UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE ESTUDIOS SUPERIORES ZARAGOZA

Estudio paleobotánico de las Bennettitales del área Este del Terreno Mixteco y regionalización fitogeográfica del Jurásico Medio

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

DIEGO ENRIQUE LOZANO CARMONA

TUTOR PRINCIPAL DE TESIS:
DRA. MARÍA PATRICIA VELASCO DE LEÓN
FACULTAD DE ESTUDIOS SUPERIORES ZARAGOZA, UNAM

COMITÉ TUTOR:
DR. ISMAEL FERRUSQUÍA VILLAFRANCA
INSTITUTO DE GEOLOGÍA, UNAM

DR. JUAN JