ayuquila, and Tlaxiaco basins, developed during the fragmentation of the western-equatorial margin of Pangea (Campos-Madrigal et al., 2013; Martini et al., 2016; Zepeda-Martínez et al., 2021).

The succession of the Otlaltepec Basin consists of alluvial and fluvial deposits from the Tianguistengo, Piedra Hueca, and Otlaltepec formations (Morán-Zenteno et al., 1993; Verde-Ramírez, 2015; Ramírez-Calderón, 2018; Fig. 2). Detrital zircon U–Pb dating indicates a maximum depositional age of ca. 184 Ma for the Piedra Hueca Formation and ca. 167 Ma for the Otlaltepec Formation (Martini et al., 2016; Fig. 2).

In the Ayuquila Basin, a succession is exposed that comprises alluvial and fluvial deposits that have been subdivided into the La Mora, Ayuquila, and Tecmazúchil formations (Campos-Madrigal et al., 2013; Fig. 2). According to detrital zircon U–Pb dating, the maximum depositional age for the La Mora Formation is ca. 210 Ma (Silva-Romo et al., 2015), for the Ayuquila Formation is ca. 181 Ma, and for the Tecmazúchil Formation is ca. 174 Ma (Campos-Madrigal et al., 2013; Fig. 2).

Although some sedimentary and provenance studies have been conducted on the Otlaltepec and Ayuquila basins (Campos-Madrigal et al., 2013; Verde-Ramírez, 2015), a comprehensive analysis of their tectono-sedimentary evolution remains lacking. The available information is insufficient to determine whether these basins evolved independently or were physically connected

at some stage, which makes detailed correlation particularly challenging. However, because the existing geological data generally treats the Otlaltepec and Ayuquila basins as distinct tectono-sedimentary entities, they are considered separately in the present study.

The Jurassic record of the Tlaxiaco Basin comprises volcano-sedimentary rocks of the Diquiyú, Rosario, and Las Lluvias Ignimbrite formations; alluvial deposits of the Cualac Formation; fluvial deposits of the lower Tecocoyunca Group; and marine deposits of the upper Tecocoyunca Group (Erben, 1956; Morán-Zenteno et al., 1993; Zepeda-Martínez et al., 2021). The alluvial fan deposits of the Cualac Formation have been interpreted as a sedimentary response to tectonic uplift along the northern margin of the Tlaxiaco Basin, driven by activity of the Salado River–Axutla Fault (SRAF) (Martini et al., 2012; Zepeda-Martínez et al., 2021).

The activity of the SRAF generated a region of topographically high relief that acted as a physical barrier, separating the Tlaxiaco Basin from the Otlaltepec and Ayuquila basins. When this topographic relief reached a significant elevation, it became an obstacle, blocking air passage and trapping humidity (Zepeda-Martínez and Martini, 2024). This process presumably created a climatic contrast among these basins; while the Otlaltepec and Ayuquila basins experienced arid conditions, the Tlaxiaco Basin maintained humid conditions (Martini et al., 2024; Zepeda-Martínez and Martini, 2024). Based on U–Pb zircon ages from the volcano-sedimentary rocks, which range between ca. 197–177 Ma (Campa-Uranga et al., 2004; Durán-Aguilar, 2014; Fig. 2), and ammonite ages from the first marine deposits in the basin, indicating a Bajocian age

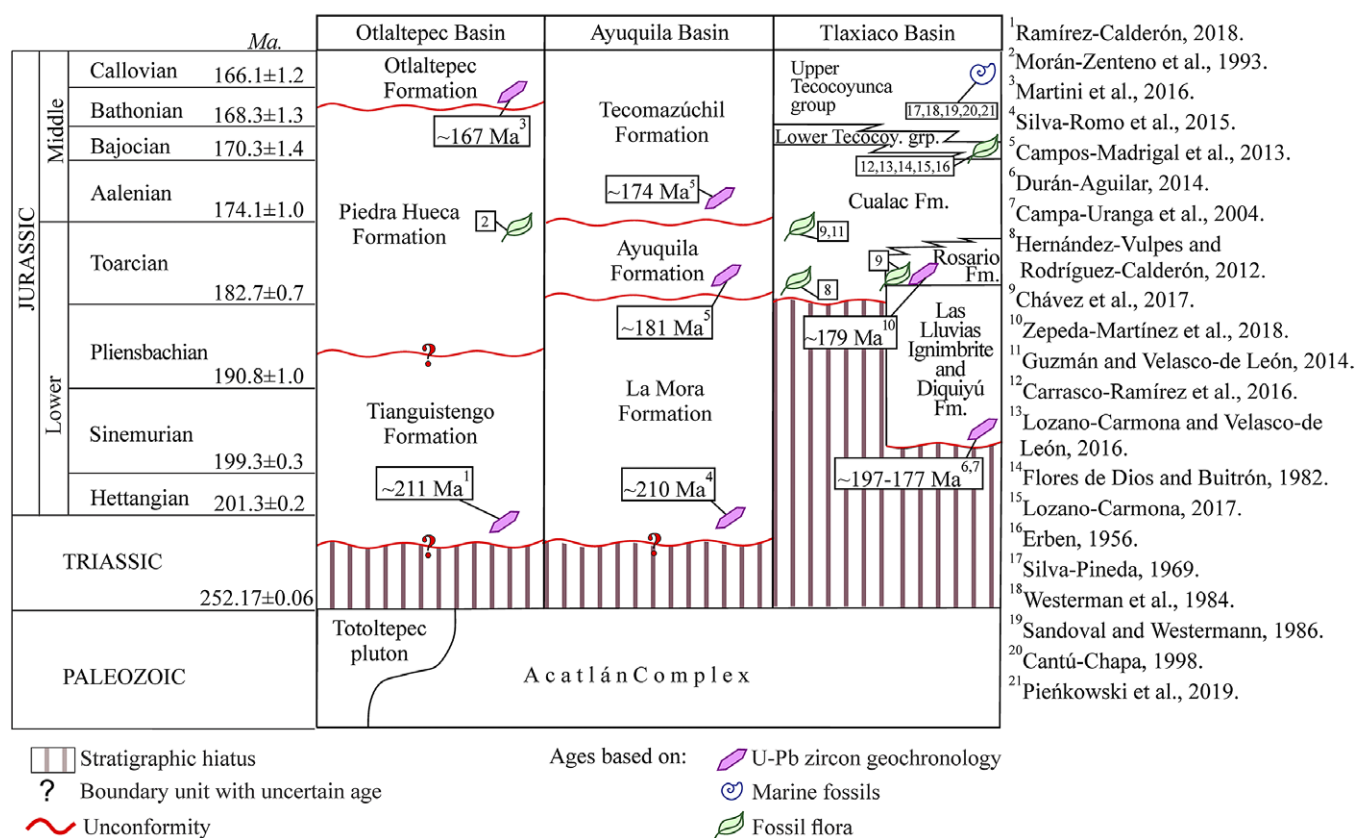


Figure 2. Chronostratigraphic chart for the Jurassic successions of the Otlaltepec, Ayuquila, and Tlaxiaco basins according to previous works. In this study, the informal subdivision of the Tecocoyunca Group is adopted (Zepeda-Martínez et al., 2021), distinguishing between the lower Tecocoyunca Group (which includes the Zorrillo, Taberna, and Simón formations from Erben, 1956) and the upper Tecocoyunca Group (which comprises the Otatera and Yucuiñti formations from Erben, 1956). Modified from Zepeda-Martínez and Martini (2024). The time scale is according to Gradstein et al. (2012).

(Sandoval and Westermann, 1986; Cantú-Chapa, 1998; Pieńkowski et al., 2019; Figure 2), the continental deposits within this basin can be constrained to the Toarcian–Aalenian (Zepeda-Martínez et al., 2021).

This study presents the first systematic description of Bennettitaleae from the Otlaltepec Formation in the Otlaltepec Basin and explores how this extinct gymnosperm lineage responded to landscape changes resulting from the fragmentation of Pangea during the Jurassic. Our results suggest that certain bennettitalean foliage types, which were consistently present across different basins, represent a generalist ecological component within this regional landscape. In contrast, other foliage and reproductive structures follow two distinct distributional patterns: some remain restricted to a single basin over time, while others emerged only during

specific intervals in each basin's history. This highlights the importance of recognizing generalist and specialist patterns in the plant fossil record for defining a comprehensive biogeographical region in the low latitudes of Western Laurasia, as these patterns offer valuable insights into plant distribution and ecological resilience.

Material and methods

Fossil samples were obtained from the locality of Santo Domingo Tianguistengo situated in the Totoltepec de Guerrero Municipality, Puebla, between Santo Domingo Tianguistengo and Santa Cruz Nuevo (18.18°N, 97.40°W; Fig. 3). The site is located along Magdalena Creek, where the clastic succession of the Otlaltepec Basin is exposed (Fig. 3.2). The fossils were recovered from the clastic

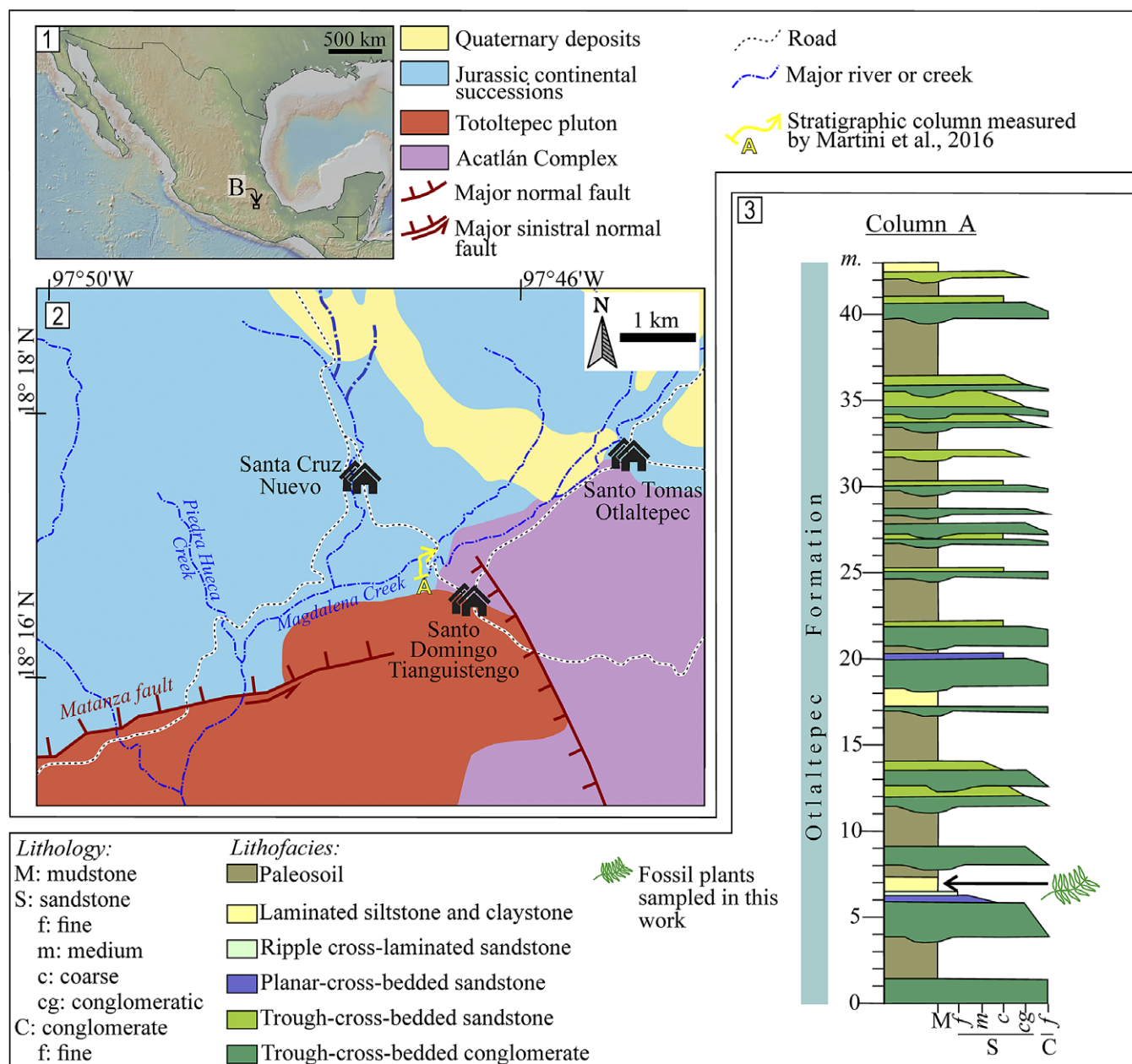


Figure 3. (1) Map of Mexico showing location of the study area. (2) Schematic geological map of a sector of the Otlaltepec Basin, indicating the location of the representative stratigraphic column of the Otlaltepec Formation measured at Magdalena Creek (modified from Martini et al., 2016). (3) Representative stratigraphic column of the Otlaltepec Formation, highlighting the horizon sampled in this study (modified from Martini et al., 2016).

succession of the Otlaltepec Formation, which comprises conglomeratic sandstone and very fine-grained lithofacies such as paleosols (Fig. 3.3). Detailed information on the sedimentary characteristics of the section can be found in Martini et al. (2016). The bennettitalean remains were found in horizontally interlaminated, very fine-grained shales, siltstones, and sandstones (Figure 3.3). Over the past few years, various plant fossil taxa have been discovered at this site, including a significant amount of fern and related foliage (Morales-Toledo et al., 2022), as well as conifers (Morales-Toledo and Cevallos-Ferriz, 2023). Further discussion of the basins can be found in Morales-Toledo and Cevallos-Ferriz (2023).

The fossil material consists of well-preserved impressions of reproductive and vegetative organs. Cuticle recovery of this material was unsuccessful. The species identified here bear the morphological characters of the bennettitalean foliage *Zamites* Brongniart emend. Harris, 1969. Other foliage types that could be assignable to different gymnosperm lineages are discussed in depth but have not been assigned to the Bennettitales. Photographs of the leaves and reproductive structures were taken with a digital camera (Canon EOS Rebel T2i), while detailed structures were identified with Axio Zoom V16 and Discovery.V8 microscopes. We conducted a detailed review of the published data for Bennettitales diversity and sedimentary environments of the Tlaxiaco Basin and Ayuquila Basin.

Repositories and institutional abbreviations. Type, figured, and other specimens examined in this study are deposited in the following institutions: Instituto de Geología (IGM), UNAM; and Collection de Paléobotanique, Muséum National d'Histoire Naturelle (MNHN), Paris, France.

Systematic paleontology

Order **Bennettitales** Engler, 1892

Family **Incertae sedis**

Genus ***Zamites*** Brongniart, 1828, emend. Harris, 1969

Type species. *Zamites gigas* (Lindley and Hutton, 1833) Morris, 1841. From the Middle Jurassic of Yorkshire, England.

Zamites ambigua new species

Figure 4

Holotype. IGM-PB 1625, Middle Jurassic (late Bathonian–Callovian; 163.5 ± 1 and 167 ± 4 Ma), Otlaltepec Formation, Santo Domingo Tianguistengo locality, located at Magdalena Creek between the towns Santo Domingo Tianguistengo, Oaxaca, and Santa Cruz Nuevo, Puebla, at 18.18°N , 97.40°W .

Material. IGM-PB 1626 to IGM-PB 1628.

Diagnosis. Leaves pinnate, with a smooth rachis. Pinnae alternate, attached on the adaxial side of the rachis, and not imbricate though sometimes slightly overlapping. Margins entire, symmetrically contracted cordate bases. The alignment of the pinna apices produces a parallel-sided lamina outline. Venation parallel, dichotomizing several times, with middle veins extending to the apex and lateral veins directed toward the basal margins. Middle pinnae narrowly oblong to oblong with obtuse apices; apical pinnae narrowly elliptical with acute apices.

Description. Several incomplete, pinnate leaves (Fig. 4.1 and 4.2) with preserved fragments of the lamina measuring at least 20 cm

long and 6 cm wide (Fig. 4.1) were studied. Leaves have a smooth rachis, 2 mm wide. Pinnae are alternate along the rachis, sessile (Fig. 4.3–4.5) and are 2–3.5 cm long and 0.3–1.2 cm wide. Pinnae are attached on the adaxial side of the rachis every centimeter at divergence angles of $5\text{--}10^\circ$ in the middle leaf zone, and $22\text{--}26^\circ$ for more apical pinnae. The length of the pinnae remains constant along the lamina and starts to taper only in the last three or four apical pinnae (Fig. 4.3–4.5), producing a parallel-sided lamina outline. Pinnae are not commonly imbricate but are sometimes overlapping (Fig. 4.3). Pinnae in the middle zone are narrowly oblong to oblong (Fig. 4.4) with an obtuse apex (Fig. 4.4). Apical pinnae are narrowly elliptical with an acute apex (Fig. 4.3–4.5). Pinnae have an entire margin and symmetrically contracted cordate base (Fig. 4.5). Venation is parallel and dichotomizes several times along each pinna. The middle veins extend towards the pinna apex, while the basal acroscopic lateral veins extend towards the superior basal margin, and the basal basiscopic lateral veins extend towards the inferior basal margin (Fig. 4.5). Vein density in the middle zone is 40 veins per cm.

Etymology. From Latin *ambiguous* (of doubtful nature).

Remarks. The specimens have morphological characters of the genus *Zamites*, such as a symmetrically contracted (cordate) pinnae base and parallel dichotomizing veins reaching the apex of the pinnae (Harris, 1969). Our material includes more than 35 well-preserved specimens (IGM-PB 1629 to IGM-PB 1663), of which nine representative examples are illustrated (Fig. 4), and consistently show the morphological variability of this new species. We compared our fossil material with morphologically similar *Zamites* specimens previously reported from the Middle Jurassic of Mexico, as well as with the type species and other *Zamites* species exhibiting comparable pinna morphology and found that our material exhibits a unique combination of features (Table 1). The comparison between *Z. ambigua* n. sp. and *Zamites lucerensis* (Wieland, 1914–1916) Person and Delevorayas, 1982, is available in the next remarks section.

Our specimens are similar to the material from the Jurassic of Tecmatlán, Puebla, identified as *Zamites feneonis* Brongniart, 1828, by Silva-Pineda (1969) from the lower Tecocoyunca Group, in the Tlaxiaco Basin. They share key characters such as alternate pinnae that are oblong to elliptic in shape, with obtuse apices (characters interpreted from plates of Silva-Pineda, 1969), and 40 veins per cm. Lozano-Carmona and Velasco-de León (2016) reported additional material from the same species in the Middle Jurassic of the lower Tecocoyunca Group, situated in the Tlaxiaco area within the Tlaxiaco Basin. They illustrated a single detached pinna for *Z. feneonis*, which exhibits an elliptic shape with veins running toward an obtuse apex (e.g., Fig. 3.3). However, *Z. feneonis* is conventionally characterized by linear lanceolate pinnae with acute apices (Fig. 5), terminating in a small mucro (Barale, 1981) (Fig. 5.4), and the overall shape of the leaf is ellipsoid (Fig. 5.1 and 5.2), while in our specimens, the alignment of the pinna apices produces a more parallel-sided lamina outline (Fig. 4.1) that we interpret as ligulate in shape (strap-shaped, narrow and with parallel sides, Beentje, 2016).

These diagnostic features have been observed in other specimens from the Upper Jurassic of Causse Méjean, France (Moreau et al., 2022) but are notably absent in our material and in specimens reported by Silva-Pineda (1969) and Lozano-Carmona and Velasco-de León (2016). Furthermore, reports from the Ayuquila Formation in the Ayuquila Basin (Velasco-de León et al., 2019)



Figure 4. *Zamites ambigua* new species. (1) Holotype (IGM-PB 1625), general morphology of the leaves with oblong pinnae that are constant in length along the lamina; (2, 5) (IGM-PB 1626), (2) associated leaves showing the apical area of the lamina (left) and mid zones of the lamina (right), and (5) detailed section of the apical pinnae showing venation patterns; (3) (IGM-PB 1627), leaf with apical pinnae narrowly elliptical with an acute apex; (4) (IGM-PB 1628), leaf with oblong to narrowly oblong pinnae that are not imbricate, and apical pinnae narrowly elliptical with an acute apex. Scale bars: (1, 2) = 2 cm; (3–5) = 1 cm.

Table 1. Useful characters that distinguish *Zamites ambigua* n. sp. from other species of the genus.

<i>Zamites</i> character	<i>Z. ambigua</i> n. sp.	<i>Z. feneonis</i>	<i>Z. lucerensis</i>	<i>Z. gigas</i>	<i>Z. carruthersii</i>	<i>Z. manoniae</i>	<i>Z. notokenensis</i>
Leaf general outline	Ligulate with an acute apex	Ellipsoid	Unknown	Broadly lanceolate	Lanceolate with an acute apex	Unknown	Unknown
Pinna disposition (arrangement)	Alternate	Alternate	Alternate	Alternate*	Alternate or subopposite	Alternate	Unknown
Shape of apical pinnae	Narrowly elliptical	Linear	Elliptical	Linear lanceolate, sometimes curving towards the apex of the leaf	Narrowly elliptical*	Unknown	Unknown
Proximal pinnae shape	Narrowly oblong to oblong	Linear lanceolate	Elliptical to rounded	Broadly lanceolate	Broadly oval or oblong to elongate (narrow and parallel-sided)	Oval	Oval
Apical pinnae apex	Acute	Acute, terminating in a small mucro	Obtuse	Acute	Rounded*	Unknown	Unknown
Proximal pinnae apex	Obtuse	Acute, terminating in a small mucro	Obtuse to round	Acute	Bluntly rounded or truncate	Obtuse*	Round
Vein density	40/cm	23/cm	15–30/cm	15/cm	50/cm (5/mm in the publication)	50/cm (5/mm in the publication)	40–50/cm (4–5/mm in the publication)
Reference	This work	Barale, 1981	Person and Delevoryas, 1982, and this work	Harris, 1969	Watson and Sincock, 1992	Watson and Sincock, 1992	Watson and Sincock, 1992

*Characters interpreted from plates and illustrations.

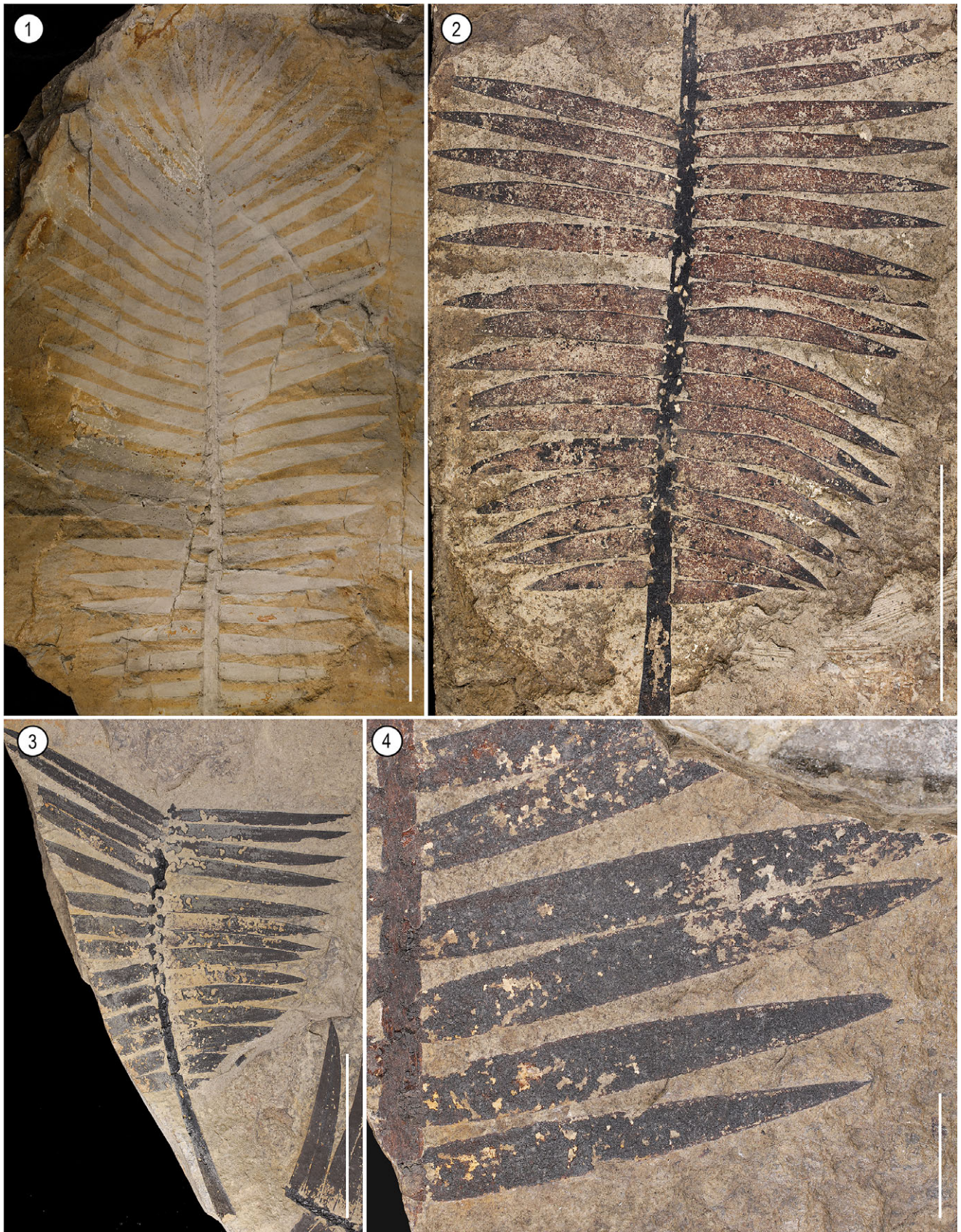


Figure 5. *Zamites feneonis* deposited in Muséum National d'Histoire Naturelle (MNHN). (1) (1587), general morphology of the leaf, showing a general ellipsoid shape; (2) (6499), proximal and middle pinnae arranged approximately perpendicularly to the rachis; (3) (10481), proximal part of the leaf, showing a prominent petiole; (4) (1588), linear-lanceolate pinnae showing a mucronate apex. Scale bars: (1, 3) = 5 cm; (2) = 2 cm; (4) = 1 cm.

attribute *Z. feneonis* to the region. We contend that these specimens do not accurately represent the leaves of *Z. feneonis* and instead belong to *Zamites ambigua* n. sp.

Zamites gigas from the Middle Jurassic of Yorkshire, UK, has a broadly lanceolate leaf outline, with apical pinnae that are linear-lanceolate and sometimes curved toward the leaf apex, and proximal pinnae that are broadly lanceolate with acute apices and a vein density of 15 per cm (Harris, 1969), unlike *Z. ambigua* n. sp. *Zamites carruthersii* Seward, 1895, from the Lower Cretaceous Wealden succession of England has proximal pinnae that are broadly oval to oblong-elongate (Watson and Sincock, 1992), contrasting with the narrowly oblong to oblong proximal pinnae of *Z. ambigua* n. sp. Furthermore, the bluntly rounded or truncate apices and higher vein density (50 veins per cm) of *Z. carruthersii* (Watson and Sincock, 1992) differ from the obtuse apices and lower vein density (40 veins per cm) of *Z. ambigua* n. sp.

Finally, *Z. ambigua* n. sp. exhibits some superficial similarities to *Zamites manoniae* Watson and Sincock, 1992, and *Zamites notokenensis* Watson and Sincock, 1992, from the Lower Cretaceous Wealden succession of England. However, the proximal oval pinnae with rounded apices and a vein density of 50 veins per cm in those species (Watson and Sincock, 1992) contrast with the oblong proximal pinnae with obtuse apices and a vein density of 40 per cm in *Z. ambigua* n. sp., distinguishing the Mexican material. Therefore, we propose that *Z. ambigua* n. sp. represents a distinct lineage, providing evidence for a new species restricted to the Middle Jurassic of Mexico.

Zamites lucerensis (Wieland, 1914–1916) Person and Delevoryas, 1982
Figure 6

- 1914–1916 *Otozamites reglei* var. *oaxacensis* Wieland, pl. 10, fig. 3; pl. 27, fig. 7; pl. 28.
- 1914–1916 *Otozamites molinianus* var. *oaxacensis* Wieland, pl. 12, fig. 2; pl. 16, figs. 2–4; pl. 28.
- 1982 *Zamites lucerensis*; Person and Delevoryas, pl. 2, fig. 15; pl. 4, fig. 24.
- 1984 *Zamites lucerensis*; Silva-Pineda, pl. 7, fig. 2.

Lectotype. *Zamites lucerensis* (IGM-PB 15) from the Rosario Formation, Middle Jurassic of Oaxaca (Person and Delevoryas, 1982, pl. 2, fig. 15; pl. 4, fig. 24; Silva-Pineda, 1984, pl. 7, fig. 2).

Materials. IGM-PB 1664 to IGM-PB 1668.

Description. Several specimens of fragmented, pinnate leaves (Fig. 6.1–6.5). The preserved fragment of the lamina is 8 cm long, 3.5 cm wide (Fig. 6.1). The petiole is 0.7 cm in length (Fig. 6.1) while the rachis is smooth, 2 mm wide. Alternate pinnae, uniting towards the middle of the base, attached on the adaxial side of the rachis (Fig. 6.1–6.5), at angles of 22–38° every 0.8 cm. Pinnae are not imbricate throughout the lamina, and measure 1.6–2 cm long and 0.6–0.7 cm wide. The size of the pinnae remains constant for most of the length of the leaf but decreases in the apical part of the lamina (Fig. 6.2). Pinnae in the middle zone of the leaf are elliptical (Fig. 6.1, 6.2, 6.5) to rounded (Fig. 6.3 and 6.4) in shape, with an obtuse (Fig. 6.1 and 6.2) to rounded apex (Fig. 6.3 and 6.4), infrequently subacute (Fig. 6.5). Apical pinnae are elliptical with an obtuse apex (Fig. 6.2). Pinnae have entire margins and symmetrically contracted cordate bases (Fig. 6.1–6.5). Veins are parallel and dichotomize several times (Fig. 6.1 and 6.3). Middle veins extend up to the pinna

apex, while the acroscopic basal laterals extend toward the upper basal margin and then extend to the apex, and the basiscopic basal laterals extend toward the lower basal margin. Vein density in the middle zone of the pinna is 30 veins per cm.

Remarks. Wieland (1914–1916) first reported similar leaves from the Middle Jurassic of Oaxaca, and Person and Delevoryas (1982) subsequently assigned them to *Zamites lucerensis*. Our material shares key characters with some specimens of *Z. lucerensis* from Oaxaca, including alternate elliptical-rounded pinnae with symmetrically contracted cordate bases and obtuse to rounded apices (referred to as rounded-truncate in Person and Delevoryas, 1982). Person and Delevoryas (1982, p. 98) noted that “more than one species is represented in the assemblage described as *Zamites lucerensis*”, and that being able to separate the rounded foliage of *Z. lucerensis* from specimens with asymmetrical foliage (with acroscopic margin generally shorter than the basiscopic margin) could be extremely difficult due to the gradation of the characters. However, our new material provides evidence that the apical pinnae have valuable morphological data to distinguish between *Z. lucerensis* and other leaves with similar pinnae. Our specimens with well-preserved apical pinnae exhibit obtuse apices (Fig. 6.2 and 6.5), in contrast to apical pinnae with acute apices presented by Person and Delevoryas (1982, pl. 2, fig. 14). We suggest that the Person and Delevoryas (1982) material should be reviewed and that the only specimen that represents *Z. lucerensis* is IGM-PB 2624-387 (Fig. 6.6); meanwhile, other specimens reported in the plates from Person and Delevoryas (1982) likely represent the apical part of a leaf from *Z. ambigua* n. sp.

Zamites lucerensis has also been identified in the Rosario Formation and lower Tecocoyunca Group (Zorrillo Formation: Erben, 1956) within the Tlaxiaco Basin (Person and Delevoryas, 1982), in the Ayuquila Formation and the Tecomazuchil Formation within the Ayuquila Basin (Velasco-de León et al., 2019; Lozano-Carmona et al., 2021), and new material in the Otlaltepec Basin. These findings demonstrate a wide geographical and temporal distribution for this species during the Middle Jurassic in low latitudes of Western Laurasia.

Zamites oaxacensis (Wieland, 1914–1916) Person and Delevoryas, 1982
Figure 7

- 1914–1916 *Otozamites* (*Williamsonia*) *oaxacensis* Wieland, pl. 19, figs. 4, 5.
- 1914–1916 *Otozamites* (*Williamsonia*) *paratypus* Wieland, pl. 2; pl. 16, fig. 8.
- 1914–1916 *Otozamites* (*Williamsonia*) *aguilarianus* Wieland, pl. 19, fig. 2.
- 1914–1916 *Otozamites* (*Williamsonia*) *aguilerai* Wieland, pl. 20, figs. 1, 3.
- 1914–1916 *Otozamites* (*Williamsonia*) *diazii* Wieland, pl. 21.
- 1914–1916 *Otozamites* sp. Wieland, pl. 20, fig. 2.
- 1982 *Zamites oaxacensis*; Person and Delevoryas, pl. 3, fig. 20; pl. 7, fig. 44.
- 1984 *Zamites oaxacensis*; Silva-Pineda, pl. 10, fig. 2.

Lectotype. *Zamites oaxacensis* (IGM-PB 42) from the Rosario Formation, Middle Jurassic of Oaxaca (Person and Delevoryas, 1982, pl. 3, fig. 20, pl. 7, fig. 44; Silva-Pineda, 1984, pl. 10, fig. 2).

Materials. IGM-PB 1669 to IGM-PB 1671.

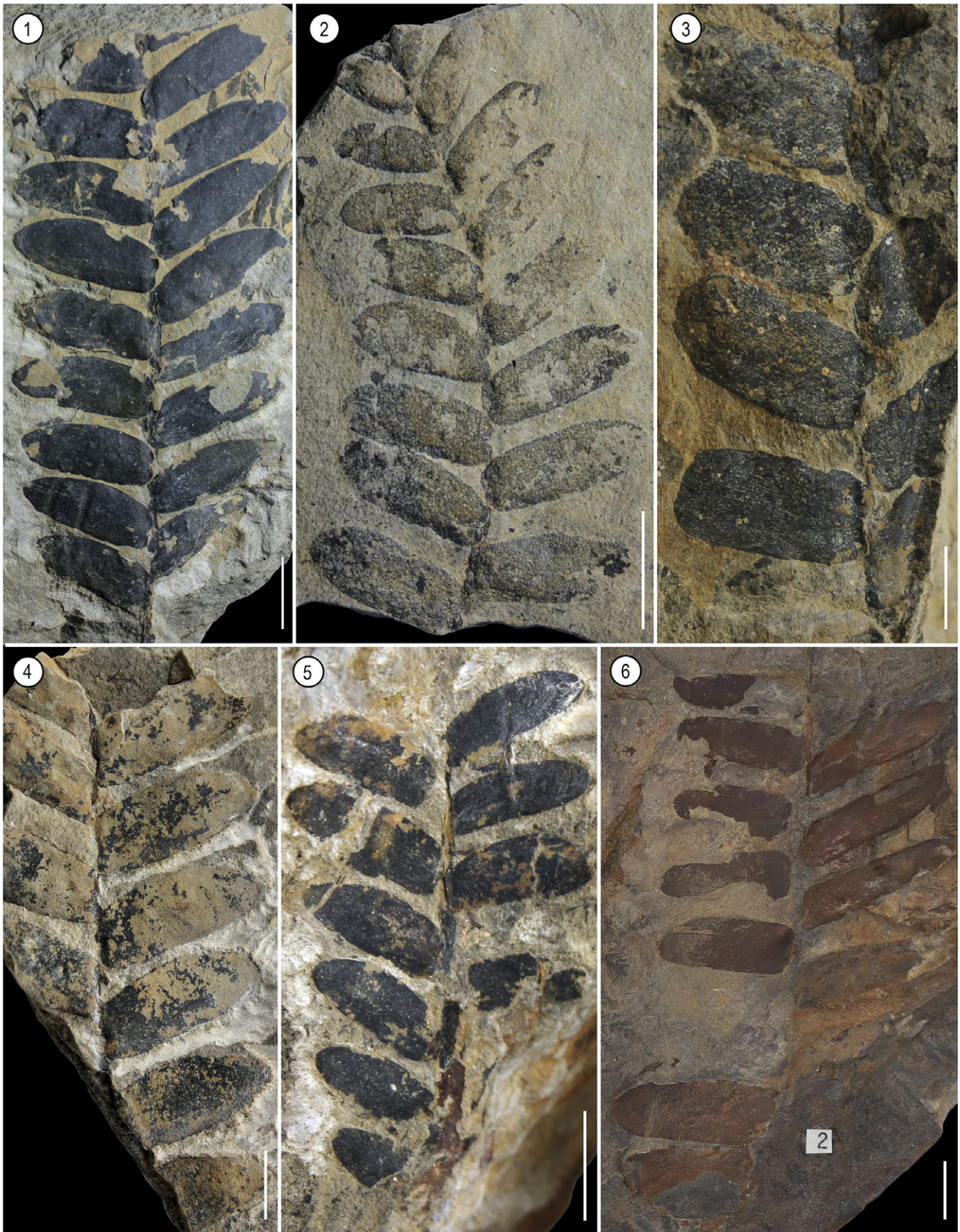


Figure 6. *Zamites lucerensis*. (1) (IGM-PB 1664), general morphology of the lamina; (2) (IGM-PB 1665), morphology of the apical area of the lamina; (3, 4) (3) (IGM-PB 1666), (4) (IGM-PB 1667), specimens showing rounded pinnae with rounded apices; (5) (IGM-PB 1668), specimen showing elliptical pinnae with rounded to subacute apices; (6) (IGM-PB 2624-387), *Zamites lucerensis* as described in Person and Delevoryas (1982, pl. 4, fig. 24). All scale bars = 1 cm.

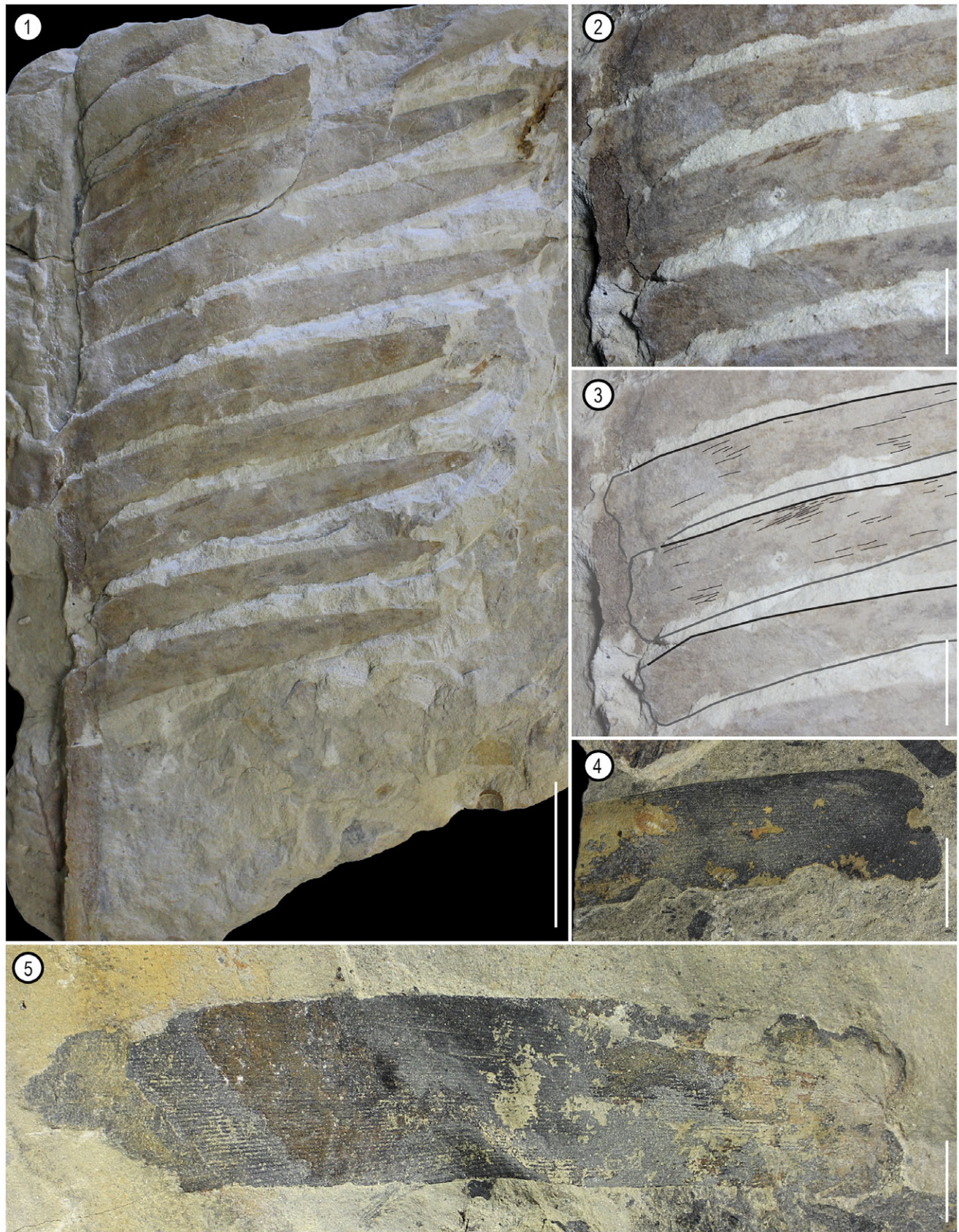


Figure 7. *Zamites oaxacensis*. (1–3) (IGM-PB 1669), (1) general morphology of the petiolate leaf; (2) detailed section of (1), showing the imbricate bases of the pinnae (incubous in appearance); (3) schematic drawing of (2) showing symmetrically contracted bases and venation details; (4, 5) (IGM-PB 1670), (5) (IGM-PB 1671), specimens showing venation patterns. Scale bars: (1) = 5 cm; (2, 3) = 2 cm; (4, 5) = 1 cm.

Description. *Zamites oaxacensis* is represented by an incomplete, petiolate, pinnate leaf (Fig. 7.1) and some detached pinnae. The preserved fragment of the lamina is 29 cm long and 15 cm wide (a total width of approximately 30 cm is interpreted). The petiole is 8 cm long $\times$ 1 cm wide (Fig. 7.1). The rachis is rough and measures 1 cm wide (Fig. 7.1). Alternate pinnae, uniting in the middle of the base, and attached on the adaxial side of the rachis at angles of 16–18°, every 2 cm. Pinnae measure 11–15.5 cm long and 1.7–2 cm wide. The length of the pinnae increases towards the apex, and pinnae are imbricate (incubous appearance) (Fig. 7.2 and 7.3). Pinnae have an entire margin, are linear in shape, with an acute apex and symmetrically contracted cordate base (Fig. 7.3–7.5). Veins dichotomize at the base of the pinnae, then are parallel through the blade (Fig. 7.4 and 7.5), with a density in the middle zone of the pinna of 16–19 veins per cm (Fig. 7.3–7.5).

Remarks. The leaves assigned to this species by Person and Delevoryas (1982) are characterized by having large blades (up to 52 cm long by 27 cm wide), a long petiole, wide rachis, and 10- to 17-cm-long pinnae with a vein density of 15–20 veins per cm. All these characters are present in our material. One of the differences is that the shape of the pinna is curved towards the base of the lamina in *Z. oaxacensis* and is straight in our material. *Zamites oaxacensis* represents another foliage element in the three rift basins, reported in the Rosario Formation, lower Tecocoyunca Group (Zorrillo Formation: Erben, 1956; Person and Delevoryas, 1982; Zorrillo-Taberna Indiferenciadas Formation: Lozano-Carmona and Velasco-de León, 2016; Lozano-Carmona et al., 2019) within the Tlaxiaco Basin, the Ayuquila Formation in the Ayuquila Basin (Velasco-de León et al., 2019), and now is an element present in the Otlaltepec Formation within the Otlaltepec Basin.

Zamites tribulosus (Wieland, 1914–1916) Person and Delevoryas, 1982
Figure 8

1914–1916 *Otozamites tribulosus* Wieland, text fig. 3.

1914–1916 *Otozamites* (*Williamsonia*) *juarezii* Wieland, pl. 11; pl. 14, fig. 3; pl. 22; pl. 26.

1982 *Zamites tribulosus*; Person and Delevoryas, pl. 3, fig. 22.

Lectotype. *Zamites tribulosus* (IGM-PB 414) from the Rosario Formation, Middle Jurassic of Oaxaca (Person and Delevoryas, 1982, pl. 3, fig. 22).

Materials. IGM-PB 1672 to IGM-PB 1675.

Description. *Zamites tribulosus* is represented by incomplete, elliptical, pinnate leaves (Fig. 8.1–8.5). The preserved fragment of the lamina is 11.5 cm long and 7 cm wide (Fig. 8.1). The rachis is smooth, measuring 2–3 mm wide. Alternate pinnae, united towards the middle of the base, attached on the adaxial side of the rachis at angles of 66–73°, every 1.1–1.3 cm. Pinnae are slightly curved towards the base and the middle zone of the lamina, becoming straight towards the apex of the leaf. Pinnae are 3.2–4.5 cm long, 0.6–0.8 cm wide (Fig. 8.1), appearing shorter and wider towards the base of the leaf (Fig. 8.3–8.5), and are not imbricated in the middle and apical zones (Fig. 8.1 and 8.2), but do overlap towards the base (Fig. 8.3). Pinnae are mostly straight (Fig. 8.1 and 8.2), sometimes with a slightly falcate (Fig. 8.1 and 8.3), or lanceolate (Fig. 8.2)

appearance, with entire margin, acute apex, and symmetrically contracted cordate base (Fig. 8.1, 8.2, 8.5). Parallel veins are occasionally bifurcated, with the middle veins extending to the pinna apex, the basal acroscopic lateral veins extending to the superior margin, and the basal basiscopic lateral veins extending towards the inferior basal margin. Vein density in the middle zone of the pinna is 40 veins per cm.

Remarks. Person and Delevoryas (1982) conducted a review of the material previously collected by Wieland (1914–1916), introducing new foliar characters to distinguish *Z. tribulosus* from *Zamites oaxacensis* based on pinna size and shape. They argued that there are no intermediates between the pinnae of *Z. tribulosus* and *Z. oaxacensis*. Our findings support this interpretation, as we did not encounter leaves exhibiting intermediate size between these two species. The alternate arrangement and the mostly straight and slightly falcate pinnae with acute apices seen in the new material agree with their description of this species (Person and Delevoryas, 1982). Furthermore, the size of the pinnae is similar between the material from the Jurassic of Oaxaca and that of Santo Domingo Tianguistengo. The number of veins seems to be higher in our material, but it could be because the preservation is better in our material. Both our material and that of Person and Delevoryas (1982) have a cordate pinnae base (symmetrically contracted), and some of our specimens have pinnae slightly curved towards the base of the blade, while others have pinnae with more parallel margins, and some have both morphologies on the same plant (Fig. 8.1 and 8.2). The absence of pinnae in some specimens is likely the result of taphonomic processes, such as detachment during transport or burial (Fig. 8.3). However, the regular pattern of pinna abscission observed in certain specimens may also suggest a deciduous behavior, although this interpretation remains tentative.

Zamites tribulosus has been identified in the Middle Jurassic of the Rosario Formation and the lower Tecocoyunca Group (Zorrillo Formation: Erben, 1956) in the Tlaxiaco Basin (Person and Delevoryas, 1982), and in the Tecomazúchil Formation (Silva-Pineda, 1978) and the Ayuquila Formation (Velasco-de León et al., 2019; Lozano-Carmona et al., 2021) in the Ayuquila Basin. The material from the Middle Jurassic of the Otlaltepec Basin provides evidence that this species had a broad geographic and temporal distribution in low latitudes of Western Laurasia.

cf. *Zamites diquiyui* (Wieland, 1914–1916) Person and Delevoryas, 1982
Figure 9.1

Holotype. *Zamites diquiyui* (IGM-PB 420) from the Rosario Formation, Middle Jurassic of Oaxaca (Person and Delevoryas, 1982, pl. 6, fig. 39).

Materials. IGM-PB 1676.

Description. The preserved fragment of the pinnate lamina measures 27.5 cm long $\times$ 9 cm wide (Fig. 9.1), and a total width of 18 cm is interpreted. The rachis is 0.4 cm wide. Alternate pinnae, uniting in the middle of the base, arise from the adaxial part of the rachis at angles of 10–24°, every 1.7–2 cm, increasing in size towards the apex of the leaf, and are slightly imbricate (succubous appearance). Pinnae are 7–8.5 cm long $\times$ 1.6 cm wide, with a length/basal width ratio of 4.3. Pinnae are narrowly oblong, with an entire margin, subacute apex, and slightly symmetrically contracted cordate bases (Fig. 9.1).

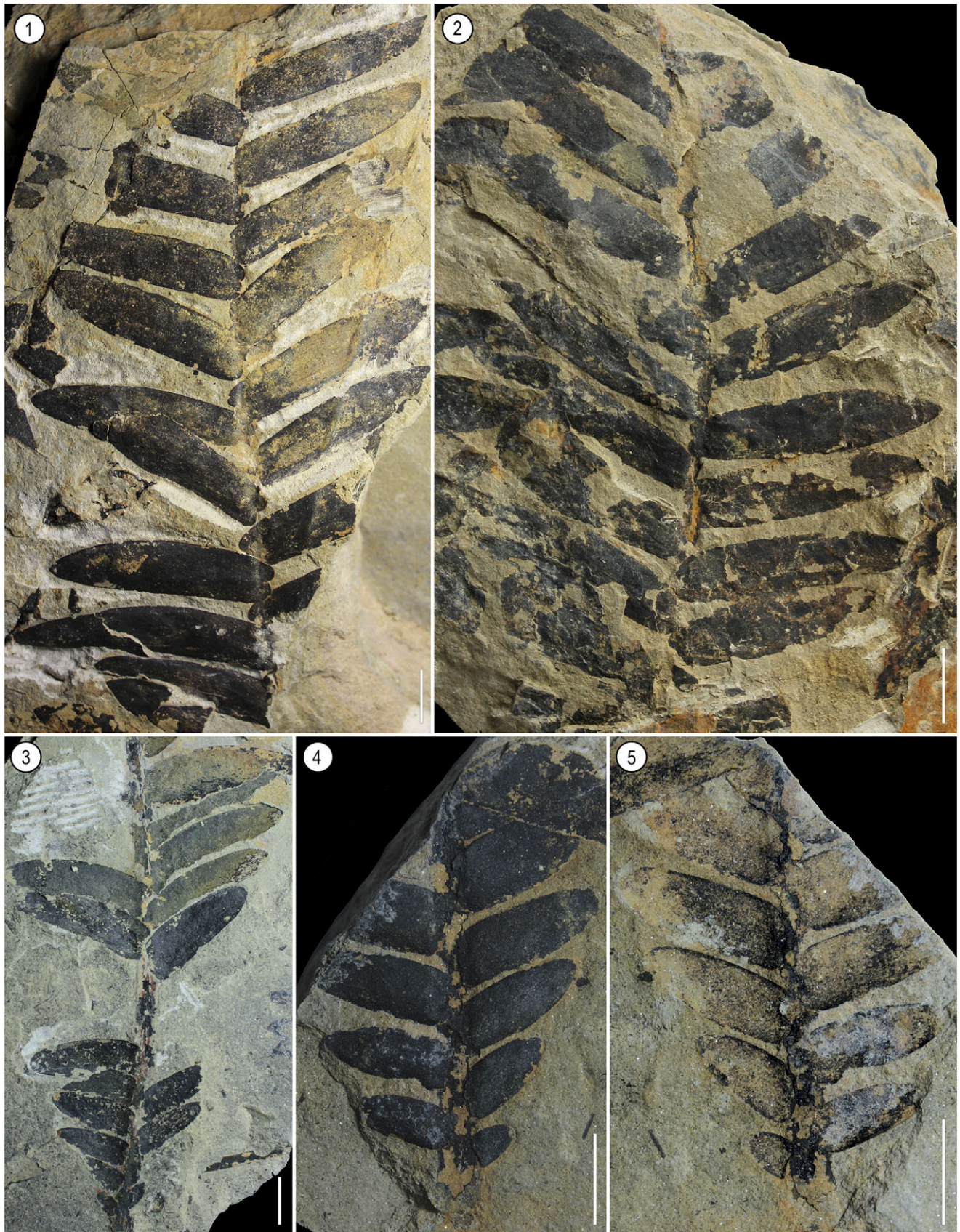


Figure 8. *Zamites tribulosus*. (1) (IGM-PB 1672), general morphology of lamina with pinnae curving towards the base; (2) (IGM-PB 1673), general morphology of the lamina, with parallel margins of pinnae; (3) (IGM-PB 1674), lamina with dehiscent pinnae; (4, 5) (IGM-PB 1675), base of lamina showing reduced basal pinnae. All scale bars = 1 cm.

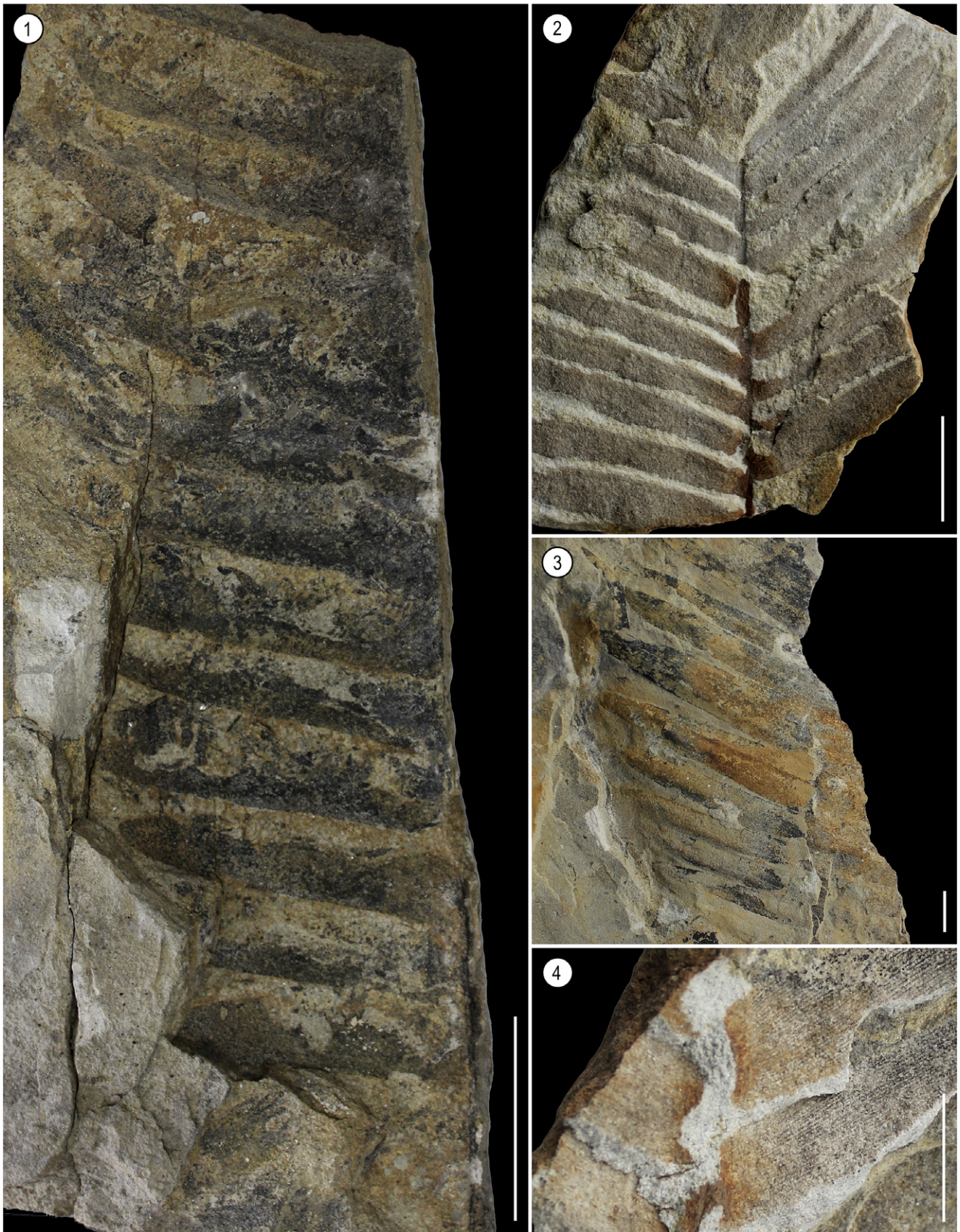


Figure 9. cf. *Zamites diquiyui*. (1) (IGM-PB 1676), general morphology of the lamina. *Zamites* sp. 1. (2) (IGM-PB 1677), general morphology of the lamina with linear pinnae with entire margin and round apex; (3) (IGM-PB 1678), distal part of pinnae with entire margin and round apex; (4) (IGM-PB 1679), symmetrically contracted pinna bases and venation. All scale bars = 1 cm.

Veins are simple and parallel, but the preservation is not good enough to provide the total number of veins per cm in each pinna.

Remarks. We assign the specimen to *Zamites* based on the symmetrically contracted base of the pinnae (Harris, 1969). The leaves of this specimen are the second largest found in the flora after *Zamites oaxacensis*. The material has poor preservation, but it differs from *Z. oaxacensis* and any other species from the region with large leaves. Unlike *Z. oaxacensis*, which has pinnae with acute apices, the Otlaltepec Formation specimen bears rounded apices, and has a narrowly oblong shape, contrasting with the large linear pinnae of *Z. oaxacensis*. However, our material could be compared with foliage of *Zamites diquiyui* (Wieland) Person and Delevoryas from the Jurassic of the Rosario Formation, lower Tecocoyunca Group (Zorrillo Formation: Erben, 1956; Person and Delevoryas, 1982) and the Cualac Formation (Velasco-de León et al., 2024), within the Tlaxiaco Basin. The shared characters between our material and the material from the Cualac formation are large leaves (~26–27 cm long, 18–19 cm wide) bearing big pinnae (4.9–10.6 cm long, 1.7–3.5 cm wide), slightly imbricate, and each pinnae with a cordate base that is quadrate in appearance, and a subacute apex (acute in the specimens from Velasco-de León et al., 2024). The only reliable way to decide if our material is *Z. diquiyui* is with the recovery of the cuticles with syndetocheilic stomata, rectangular epidermal cells and hook-shaped trichomes as reported by Velasco-de León et al. (2024), but we were unsuccessful in recovering cuticle from the Otlaltepec material.

Zamites sp. 1

Figure 9.2–9.4

Material. IGM-PB 1677 to IGM-PB 1679.

Description. This taxon is represented by an incomplete pinnate leaf (Fig. 9.2) measuring 10.5 cm long × 10 cm wide. The rachis is 0.2–0.6 cm wide. Pinnae are alternate, uniting in the middle of the base, and attached to the adaxial side of the rachis at angles of 14–42° every 0.7–0.8 cm. Pinnae are 5–6 cm long and 0.6–1.2 cm wide, tapering in size towards the apex of the leaf, and are not imbricate. Pinnae are linear, with an entire margin, rounded apex (Fig. 9.2 and 9.3), and slightly symmetrically contracted cordate base (Fig. 9.1 and 9.4). Veins are parallel from the base and extend towards the distal part of the pinna, with few bifurcations (Fig. 9.4). The vein density in the middle zone of the pinna is 31 veins per cm.

Remarks. The symmetrically contracted cordate bases of the pinnae suggest that the material belongs to *Zamites* (Harris, 1969). Of the *Zamites* species found in the locality, this is the one with the least cordate pinnae base. Furthermore, the bases do not have the morphology of similar genera such as *Otozamites* Braun, 1843, *Pterophyllum* Brongniart, 1828, or *Ptilophyllum* Morris, 1840. The leaves of *Zamites* sp. 1 differ from other species found in the locality in terms of pinna shape, base, apex, and qualitative features such as the size and vein density. Some leaves of *Otozamites hespera* Wieland, 1914–1916 from the Rosario Formation and lower Tecocoyunca Group (Zorrillo Formation: Wieland, 1914–1916; Silva-Pineda, 1969; Person and Delevoryas, 1982) have a similar morphology to *Zamites* sp. 1. However, our material lacks the enlarged acroscopic part of the pinnae base, forming an auricle, a diagnostic character of *Otozamites* (Harris, 1969). The differences discussed so far suggest that the new material is most likely related to *Zamites*, and

it is maintained apart from other species until better preserved material helps to clarify its taxonomic relationship.

Zamites sp. 2

Figure 10.1

Material. IGM-PB 1680.

Description. One specimen of an incomplete pinnate leaf (Fig. 10.1). The preserved fragment of the lamina is 7 cm long × 6 cm wide (a width of approximately 8 cm is interpreted). The rachis is covered by sediment, but the pinnae are visible (Fig. 10.1). Pinnae are alternate, united in the middle of the base, and attached to the adaxial side of the rachis at angles of 21–44°, every 0.9 cm. Pinnae are imbricate (incubous in appearance), 4.5 cm long and 0.5–0.8 cm wide. Pinnae are linear-lanceolate in shape (Fig. 10.1), with an entire margin, acuminate apex, and cordate to auriculate base (symmetrically contracted) (Fig. 10.1). Parallel veins are present, dichotomizing at times.

Remarks. The symmetrically contracted base of the pinnae suggests that the specimen belongs to *Zamites* (Harris, 1969). This specimen differs from *Zamites* sp. 1 in the shape of the pinnae and pinnae apex, and dimensions of the pinnae. The shape of the pinnae in *Zamites* sp. 1 is linear, while in *Zamites* sp. 2 pinna shape is lanceolate-linear. The pinnae apex is round in *Zamites* sp. 1, but acuminate in *Zamites* sp. 2, and the pinnae are larger in size in *Zamites* sp. 1. Due to these morphological differences, we consider the material as two different morphological types.

Different specimens of *Zamites gigas*, observed in the Paleobotany Collection of the Natural History Museum, London, have pinnae that are similar in shape to the pinnae of *Zamites* sp. 2. Pinna bases of specimen V.61612 are similar to those of our material, while the distal pinnae of specimen V5891 also lanceolate-linear in shape as in *Zamites* sp. 1. The specimen V.53000 has pinnae that are acuminate towards the apex of the leaf, strongly suggesting that the English material is like that of the Otlaltepec Formation. Person and Delevoryas (1982) compared the specimens of *Zamites gigas* with those of *Zamites oaxacensis*, keeping them as distinct species, but ‘closely comparable’. Since there are no specimens that bear the apical parts of the blade of *Z. oaxacensis*, we can only rely on gross morphological features to compare our material with *Zamites gigas* from the Middle Jurassic of Yorkshire (Harris, 1969). The only reliable way to determine if our material belongs to *Zamites gigas* is to recover cuticles in the future that show rectangular cells that bear strongly sinuous walls, with a flat surface and no papillae or trichomes (but at margins) in the adaxial epidermis, and the abaxial epidermis with sunken syndetocheilic stomata (Harris, 1969).

Genus *Bennetticarpus* Harris, 1932

Type species. *Bennetticarpus oxylepidus* Harris, 1932. From the Upper Triassic of Scoresby Sound, east Greenland.

Bennetticarpus sp. 1

Figure 10.2

Material. GM-PB 1681.

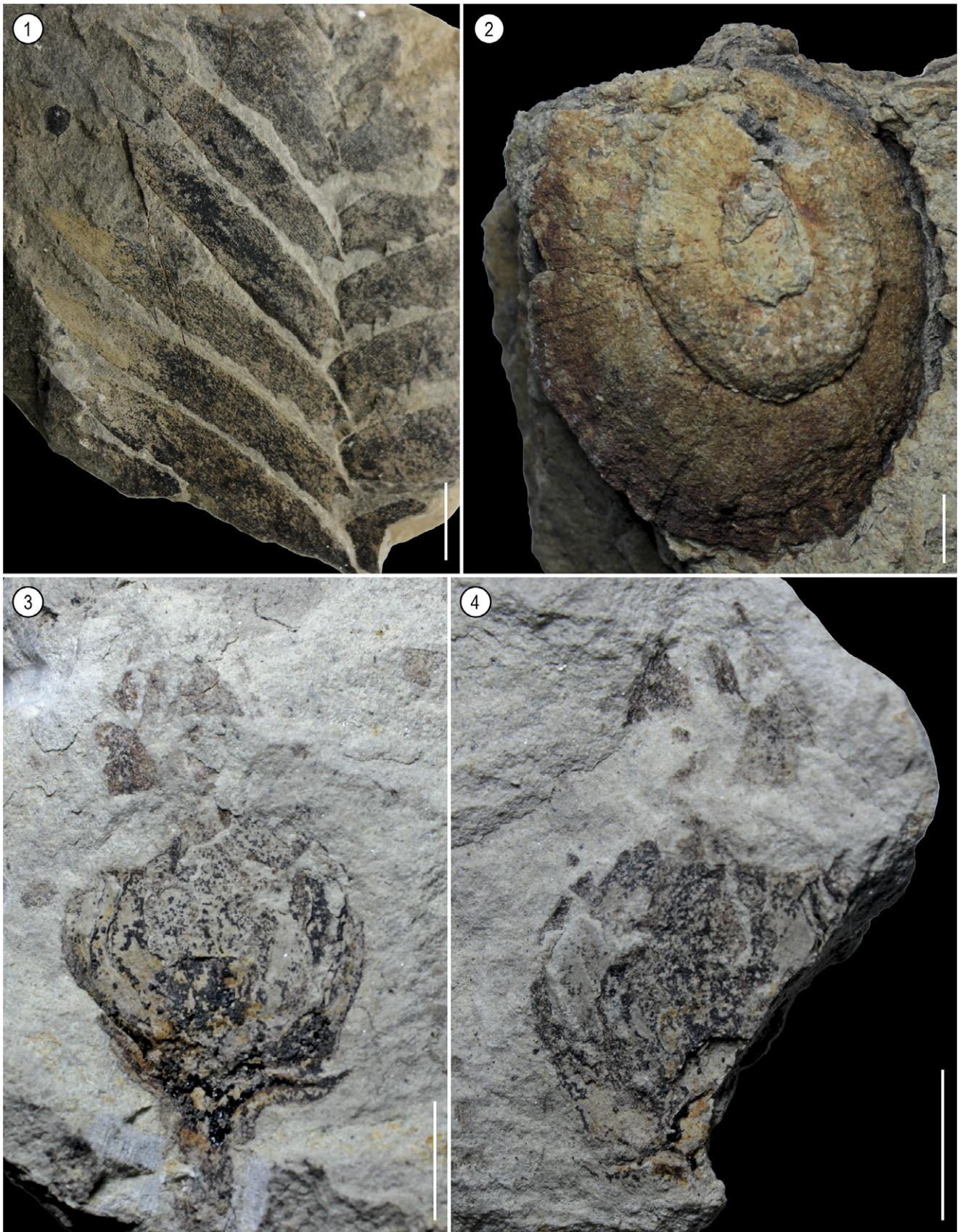


Figure 10. *Zamites* sp. 2, (1) (IGM-PB 1680), general morphology of the linear-lanceolate pinna with an acuminate apex and showing the contracted bases and venation. *Bennetticarpus* sp. 1, (2) (IGM-PB 1681), basal part of the cone showing two whorls of bracts and the scar of the peduncle. *Bennetticarpus* sp. 2, (3, 4) (IGM-PB 1682), general morphology of the immature cone attached to the peduncle with bracts covering the receptacle. Scale bars: (1, 3, 4) = 1 cm; (2) = 0.5 cm.

Description. One cone was recovered, with a basal whorl of bracts that is 3–5 mm wide. Bracts are persistent and numerous (27 bracts can be distinguished and a total of 29 are interpreted). Bracts have parallel and smooth margins, a glabrous surface, and parallel venation. However, they are incompletely preserved, and all terminate at a similar length without a preserved apex (Fig. 10.2). At the base of the cone, a peduncle scar 10 mm in diameter can be observed. There is a smaller whorl that surrounds the peduncle scar and separates it from the bracts, measuring 24 mm in diameter. No other types of structures are observed, such as the receptacle, interseminal scales or seeds with elongate micropyles.

Remarks. *Bennetticarpus* is a common Mesozoic genus established to include ovuliferous cones that exhibit clear bennettitalean characters but are insufficiently preserved or characterized to be confidently assigned to, or distinguished from, the ovuliferous cone diversity of existing genera (Harris, 1932). Our fossils have structural similarities to specimens of *Williamsonia gigas* Lindley and Hutton, 1831, from the Middle Jurassic ironstone bed at Wrack Hills, North Yorkshire, UK. Hill et al. (1985, fig. 5 E and G) show disarticulated specimens of the peduncle. The disarticulation of *W. gigas* fossils is significant (Hill et al., 1985), and the material from the Otlaltepec Basin exhibits the same condition as those from the Middle Jurassic ironstone bed at Wrack Hills, North Yorkshire. For example, in the Paleobotany Collection at the Natural History Museum, London, specimens V.2887, V.3512, V.1006, 46633, V.61617a, and V.61617b are disarticulated. Specimen V.1006 is like the fossil presented here—it has numerous bracts, and the scar of the receptacle is of similar dimensions. In specimen 46633 a striated section is seen between the receptacle scar and the area where the bracts begin. It is interpreted that this section may be equivalent to the smallest whorl, but that in specimen 46633 has been lost. The specimens V.61617a and V.61617b also show traces of this ‘ring’, from which the bracts that make up the perianth begin to grow.

The Otlaltepec Basin fossil does not have remains of the ovuliferous organ, but persistent, imbricate, and numerous bracts with a smooth parallel margin are similar to the bracts described for *W. gigas* (Harris, 1969). We suggest that future research should focus on recovering material that shows characters from the receptacle to determine if the specimens from the Otlaltepec Formation represent a species from the Middle Jurassic of Yorkshire or a regional species from the Middle Jurassic of Mexico.

***Bennetticarpus* sp. 2**

Figure 10.3, 10.4

Material. IGM-PB 1682.

Description. *Bennetticarpus* sp. 2 is represented by a partial, immature cone 2.4 cm long × 2.5 cm wide (Figure 10.3 and 10.4). A peduncle, 0.6 cm long × 0.4 cm wide, is covered by unfused striated bracts measuring 1.7–2.2 cm long × 0.2–0.3 mm wide (Fig. 10.3 and 10.4). The number of bracts is interpreted as 12. There are differentiated basal bracts 0.8 mm long (Fig. 10.3 and 10.4). Receptacle characters cannot be observed.

Remarks. The material is interpreted as an immature ovuliferous cone because it is still attached to the peduncle and the bract whorls enclose the receptacle. The species found in Mexico have cones, or receptacles, that separate from the peduncle (Delevoryas and Gould, 1973; Silva-Pineda, 1984). For example, *Williamsonia*

netzahualcoyotlii Wieland, 1914–1916 (Delevoryas and Gould, 1973; Person and Delevoryas, 1982; Flores-Barragán et al., 2017), and *Williamsonia oaxacensis* Delevoryas and Gould, 1973 (Delevoryas and Gould, 1973; Person and Delevoryas, 1982), have deciduous receptacles with interseminal scales and ovules with well-developed micropyles. *Williamsonia nathorstii* Wieland, 1914–1916 is interpreted as a perennial plant with hexagonal interseminal scales (Silva-Pineda 1978; Flores-Barragán et al., 2017), a feature that is absent in our material. Another case of a mature deciduous cone is that of *Williamsonia diquiyui* Delevoryas and Gould, 1973, which has preserved ovules (Delevoryas and Gould, 1973). The Mexican material suggests that these structures are deciduous when mature. In contrast, the Santo Domingo Tlanguistengo material is still in organic connection with the peduncle and the receptacle is not yet exposed, likely due to its immaturity. This, along with the difficulty in associating different developmental stages to each other without intermediates to document how characters changed ontogenetically, hinders placement of this material into any known species of *Williamsonia*, and the material is included in *Bennetticarpus* (Harris, 1932).

Order **Bennettitales** Engler, 1892

Family **Williamsoniaceae** Carruthers, 1870

Genus **Weltrichia** Braun emend. Harris, 1969

Type species. *Weltrichia mirabilis* Braun, 1849. From the Lower Jurassic of Franconia, Germany.

cf. *Weltrichia xochitetlii* Lozano-Carmona and Velasco-de León, 2021

Figure 11

Holotype. *Weltrichia xochitetlii* (UTMSMX-12) from the Tecoma-zúchil Formation, northwestern Oaxaca, Mexico (Lozano-Carmona and Velasco-de León, 2021, fig. 3A–D).

Materials. IGM-PB 1683 to IGM-PB 1690.

Description. Remains of a flower-like, pollen-producing organ, composed of a cup-shaped structure of 8–9 microsporophylls that are connate basally (Fig. 11.1–11.8). Microsporophylls are 1.1–2 cm long and 0.4–0.9 cm wide at the point of separation of the fused bases (Fig. 11.1–11.5). Microsporophylls are filiform (Fig. 11.4 and 11.5), with an entire margin, an acute apex (Fig. 11.1–11.8), and a prominent middle ridge that diverges from the central part of the structure and runs towards the apex of each microsporophyll (Fig. 11.1, 11.4, 11.6). Striations run parallel to the ridge (Fig. 11.1). No evidence of hairs or trichomes is seen on microsporophylls. The central diameter of the pollen-producing organ is 0.3–0.6 cm (Fig. 11.4 and 11.5). No inner appendages (centripetal rays) or pollen sacs are preserved on microsporophylls.

Remarks. *Weltrichia* is a Mesozoic bennettitalean pollen-producing structure that is ‘cup-shaped’ with fusion of the proximal part of the microsporophylls (also referred to as rays, or centrifugal rays), and sometimes with inner appendages (also referred as centripetal rays) (Harris, 1969; Popa 2014, 2019). These characters are present in our material. However, it lacks cuticles or any pollen sacs. Therefore, we can only rely on general morphology for comparison. Our material is similar to *Weltrichia xochitetlii* from the Middle Jurassic of the Tecoma-zúchil Formation in the Ayuquila Basin. This species has

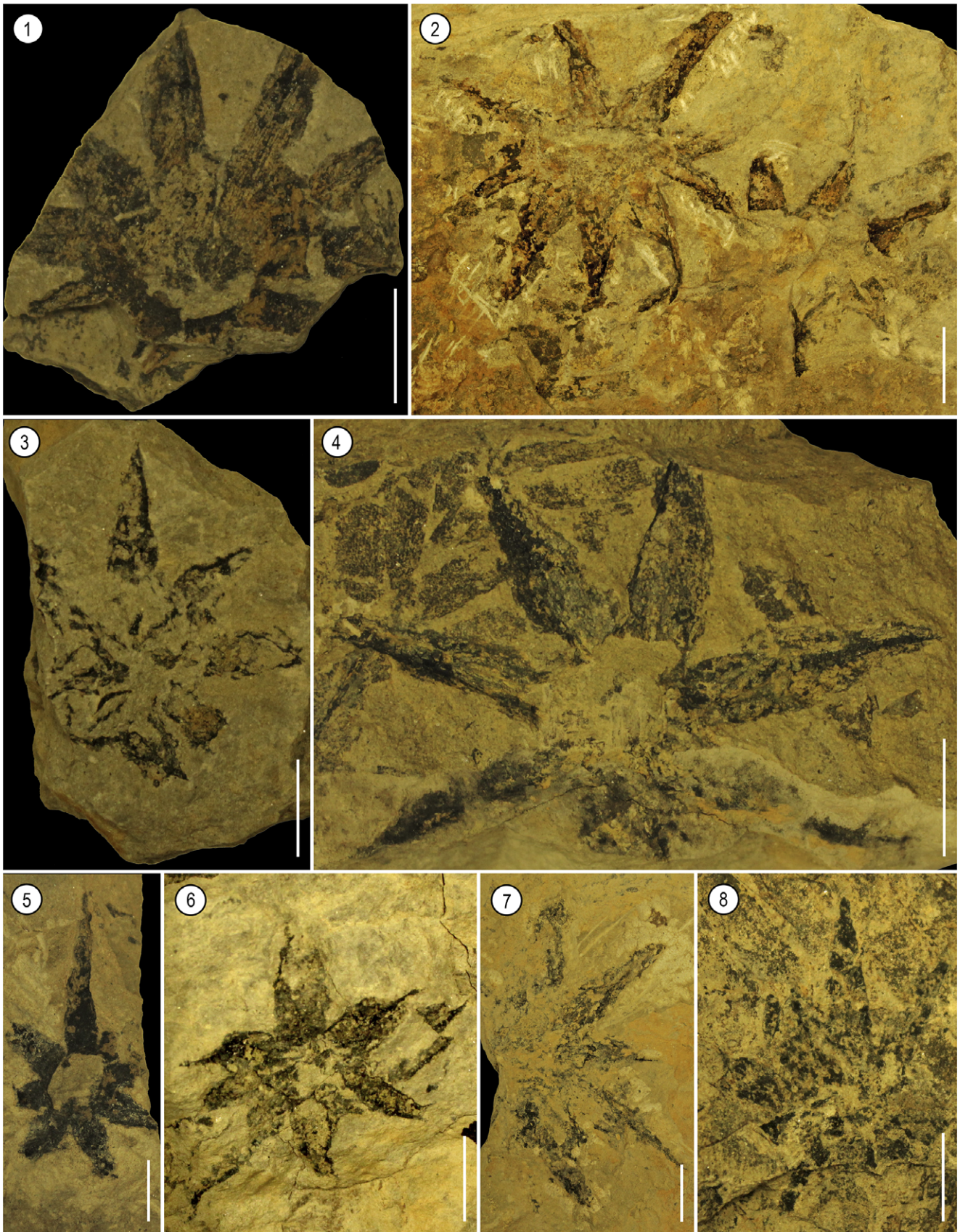


Figure 11. cf. *Weltrichia xochitellii*. (1) (IGM-PB 1683), abaxial view of the pollen-producing organ composed of fused bracts with one middle vein each, and sterile scales in the central part of the structure; (2) (IGM-PB 1684), two associated pollen-producing organs; (3) (IGM-PB 1685), pollen-producing organ showing eight microsporophylls, and the remains of sterile scales in the central part of the structure; (4) (IGM-PB 1686), remains of the fused microsporophylls with a midvein, and showing the attachment scar; (5–8) more specimens showing the fused microsporophylls in different degrees of preservation, (5) (IGM-PB 1687), (6) (IGM-PB 1688), (7) (IGM-PB 1689), (8) (IGM-PB 1690). All scale bars = 1 cm.

eight to nine fused microsporophylls that are filiform in appearance with a prominent middle ridge diverging from the central part of the structure and running towards the apex of each microsporophyll, with striations that run parallel to the ridge (Lozano-Carmona et al., 2021). However, the presence of three rows of semicircular to oval pollen sacs on each side of the distal part of the microsporophylls is needed to confirm that our material is *W. xochiteltii* as reported by Lozano-Carmona et al. (2021).

Our material can be distinguished from other Middle Jurassic *Weltrichia* species found in the region due to the number of microsporophylls present in the structure. *Weltrichia microdigitata* Delevoryas, 1991, and *Weltrichia mixtequensis* Silva-Pineda et al., 2011, have 14 microsporophylls (Delevoryas, 1991; Silva-Pineda et al., 2011), while *Weltrichia ayuquilana* Delevoryas, 1991, has 10 microsporophylls (Delevoryas, 1991). Furthermore, *Weltrichia huitzilopochtlii* (Wieland, 1914–1916) Lozano-Carmona and Velasco-de León in Lozano-Carmona et al., 2024, from the Rosario Formation has seven microsporophylls; they are lanceolate to slightly ovate in shape, and each microsporophyll is widest in the middle (Lozano-Carmona et al., 2024), contrasting with the narrow filiform microsporophylls from our material. *Weltrichia xochiteltii* has been compared with the known diversity of the genus, and it represents an endemic species from the Middle Jurassic of Mexico (Lozano-Carmona et al., 2021). The possible presence of this species in the Otlaltepec Formation suggests that this species had a broader regional distribution among the rift basins of Western Laurasia for the Middle Jurassic.

Incertae sedis

Leaf type 1

Figure 12.1–12.3

Studied material. IGM-PB 1691 to IGM-PB 1693.

Description. This taxon is represented by incomplete pinnate leaves (Fig. 12.1–12.3) and are visible on the adaxial surface. The preserved fragments of the lamina are 7 cm long × 15 cm wide. The rachis is 0.3 cm wide (Fig. 12.1), and it is partially masked by the bases of the pinnae. Alternate pinnae are sessile and attached to the adaxial side of the rachis at angles of 27–39°, every 0.7 cm. Pinnae are of a similar size throughout the preserved fragment, 7.2–7.5 cm long and 0.4–0.7 cm wide, and not imbricate (although they touch in several places; Fig. 12.1–12.3). Pinnae are linear with an entire margin, acute apex, and base apparently oblique (asymmetric), with the upper basal margins overlapping a little, giving an incubous appearance (Fig. 12.1 and 12.2). Simple parallel veins arise from the base, with a density of 30 veins per cm in the middle zone of the pinnae.

Remarks. The morphology of the leaves is similar to the fossil genera *Otozamites* and *Ptilophyllum*. In *Otozamites* the basal acroscopic side of the pinnae is enlarged, forming an auricle (Harris, 1969). *Ptilophyllum* differs in that the leaflets have a decurrent basiscopic base (Harris, 1969). Some specimens from Santo Domingo Tianguistengo preserve the base of the leaflets with an enlarged acroscopic base (Fig. 12.1), while others do not have any preserved base (Fig. 12.3). Furthermore, the material lacks cuticles, so we can only rely on general leaf morphology for character comparison. For this reason, the material is difficult to assign to a bennettitalean genus. A similar type of foliage has been referred as cf. *Ptilophyllum acutifolium* (Morris) Bose and Kasat, 1970, by Person and Delevoryas (1982) for the Rosario Formation. Silva-Pineda (1978) also reported this type of lamina for the

Tecomazúchil Formation and lower Tecocoyunca Group (Zorrillo Formation: Erben, 1956). The shared characters between the Santo Domingo Tianguistengo specimens and the specimens described here are the linear pinnae, similar pinna width (0.3 cm), and acute pinna apex. The description of Silva-Pineda (1978) has few details, hindering character comparison. Furthermore, the Tecomazúchil and lower Tecocoyunca Group specimens are poorly preserved, so caution should be taken when referring to them as *Ptilophyllum acutifolium* Morris, 1841.

Ptilophyllum acutifolium is characterized by a lamina that is broadly lanceolate, with linear, elongated, and narrow pinnae having a straight margin and acute apex (Bose and Kasat, 1970). The base of the pinnae exhibits a slightly rounded acroscopic margin and a decurrent basiscopic margin (Bose and Kasat, 1972). The emended diagnosis proposed by Bose and Kasat (1972) for the species lacks any cuticular characters. Despite this, the species has been recognized as having a wide Gondwanan distribution across space and time, being found in the Cretaceous of Argentina (Passalia, 2007), Antarctica (Césari et al., 1999), Australia (McLoughlin, 1996), and India (Bose and Kasat, 1972). If *P. acutifolium* is indeed present in the Jurassic stratigraphic record of Mexico, it could potentially represent the geographical origin of the species, thus holding global relevance. However, to discuss the significance of this species, better-preserved specimens bearing diagnostic characters of the base of the leaflets and cuticular data are needed. If confirmed, the Mexican specimens could be the oldest record of the species.

Leaf type 2

Figure 12.4, 12.5

Studied material. IGM-PB 2694 to IGM-PB 1695.

Description. Two incomplete pinnate leaves (Fig. 12.4 and 12.5). The preserved fragment of the lamina is 17 cm long × 6.5 cm wide, but a total width of 14 cm is inferred. The rachis is smooth, 1 cm wide (Fig. 12.5). The leaves are preserved showing only the abaxial surface. Pinnae are opposite, sessile, attached to the adaxial side of the rachis at angles of 5–15°, every 1–1.5 cm, and are not imbricate (Fig. 12.4). Pinnae measure 2–6 cm long, 1–1.3 cm wide, getting wider towards the apex of the leaf (Fig. 12.4). It is important to note that the measurements are for incomplete pinnae. Pinnae are transversely oblong and narrow (more than two times longer than broad), with an entire margin that is parallel sided. The apices of the pinnae are not preserved, but they have expanded (Fig. 12.5), or slightly contracted (Fig. 12.5) bases. Parallel veins, without observable bifurcations, have a density of approximately 24 veins per cm in the middle zone.

Remarks. The adaxial attachment of the pinnae and the gross leaf morphology of the leaves are similar to various fossil genera of Bennettitales (e.g., *Ptilophyllum* or *Zamites*) and Cycadales (*Nilssonia* Brongniart, 1825, or *Lepidozamia* Regel, 1857). However, since the material lacks cuticles, and it is preserved showing only the abaxial surface, masking the adaxial side and the bases of the pinnules, the affinities to either Bennettitales or Cycadales cannot be confidently resolved. However, the large size of the specimens, with pinnae more than twice as long as broad, and having parallel-sided margins, makes them unique within this fossil assemblage. The confident assignment of our material to any of these genera would require key diagnostic features from the cuticles or pinna bases.

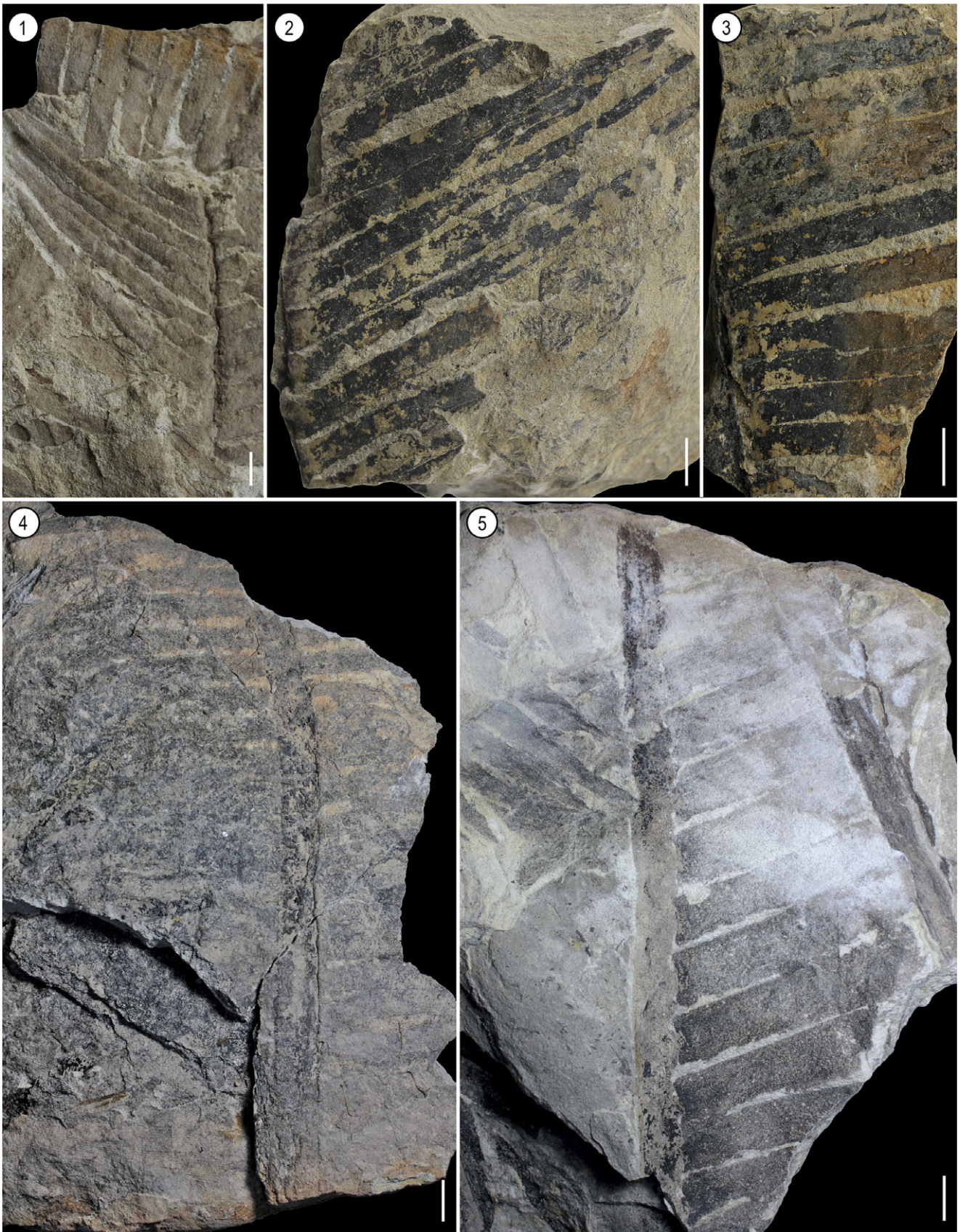


Figure 12. 'Leaf type 1', (1–3) Preserved material showing the adaxial side of the lamina; (1) (IGM-PB 1691), general morphology of the lamina with linear pinnae bearing acute apices; (2) (IGM-PB 1692), distal part of the linear pinnae with acute apices; (3) (IGM-PB 1693), proximal part of the pinnae showing that the bases are not preserved. 'Leaf type 2', (4, 5) Preserved specimens showing the abaxial side of the lamina, (4) (IGM-PB 1694), general morphology of the lamina showing opposite pinnae; (5) (IGM-PB 1695), general morphology of the lamina showing slightly contracted pinnae bases. All scale bars = 1 cm.

Results

The Bennettitales are an abundant and important lineage in the Middle Jurassic, being dominant elements in several floras of the world (e.g., Harris, 1969; Pott and McLoughlin, 2009; Pott et al., 2010; Moisan et al., 2011; Barboni and Lindner-Dutra, 2013; Popa, 2014). During the Middle Jurassic in Mexico, different geographically close plant communities developed a substantial bennettitalean diversity in different rift basins (e.g., Wieland, 1914–1916; Delevoryas and Gould, 1971, 1973; Silva-Pineda, 1978, 1984; Person and Delevoryas, 1982; Silva-Pineda and González-Gallardo, 1988; Velasco de León et al., 2013; Lozano-Carmona and Velasco de León, 2016). Bennettitales in the Otlaltepec Formation contribute to the understanding of species continuity over time and space in Mexican rift basins. Regional similarity in the fossil record is driven by leaves of different species of *Zamites*, and by reproductive structures related to species of *Bennetticarpus* and *Weltrichia*. Some other foliage with uncertain gymnosperm affinities increases the foliar gymnosperm diversity found in the Otlaltepec region, such as Leaf types one and two. *Zamites* represents the most diverse genus among bennettitalean foliage, being the most abundant in number of specimens and species recognized.

Bennettitalean taxa that share a broad temporal–spatial distribution among the three rift basins during the Early–Middle Jurassic are interpreted as species that are more generalist (Table 2). The shared foliage between the Tlaxiaco Basin, the Ayuquila Basin, and the Otlaltepec Basin includes *Zamites ambigua* n. sp. (historically treated in the region as *Zamites feneonis*), *Z. lucerensis*, *Z. oaxacensis*, and *Z. tribulosus* (Table 2). *Otozamites hespera* has a distribution that encompasses the Rosario Formation to the Lower Tecocoyunca Group, the Ayuquila and Tecomazúchil formations, and Otlaltepec Formation. Finally, *Williamsonia netzahualcoyotlii* ranges from the Rosario Formation to the lower Tecocoyunca Group, the Ayuquila Formation, and the Otlaltepec Formation. These shared foliar species are widely distributed across the three rift basins, occurring in diverse localities, sedimentary environments, and temporal deposits, and thus likely represent generalist elements of the flora.

Furthermore, some other fossils found in the Otlaltepec Formation, such as cf. *Zamites diquiyui* or ‘Leaf type 1’, have comparable morphological characters that could increase the species consistency among the three rift-associated basins. *Zamites diquiyui* is present in the Rosario Formation to the lower Tecocoyunca Group and possibly in the Otlaltepec Formation, while ‘Leaf type 1’ (treated historically in the region as *Ptilophyllum acutifolium*), is present in the Rosario Formation to the lower Tecocoyunca Group, the Ayuquila and Tecomazúchil formations, and the Otlaltepec Formation.

On the other hand, species found solely in a single basin represent a restricted pattern that we interpret as specialists. The first specialist pattern involves species with a broad temporal distribution within a single basin, such as *Weltrichia huitzilopochtlii*, found from the Rosario Formation to the lower Tecocoyunca Group in the Tlaxiaco Basin (Table 2), or *W. microdigitata* and *W. mixtequensis*, found from the Ayuquila Formation to the Tecomazúchil Formation in the Ayuquila Basin, but so far not yet in the Otlaltepec Formation. Despite the topographic changes caused by the formation of the mountains uplifted by the activity of the Salado River–Axutla fault, these species persisted within each basin, showing evidence of resilience to the possible changes in niches.

The second specialist pattern consists of species with a restricted temporal range within each basin. For example, within the Tlaxiaco

Basin, *Pterophyllum spinosum* Person and Delevoryas, 1982 (Tezoatlán Area), *Weltrichia magna* Guzmán-Madrid and Velasco-de León, 2021 (Tlaxiaco Area), and *Williamsonia diquiyui* (Tezoatlán) are restricted to the lower Tecocoyunca Group, while *Williamsoniella rosarensis* Velasco-de León et al., 2024, is restricted to the Cualac Formation. Similarly, in the Ayuquila Basin *Weltrichia ayuquilana*, *Weltrichia microdigitata*, and *Williamsonia oligosperma* Delevoryas, 1991, are species found only in the Tecomazúchil Formation (Table 2). The restriction of this species to specific stratigraphic units so far suggests a localized pattern of endemism, highlighting the distinct paleoenvironmental and niche changes as responses to the activity of the Salado River–Axutla fault.

Discussion

Understanding the mechanisms that generate biodiversity or affect its distribution is a central goal of evolutionary biology (Kim et al., 2023). Examining the interaction between tectonic evolution and biological patterns provides essential insights for this research area. The stratigraphic and paleontological records related to the breakup of Pangea preserved in southern Mexico offer a natural laboratory to explore how geological processes shaped landscapes and influenced biodiversity during a continental rifting process. Different authors have documented that during the breakup of Pangea there was a constant change of regional landscapes, and the related shifts in temperature and humidity conditions shaped distinct local climate conditions across the Tlaxiaco, Ayuquila, and Otlaltepec basins (Martini et al., 2016, 2024; Morales-Toledo and Cevallos-Ferriz, 2023; Zepeda-Martínez and Martini 2024). Therefore, studying the bennettitalean fossil record preserved in these extensional basins provides critical insights into how these extinct lineages responded to these changes, highlighting the interplay between plate tectonics and the evolution of terrestrial ecosystems.

Basins formed during crustal thinning are initially limited in extent and isolated from each other. As the boundary faults of these basins mature, a fault pattern begins to emerge, promoting interconnections between different rift basins (Gawthorpe and Leeder, 2000). In rift systems, the evolving topography creates favorable conditions for diverse ecosystems. These processes contribute to the geographic isolation of populations, often due to physical barriers, such as mountains, which are recognized as drivers of biological diversification by supporting higher biodiversity than lowland areas (Rahbek et al., 2019). The mountain-building associated with tectonic or volcanic activity induces landscape and climatic changes that establish ecological gradients and create new habitats (Hoorn et al., 2013). Such isolation promotes allopatric speciation by preventing gene flow between separated groups, leading to adaptation to different environments and, over time, to the emergence of new species (e.g., Lehman and Tilman, 2000; Perrigo et al., 2020). Depending on the ecological and physiological characteristics of the species involved, mountains may also act as corridors facilitating dispersal (Perrigo et al., 2020).

In the case of Mexico, rift basins formed during the breakup of Pangea, such as the Ayuquila and Otlaltepec basins, still present significant uncertainties regarding their internal architecture, boundaries, and the depositional age of their preserved clastic successions. In contrast, the Tlaxiaco Basin, whose tectono-sedimentary evolution is associated with the activity of the SRAF and is well constrained in both time and space, serves as a valuable reference for interpreting the tectonic processes that occurred in southern Mexico during this period.

Table 2. Comparison of bennettitalean diversity in the Early to Middle Jurassic floras in places where plant localities have been reported. From East to West, Tlaxiaco Basin, Ayuquila Basin, and Otlaltepec Basin.

Tlaxiaco Basin							
Olinalá Area		Tecomatlán Area		Tezoatlán Area		Tlaxiaco Area	
lower Tecocoyunca Group	<i>Zamites lucerensis</i> ; <i>Otozamites hespera</i>	lower Tecocoyunca Group	<i>Ptilophyllum acutifolium</i> ?; <i>Zamites feneonis</i> ?; <i>Zamites lucerensis</i> ; <i>Zamites truncatus</i> ? Zeiller, 1903; <i>Otozamites hespera</i> ; <i>Otozamites obtusus</i> ? (Lindley and Hutton, 1834) Brongniart, 1849	lower Tecocoyunca Group	<i>Anomozamites</i> sp.; <i>Cycadolepis mexicana</i> Wieland, 1914–1916; <i>Otozamites hespera</i> ; <i>Pterophyllum</i> sp. A; <i>Pterophyllum spinosum</i> ; <i>Weltrichia huitzilopochtlii</i> ; <i>Williamsonia diquiui</i> ; <i>Williamsonia netzahualcoyotlii</i> ; <i>Williamsonian</i> stems; <i>Williamsonia oaxacensis</i> ; <i>Zamites diquiui</i> ; <i>Zamites lucerensis</i> ; <i>Zamites oaxacensis</i> ; <i>Zamites tribulosus</i> ; cf. <i>Ptilophyllum acutifolium</i> ; cf. <i>Ptilophyllum</i> sp. A	lower Tecocoyunca Group – Inferior	<i>Anomozamites angustifolium</i> Pott and McLoughlin, 2009; <i>Anomozamites</i> cf. <i>A. triangularis</i> (Nathorst, 1879) Pott and McLoughlin, 2009; <i>Anomozamites</i> sp. 2; <i>Anomozamites</i> sp. 3; <i>Bennetticarpus</i> sp. 1; <i>Otozamites gramineus</i> ? (Phillips, 1875) Harris, 1969; <i>Otozamites hespera</i> ; <i>Ptilophyllum acutifolium</i> ?; <i>Weltrichia magna</i> ; <i>Williamsonia nathorstii</i> ; <i>Williamsonia netzahualcoyotlii</i> ; <i>Williamsonia oaxacensis</i> ; <i>Williamsonia sanjuanensis</i> Lozano-Carmona and Velasco-de León, 2021; <i>Williamsonia</i> sp.1; <i>Williamsoniella</i> sp.; <i>Zamites feneonis</i> ?; <i>Zamites lucerensis</i> ; <i>Zamites oaxacensis</i> ; <i>Zamites truncatus</i> ?
Cualac Formation		Cualac Formation		Cualac Formation	<i>Anomozamites</i> sp.; <i>Cycadolepis</i> aff. <i>C. mexicana</i> ; <i>Williamsoniella rosarensis</i> ; <i>Zamites diquiui</i>	Cualac Formation	
				Rosario Formation	<i>Anomozamites</i> sp.; <i>Bennetticarpus</i> sp.; <i>Cycadolepis mexicana</i> ; <i>Otozamites hespera</i> ; <i>Pterophyllum</i> sp. A; <i>Weltrichia huitzilopochtlii</i> ; <i>Wielandiella</i> sp.; <i>Williamsonia netzahualcoyotlii</i> ; <i>Williamsonian</i> stems; <i>Zamites diquiui</i> ; <i>Zamites lucerensis</i> ; <i>Zamites oaxacensis</i> ; <i>Zamites tribulosus</i> ; cf. <i>Ptilophyllum acutifolium</i> ; cf. <i>Weltrichia</i>		
				Diquiyú Formation			
	Flores de Dios and Buitrón, 1982		Silva-Pineda, 1969		Delevoryas and Gould, 1973; Person and Delevoryas, 1982; Lozano-Carmona et al., 2024; Velasco-de León et al., 2024		Guzmán-Madrid and Velasco-de León, 2021; Lozano-Carmona and Velasco-de León, 2016, 2021; Flores-Barragán et al., 2017; Lozano-Carmona et al., 2019,

(Continued)

Table 2. (Continued)

Ayuquila Basin					Otlaltepec Basin	
San José Ayuquila Area		Chilixtlahuaca Area		Santa Maria Xochixtlapilco Area	Santo Domingo Tianguistengo Area	
Tecomazúchil Formation	<i>Ptilophyllum acutifolium?</i> ; <i>Weltrichia ayuquilana</i> ; <i>Weltrichia microdigitata</i> ; <i>Weltrichia mixtequensis</i> ; <i>Williamsonia microdigitata</i> ; <i>Williamsonia oligosperma</i> ; <i>Zamites tribulosus</i>	Tecomazúchil Formation		Tecomazúchil Formation	<i>Ptilophyllum?</i> sp.; <i>Weltrichia xochitetlii</i> ; <i>Zamites feneonis?</i> ; <i>Zamites lucerensis</i> ; <i>Zamites tribulosus</i>	Otlaltepec Formation 'Leaf Type 1' (<i>Ptilophyllum acutifolium?</i>); 'Leaf Type 2'; <i>Otozamites hespera</i> ; cf. <i>Weltrichia xochitetlii</i> ; <i>Williamsonia netzahualcoyotlii</i> ; <i>Zamites ambigua</i> n. sp.; <i>Zamites lucerensis</i> ; <i>Zamites oaxacensis</i> ; <i>Zamites</i> sp. 1; <i>Zamites</i> sp. 2; <i>Zamites tribulosus</i> ; cf. <i>Zamites diquiyui</i> ; aff. <i>Williamsonia</i> sp 1; <i>Williamsonia</i> sp. 2
Ayuquila Formation	<i>Otozamites hespera</i> ; <i>Ptilophyllum acutifolium?</i> ; <i>Williamsonia nathorstii</i> ; <i>Weltrichia mixtequensis</i> ; <i>Weltrichia</i> sp. 1; <i>Williamsonia netzahualcoyotlii</i> ; <i>Zamites lucerensis</i> ; <i>Zamites oaxacensis</i> ; <i>Zamites tribulosus</i>	Ayuquila Formation	<i>Otozamites hespera</i> ; <i>Williamsonia netzahualcoyotlii</i> ; <i>Williamsonia oaxacensis</i> ; <i>Zamites feneonis?</i> ; <i>Zamites lucerensis</i> ; <i>Zamites tribulosus</i>	Ayuquila Formation		Piedra Hueca Formation
						Tianguistengo Formation
Silva-Pineda, 1978; Delevoryas, 1991; Silva-Pineda et al., 2011; Velasco-de León et al., 2019		Velasco-de León et al., 2019		Lozano-Carmona et al., 2021		Velasco-de León et al., 2019; this work

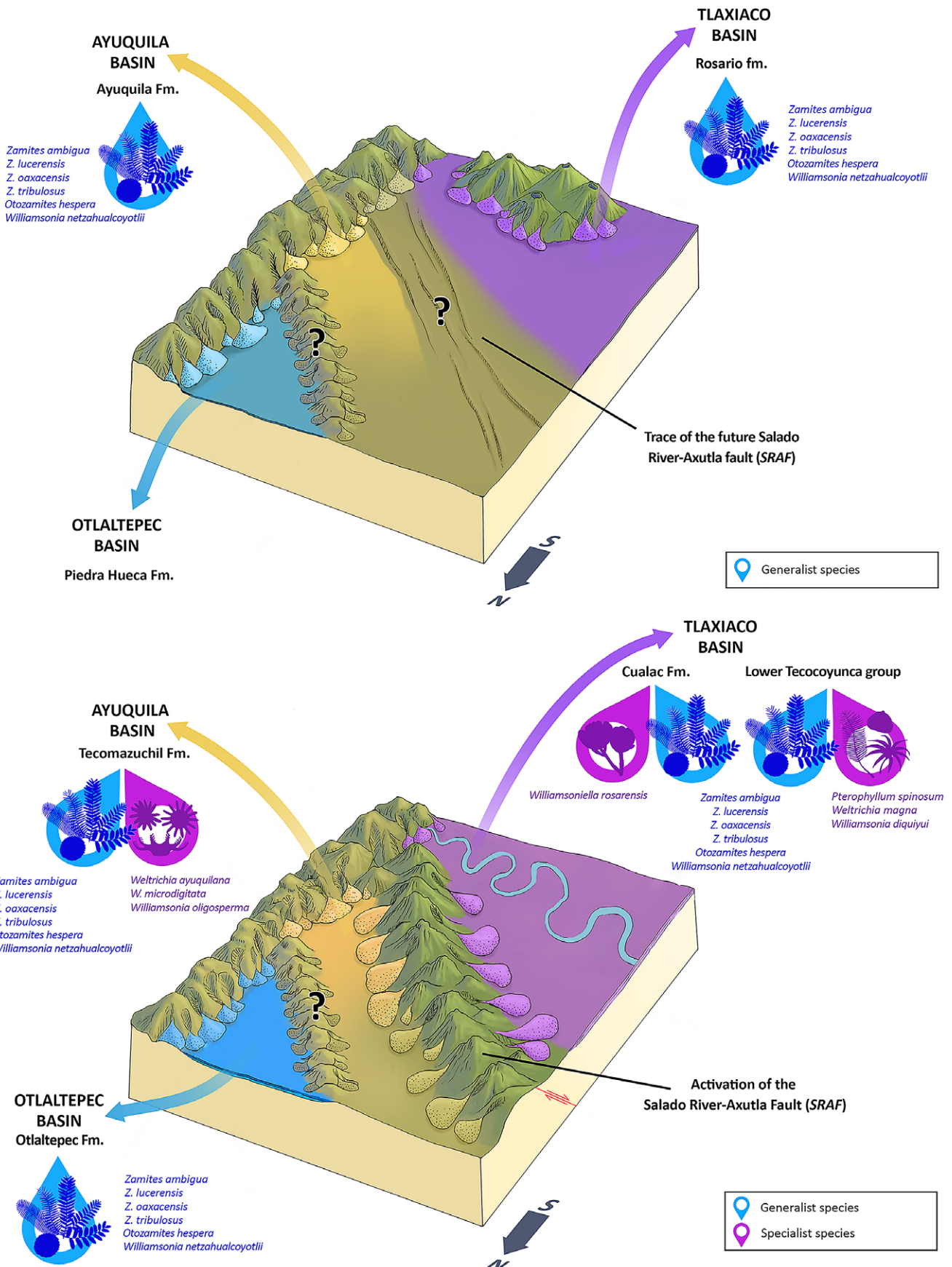


Figure 13. Schematic model showing the distribution of generalist and specialist species during the Early–Middle Jurassic time in the Otlaltepec, Ayuquila, and Tlaxiaco basins. The upper model represents the time prior to the activation of the Salado River–Axutla Fault System (SRAFS). This reconstruction is based on available sedimentological, structural, and paleontological data (see text for references). The unresolved internal architecture and boundaries between the Ayuquila, Otlaltepec, and Tlaxiaco basins are marked with question

Although constraining the precise timing of sedimentation in the Ayuquila and Otlaltepec basins is challenging due to the lack of interbedded volcanic rocks, currently available stratigraphic and geochronologic data offer a preliminary chronological framework for interpreting evolution of the basins. The paleobotanical data presented in this study, together with previously published records and the established chronological framework (Fig. 2), support the interpretation that the Otlaltepec and Ayuquila basins underwent distinct evolutionary histories. This evidence suggests that their individual tectono-sedimentary evolution favored the differential preservation of bennettitalean species during successive stages of basin development.

The influence of taphonomic and depositional factors on the composition of the Jurassic plant assemblages of Mexico was discussed in detail in Morales-Toledo and Cevallos-Ferriz (2023). These authors documented that despite differences in energy levels and sedimentary environments among the Cualac, Ayuquila, and Otlaltepec formations, comparable plant communities are preserved in lithologies of similar grain size, suggesting that the observed floristic patterns are not primarily taphonomic artifacts but are instead linked to broader geological processes such as rifting.

However, additional sources of bias may still influence the interpretation of bennettitalean diversity and distribution presented in this work. Differences in sampling effort among localities may obscure true diversity patterns because some basins have been more thoroughly collected or studied than others. Moreover, the incomplete preservation of diagnostic features, particularly cuticular and reproductive structures, limits taxonomic resolution and may lead to either lumping or splitting of species. Nonetheless, our findings on the bennettitalean fossil record and an updated geological framework for the region paves the way for new research opportunities that address these biases and provide more data to understand ecological patterns of extinct species in deep time.

The patterns observed so far include species shared among multiple basins, as well as species restricted to individual basins, potentially reflecting meaningful differences in the fossil record of generalist and specialist forms. The development of physical barriers generated by Pangea rifting tectonics restricted the distribution of certain plant communities between adjacent basins, as evinced by the specialist bennettitalean fossil record documented in this study. Formation of the topographic barrier between the Jurassic basins driven by the SRAF activity may have led to the emergence of specialist species. Another case that documented the process of diversification of certain species associated with rift basin evolution during the Early–Middle Jurassic in southern Mexico is the notable diversity of conifers in the Otlaltepec Basin, which has not been observed in other nearby Jurassic basins in southern Mexico (Morales-Toledo and Cevallos-Ferriz, 2023).

These patterns in the bennettitalean fossil record suggest that the breakup of Pangea and the evolution of these basins played a crucial role in diversification of extinct lineages. In this context, the topographic barrier developed as a result of the activity of the SRAF, which progressively influenced regional moisture distribution and led to the establishment of contrasting microclimates across the

area. The Tlaxiaco Basin, being located closer to the sea, would have experienced higher moisture availability, whereas drier conditions likely prevailed in the more inland Otlaltepec and Ayuquila basins (Martini et al., 2024; Zepeda-Martínez and Martini, 2024) (Fig. 4). This climatic differentiation, driven by the uplift associated with the SRAF, may have further shaped plant biogeographic patterns by modifying niche conditions and constraining species distribution across the region.

Physical barriers generated during the rifting of continental masses significantly contributed to extant species diversification, often facilitating allopatric speciation (e.g., Lehmann et al., 2000; Evans et al., 2011). However, this process alone does not fully explain species responses and interactions; it was accompanied by the presence of generalist species that demonstrated resilience to ongoing climate and topographic changes associated with such tectonic activity (Fig. 13). In southern Mexico, the activation of the SRAF and the subsequent uplift of northern mountains that separated the Jurassic rift basins played a key role in the diversification of Bennettitales within rift basins. The Jurassic bennettitalean diversity patterns observed in southern Mexico offer a valuable framework for understanding the interactions between extinct plant lineages and the dynamic topographic transformations resulting from the breakup of Pangea.

Conclusions

Middle Jurassic plant communities of the Otlaltepec Formation exhibit a remarkable diversity of Bennettitales, which largely dominate the flora. Our findings reveal that, despite the physical separation of plant communities by geological barriers formed during rifting, a consistent regional flora persisted across the Otlaltepec, Tlaxiaco, and Ayuquila basins. This suggests that some Bennettitales functioned as generalists, maintaining their distribution across varying depositional environments and moisture regimes, while others were more specialized, restricted to specific basins or time intervals.

The preservation of these fossils in diverse sedimentary settings further underscores the ecological flexibility of Bennettitales, shedding light on their ability to persist through environmental shifts driven by tectonic activity. Moreover, their association with ferns and conifers highlights the structural complexity of Middle Jurassic terrestrial ecosystems in the low latitudes of Western Laurasia.

More broadly, this study provides new insights into how ancient plant lineages responded to landscape fragmentation, climate variability, and environmental change over geological timescales. By integrating paleobotanical and stratigraphic data, we contribute to a deeper understanding of the interplay among tectonics, paleoecology, and plant evolution, reinforcing the role of rift basins as natural laboratories for studying biodiversity dynamics during the breakup of Pangea.

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Figure 13. (Continued)

marks. Generalist species were already established during deposition of the alluvial fan system of Rosario Formation, as well as in braided drainages of the Ayuquila Formation (Ayuquila Basin), presumably before the onset of tectonic activity associated with the SRAFS. The lower model represents the time after activation of the SRAFS. Despite current limitations in understanding of the internal architecture and precise boundaries of the Ayuquila and Otlaltepec basins, the paleobotanical data from the Otlaltepec Formation provide evidence of the maintenance of the generalist elements (blue) among all basins following the activation of the SRAF, an event recorded in the stratigraphic record of the Tlaxiaco Basin. On the other hand, the specialist species present in adjacent basins provide evidence of the restriction of certain Bennettitales to specific stratigraphic units, which we interpret as the result of paleoenvironmental and niche changes due to the activity of the SRAFS.

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Competing interests. The authors declare none.

References

- Barale, G., 1981, La paléoflore Jurassique du Jura Français: Étude Systématique, aspects Stratigraphiques et Paléoécologiques: *Documents des Laboratoires de Géologie de Lyon*, n. 81, 467 p.
- Barboni, R., and Lindner-Dutra, T., 2013, New “flower” and leaves of Bennettitales from southern Brazil and their implication in the age of the lower Mesozoic deposits: *Ameghiniana*, v. 50, p. 14–32.
- Beentje, H.J., 2016, *The Kew Plant Glossary: An Illustrated Dictionary of Plant Terms* (Second edition): Richmond, Surrey, Kew Publishing.
- Bose, M.N., and Kasat, M.L., 1970, The genus *Ptilophyllum* in India: *Journal of Palaeosciences*, v. 19, p. 115–145.
- Bose, M.N., and Kasat, M.L., 1972, The genus *Ptilophyllum* in India: *The Palaeobotanist*, v. 19, p. 115–145.
- Boyce, K.C., Lee, J.E., Field, T.S., Brodribb, T.J., and Zwieniecki, M.A., 2010, Angiosperms helped put the rain in the Rainforest: the impact of plant physiological evolution on tropical diversity: *Annals of the Missouri Botanical Garden*, v. 97, p. 527–540.
- Braun, C.F.W., 1843, Beiträge zur Urgeschichte der Pflanzen, in Münster, G.G., ed., *Beiträge zur Petrefactenkunde*, v. 6, p. 1–100, Bayreuth.
- Braun, C.F.W., 1849, *Weltrichia*, eine neue Gattung fossiler Rhyzantheen: *Flora*, v. 32, p. 705–712.
- Brongniart, A., 1825, Observations sur les végétaux fossiles renfermés dans les Grès de Hoer en Scanie: *Annales des Sciences Naturelles*, v. 4, p. 200–224.
- Brongniart, A., 1828, Prodrome d'une histoire des végétaux fossiles, in *Dictionnaire des Sciences Naturelles*, v. 57, p. 16–212, Paris, F. G. Levrault.
- Brongniart, A., 1849, Tableau des genres de végétaux fossiles considérés sous le point de vue de leur classification botanique et de leur distribution géologique (extrait du Dictionnaire universel d'histoire naturelle): v. 13, p. 1–127 (52–176).
- Büchi, L., and Vuilleumier, S., 2014, Coexistence of specialist and generalist species is shaped by dispersal and environmental factors: *The American Naturalist*, v. 183, p. 612–624.
- Campa-Uranga, M.F., García-Díaz, J.L., and Iriondo, A., 2004, El arco sedimentario del Jurásico Medio (Grupo Tecocoyunca y Las Lluvias) de Olinalá, Guerrero: *GEOS: Unión Geofísica Mexicana*, v. 24, p. 174.
- Campos-Madrugal, E., Centeno-García, E., Mendoza-Rosales, C.C., and Silva-Romo, G., 2013, Sedimentología, reconstrucción paleoambiental y significado tectónico de las sucesiones clásticas del Jurásico Medio en el área de Texcalapa, Puebla–Huajuapande León, Oaxaca: revisiones de las formaciones Ayuquila y Tecamazúchil: *Revista Mexicana de Ciencias Geológicas*, v. 30, p. 24–50.
- Canú-Chapa, A., 1998, Las transgresiones Jurásicas en México: *Revista Mexicana de Ciencias Geológicas*, v. 15, p. 25–37.
- Carruthers, W., 1870, On fossil cycadean stems from the secondary rocks of Britain: *Transactions of the Linnean Society of London*, v. 26, p. 675–708.
- Césari, S.N., Parica, C., Remesal, M., and Salani, F., 1999, Paleoflora del Cretácico Inferior de península Byers, islas Shetland del Sur, Antártida: *Ameghiniana*, v. 36, p. 2–22.
- Condamine, F.L., Silvestro, D., Koppelhus, E.B., and Antonelli, A., 2020, The rise of angiosperms pushed conifers to decline during global cooling: *Proceedings of the National Academy of Sciences of the United States of America*, v. 117, p. 28867–28875.
- Delevoryas, T., 1991, Investigations of North American cycadeoids: *Weltrichia* and *Williamsonia* from the Jurassic of Oaxaca, Mexico: *American Journal of Botany*, v. 78, p. 177–182.
- Delevoryas, T., and Gould, R.E., 1971, An unusual fossil fructification from the Jurassic of Oaxaca, México: *American Journal of Botany*, v. 58, p. 616–620.
- Delevoryas, T., and Gould, R.E., 1973, Investigations of North America cycadeoids, Williamsonian cones from the Jurassic of Oaxaca, Mexico: *Review of Paleobotany and Palynology*, v. 15, p. 27–42.
- Durán-Aguilar, R.F., 2014, Sedimentología y geocronología de los lechos rojos del Jurásico, Región Norte de la Cuenca de Tlaxiaco, Tezoatlán, Oaxaca: correlaciones y procedencia [Tesis de Maestría]: México City, Instituto de Geología, Universidad Nacional Autónoma de México, México D.F., 92 p.
- Edwards, D., Kenrick, P., and Dolan, L., 2017, History and contemporary significance of the Rhynie cherts—our earliest preserved terrestrial ecosystem: *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*: v. 373, 20160489, <https://doi.org/10.1098/rstb.2016.0489>.
- Engler, A., 1892, *Syllabus der Vorlesungen Spezielle und Medicinisch-Pharmaceutische Botanik*: Berlin, Gebrüder Borntraeger, 184 p.
- Erben, H.K., 1956, *El Jurásico Medio y el Cretácico de México*: Vigésimo Congreso Geológico Internacional, D.F. México.
- Evans, B.J., Bliss, S.M., Mendel, S.A., and Tinsley, R.C., 2011, The rift valley is a major barrier to dispersal of African clawed frogs (*Xenopus*) in Ethiopia: *Molecular Ecology*, v. 20, p. 4216–4230.
- Flores-Barragán, M.A., Velasco-de León, M.P., and Corro-Ortiz, M.G., 2017, El género *Williamsoniella* (Thomas) y la flora asociada de la Formación Zorrillo-Taberna Indiferenciadas (Jurásico Medio) Oaxaca, México: *Paleontología Mexicana*, v. 6, p. 59–65.
- Flores de Dios, A., and Buitrón, B.E., 1982, Revisión y aportes a la estratigrafía de la Montaña de Guerrero: *Universidad Autónoma de Guerrero, Serie Técnico Científica*, v. 12, p. 1–28.
- Gawhorpe, R.L., and Leeder, M.R., 2000, Tectono-sedimentary evolution of active extensional basins: *Basin Research*, v. 12, p. 195–218.
- Goldhammer, R.K., 1999, Mesozoic sequence stratigraphy and paleogeographic evolution of northeast Mexico, in Bartolini, C., Wilson, J.L., and Lawton, T.F., eds., *Mesozoic Sedimentary and Tectonic History of North-Central Mexico: Geological Society of America, Special Paper*, v. 340, p. 1–58.
- Gradstein, F.M., Ogg, J.G., Schmitz, M.D., and Ogg, G. E., 2012, *The geologic time scale*: Boston, Elsevier, p. 1144.
- Guzmán-Madrid, D.S., and Velasco-de León, M.P., 2021, *Weltrichia magna* sp. nov., a new record for the Middle Jurassic of Oaxaca, México: *Acta Palaeobotanica*, v. 61, p. 95–106.
- Harris, T.M., 1932, The fossil flora of Scoresby Sound East Greenland. Part 3: Caytoniales and Bennettitales: *Meddeleser om Grønland*, v. 85, no. 5, p. 1–133.
- Harris, T.M., 1969, *The Yorkshire Flora III Bennettitales*: London, Trustees of the British Museum (Natural History).
- Hill, C.R., Moore, D.T., Greensmith, J.T., and Williams, R., 1985, Palaeobotany and petrology of a Middle Jurassic ironstone bed at Wrack Hills, North Yorkshire: *Proceedings of the Yorkshire Geological Society*, v. 45, p. 277–292.
- Hoorn, C., Mosbrugger, V., Mulch, A., and Antonelli, A., 2013, Biodiversity from mountain building: *Nature Geoscience*, v. 6, 154, <https://doi.org/10.1038/ngel1742>.
- Kim, D., Stokes, M.F., Ebersole, S., and Near, T.J., 2023, Erosional exhumation of carbonate rock facilitates dispersal-mediated allopatric speciation in freshwater fishes: *Evolution*, v. 77, 2442–2455.
- Lehman, C.L., and Tilman, D., 2000, Biodiversity, stability, and productivity in competitive communities. *The American Naturalist*, v. 156, 534–552.
- Lehmann, T., Blackston, C.R., Besansky, N.J., Escalante, A.A., Collins, F.H., and Hawley, W.A., 2000, The Rift Valley complex as a barrier to gene flow for

- Anopheles gambiae* in Kenya: the mtDNA perspective: *Journal of Heredity*, v. **91**, p. 165–168.
- Lindley, J., and Hutton, W., 1831–1837. *The Fossil Flora of Great Britain, or figures and descriptions of the vegetable remains found in a fossil state in this country*: London, James Ridgway & Sons, v. **1**, p. 1–48 (1831); p. 49–166 (1832); p. 167–218 (1833a); v. **2**, p. 1–54 (1833b); p. 57–156 (1834); p. 157–206 (1835); v. **3**, p. 1–72 (1835); p. 73–122 (1836); p. 123–205 (1837).
- Lozano-Carmona, D.E., and Velasco-de León, M.P., 2016. Jurassic flora in southeast Mexico: importance and prospects of recent findings in the Mixteco Terrane: *Paleontología Mexicana*, v. **5**, 87–101.
- Lozano-Carmona, D.E., and Velasco-de León, M.P., 2021. Bennettitales from the Middle Jurassic of northwestern Oaxaca, Mexico: diversity, sedimentary environments, and phytogeography: *Journal of South American Earth Sciences*, v. **110**, p. 1–17.
- Lozano-Carmona, D.E., Velasco-de León, M.P., and Flores-Barragán, M.A., 2019. Jurassic flora in southern Mexico: *Anomozamites* Schimper, 1870 emend. Pott et McLoughlin, 2009 from Mixteco Terrane, phytogeographical implications of Williamsoniaceae Family (Bennettitales): *Open Journal of Geology*, v. **9**, p. 142–156.
- Lozano-Carmona, D.E., Corro-Ortiz, M., Morales, R.L., and Velasco-de León, M.P., 2021. *Weltrichia xochiteltli* sp. nov. (Bennettitales) from the Middle Jurassic of northwestern Oaxaca, Mexico: first paleobotanical evidence from the Tecomazúchil Formation: *Journal of South American Earth Sciences*, v. **108**, p. 1–11.
- Lozano-Carmona, D.E., Velasco-de León, M.P., and Jiménez-Rentería, J., 2024. Órganos reproductivos de Bennettitales del Jurásico Temprano de la colección del Museo Geológico Comunitario de Rosario Nuevo “Ing. Jorge Jiménez Rentería”, Oaxaca, México: *Paleontología Mexicana*, v. **13**, p. 17–33.
- Martini, M., and Ortega-Gutiérrez, F., 2018. Tectono-stratigraphic evolution of eastern Mexico during the break-up of Pangea: a review: *Earth-Science Reviews*, v. **183**, p. 38–55.
- Martini, M., Ramírez-Calderón, M.G., Solari, L., Villanueva-Amadoz, U., Zepeda-Martínez, M., Ortega-Gutiérrez, F., and Elías-Herrera, M., 2016. Provenance analysis of Jurassic sandstones from the Otlaltepec Basin, southern Mexico: implications for the reconstructions of Pangea breakup: *Geosphere*, v. **12**, 1842–1864.
- Martini, M., Zepeda-Martínez, M., Mori, L., Núñez-Useche, F., Velasco de León, M.P., and Solari, L., 2024. The influence of topography and transport history on the composition of clastic deposits from the Jurassic Tlaxiaco basin, southern Mexico: limitations on the use of mineral and chemical indices as proxies for paleoclimate: *Journal of Sedimentary Research*, v. **94**, p. 266–282.
- Martiny, B.M., Morán-Zenteno, D.J., Tolson, G., Silva-Romo, G., and López-Martínez, M., 2012. The Salado River fault: reactivation of an Early Jurassic fault in a transfer zone during Laramide deformation in southern Mexico: *International Geology Review*, v. **54**, p. 144–164.
- McLoughlin, S., 1996. Early Cretaceous macrofloras of Western Australia: *Records of the Western Australian Museum*, v. **18**, p. 19–65.
- Moisan, P., Voigt, S., Pott, C., Buchwitz, M., Schneider, J.W., and Kerp, H., 2011. Cycadalean and bennettitalean foliage from the Triassic Madygen Lagerstätte (SW Kyrgyzstan, Central Asia): *Review of Palaeobotany and Palynology*, v. **164**, p. 93–108.
- Morales-Toledo, J., and Cevallos-Ferriz, S.R.S., 2023. Is biodiversity promoted in rift-associated basins? Evidence from Middle Jurassic conifers from the Otlaltepec Formation in Puebla, Mexico: *Review of Palaeobotany and Palynology*, v. **318**, 104952, <https://doi.org/10.1016/j.revpalbo.2023.104952>.
- Morales-Toledo, J., Mendoza-Ruiz, A.C., and Cevallos-Ferriz, S.R.S., 2022. The ferns in a new Middle Jurassic locality from the Otlaltepec Formation, Puebla, Mexico: *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, v. **113**, p. 127–140.
- Moreau, J.D., Vullo, R., Charbonnier, S., Jattiot, R., Trincal, V., Néraudeau, D., Fara, E., Baret, L., Garassino, A., Gand, G., and Lafaurie, G., 2022. Konservat-Lagerstätten from the Upper Jurassic lithographic limestone of the Causse Méjean (Lozère, southern France): palaeontological and palaeoenvironmental synthesis: *Geological Magazine*, v. **159**, p. 761–781.
- Morris, J., 1840, in Grant, C.W., Memoir to illustrate a geological map of Cutch: *Transactions of the Geological Society of London (B)*, v. **5**, p. 289–330.
- Morris, J., 1841. Remarks upon the recent and fossil Cycadeae: *Annals & Magazine of Natural History*, v. **1**, p. 110–120.
- Morán-Zenteno, D.J., Caballero-Miranda, C.I., Silva-Romo, G., Ortega-Guerrero, B., and González-Torres, E., 1993. Jurassic–Cretaceous paleogeographic evolution of the northern Mixteca Terrane, southern Mexico: *Geofísica Internacional*, v. **32**, p. 453–473.
- Nathorst, A.G., 1879. Om floran i Skånes kolförande bildningar: *Sveriges Geologiska Undersökning, Serie C*, v. **33**, p. 53–82.
- Passalia, M., 2007. A mid-Cretaceous flora from the Kachaike Formation, Patagonia, Argentina: *Cretaceous Research*, v. **28**, p. 830–840.
- Perrigo, A., Hoorn, C., and Antonelli, A., 2020. Why mountains matter for biodiversity: *Journal of Biogeography*, v. **47**, p. 315–325.
- Person, C.P., and Delevoryas T., 1982. The Middle Jurassic flora of Oaxaca, Mexico: *Palaeontographica Abteilung B*, v. **180**, p. 82–119.
- Phillips, J., 1875. *Illustrations of the Geology of Yorkshire: or, a description of the strata and organic remains. Part I, The Yorkshire Coast*, 3rd edition: 354 pp., London, John Murray.
- Pieńkowski, G., Martini, M., and Zepeda-Martínez, M., 2019. Bajocian transgressive–regressive sequences of the Tecocoyunca Group, southern Mexico, with maximum flooding surfaces marked by *Thalassinoides*: *Geological Quarterly*, v. **63**, p. 449–459.
- Popa, M.E., 2014. Early bennettitalean reproductive structures of Romania: *Palaeobiodiversity and Palaeoenvironments*, v. **94**, p. 327–362.
- Popa, M.E., 2019. Review of the bennettitalean genus *Weltrichia*: *Journal of Palaeogeography*, v. **8**, 12, <https://doi.org/10.1186/s42501-019-0023-9>.
- Pott, C., and McLoughlin, S., 2009. Bennettitalean foliage in the Rhaetian–Bajocian (latest Triassic–Middle Jurassic) floras of Scania, southern Sweden: *Review of Palaeobotany and Palynology*, v. **158**, p. 117–166.
- Pott, C., Krings, M., Kerp, H., and Friis, E.M., 2010. Reconstruction of a bennettitalean flower from the Carnian (Upper Triassic) of Lunz, Lower Austria: *Review of Palaeobotany and Palynology*, v. **159**, p. 94–111.
- Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G., et al., 2019. Building mountain biodiversity: geological and evolutionary processes: *Science*, v. **365**, p. 1114–1119.
- Ramírez-Calderón, M.G., 2018. Formación Tianguistengo: el registro de un ambiente fluvial del triásico en el sur de México (Puebla, Oaxaca) [Tesis de Maestría]: México City, Posgrado en Ciencias de la Tierra, Universidad Nacional Autónoma de México, 211 p.
- Regel, E., 1857. Zwei neue Cycadeen, die im Botanischen Garten zu Petersburg kultivirt werden, nebst Beiträgen zur Kenntniss dieser Familie: *Bulletin de la Société des Naturalistes de Moscou*, v. **30**, p. 163–191.
- Sandoval, J., and Westermann, G.E.G., 1986. The Bajocian (Jurassic) ammonite fauna of Oaxaca, Mexico: *Journal of Paleontology*, v. **60**, p. 1220–1271.
- Seward, A.C., 1895. *The Wealden Flora. II. Gymnospermae. Catalogue of the Mesozoic Plants in the Department of Geology, British Museum (Natural History)*, 2: 259 p., London, British Museum (Natural History).
- Silva-Pineda, A., 1969. Plantas fósiles del Jurásico Medio de Tecamatlán, estado de Puebla: *Paleontología Mexicana*, v. **27**, p. 7–78.
- Silva-Pineda, A., 1978. Plantas de Jurásico Medio del sur de Puebla y noreste de Oaxaca: *Paleontología Mexicana*, v. **44**, p. 27–56.
- Silva-Pineda, A., 1984. Revisión y tipificación de las plantas Jurásicas colectadas y estudiadas por Wieland (1914) en la región de El Consuelo, Oaxaca: *Paleontología Mexicana*, v. **49**, p. 1–103.
- Silva-Pineda, A., and González-Gallardo, S., 1988. Algunas Bennettitales (Cycadophyta) y Coniferales (Coniferophyta) del Jurásico Medio del área de Cuicatlán, Guerrero: *Instituto de Geología, Revista*, v. **7**, p. 244–248.
- Silva-Pineda, A., Velasco-de León, M.P., Arellano-Gill, J., and Grimaldo, J.R., 2011. Una nueva especie de *Weltrichia* (Bennettitales) del Jurásico Medio de la Formación Tecomazúchil (Oaxaca, México): *Geobios*, v. **44**, p. 519–525.
- Silva-Romo, G., Mendoza-Rosales, C.C., Campos-Madriz, E., Centeno-García, E., and Peralta-Salazar, R., 2015. Early Mesozoic Southern Mexico–Amazonian connection based on U–Pb ages from detrital zircons: the La Mora Paleo-River in the Mixteca Terrane and its paleogeographic and tectonic implications: *Gondwana Research*, v. **28**, p. 689–701.
- Stigall, A.L., 2012. Using ecological niche modelling to evaluate niche stability in deep time: *Journal of Biogeography*, v. **39**, p. 772–781.

- Velasco de León, M.P., Ortiz-Martínez, E., Lozano-Carmona, D.E., and Silva-Pineda, A., 2013, Distribución y ambientes de las gimnospermas fósiles del terreno Mixteco: *Paleontología Mexicana*, v. 63, p. 122–143.
- Velasco-de León, M.P., Ortiz-Martínez, E.L., Lozano-Carmona, D.E., and Flores-Barragán, M.A., 2019, Paleofloristic comparison of the Ayuquila and Otlaltepec basins, Middle Jurassic, Oaxaca, Mexico: *Journal of South American Earth Sciences*, v. 93, p. 1–13.
- Velasco-de León, M.P., Ortiz-Martínez, E.L., Flores-Barragán, M.A., Guzmán-Madrid, D.S., and Martínez-Martínez, P.C., 2024, New records of Bennettitales and associated flora from the Jurassic of the Cualac Formation, Mexico: *Palaeontologia Electronica*, v. 27, a14, <https://doi.org/10.26879/1293>.
- Verde-Ramírez, M. de los A., 2015, Relación entre la tectónica y sedimentación del Jurásico, Santo Domingo Tianguistengo, Oaxaca [Master's thesis]: Mexico City, Universidad Nacional Autónoma de México, Posgrado en Ciencias de la Tierra.
- Watson, J., and Sincock, C.A., 1992, Bennettitales of the English Wealden: *Monograph of The Palaeontographical Society, London*, v. 145, p. 1–228.
- Wieland, G.R., 1914–1916, La flora Liásica de la Mixteca Alta: *Boletín del Instituto de Geología, México*, v. 31, p. 1–165.
- Zeiller, R., 1903, *Flore fossil des gîtes de charbon du Tonkin*: publiée avec la participation du gouvernement de l'Indo-Chine, Paris.
- Zepeda-Martínez, M., and Martini, M., 2024, La fragmentación de Pangea en el sur de México y sus posibles efectos sobre los ambientes naturales del Jurásico y sus ecosistemas, in Velasco de León, M.P., ed., *Paleobiota y Geología del Jurásico del Sur de México*: Zaragoza, UNAM-FES, p. 49–79.
- Zepeda-Martínez, M., Martini, M., and Solari, L., 2018, A major provenance change in sandstones from the Tezoatlán basin, southern Mexico, controlled by Jurassic, sinistral normal motion along the Salado River fault: implications for the reconstruction of Pangea: *Journal of South American Earth Science*, v. 86, p. 447–460.
- Zepeda-Martínez, M., Martini, M., Solari, L.A., and Mendoza-Rosales, C.C., 2021, Reconstructing the tectono- sedimentary evolution of the Early–Middle Jurassic Tlaxiaco Basin in southern Mexico: new insights into the crustal attenuation history of southern North America during Pangea breakup: *Geosphere*, v. 17, p. 1294–1317.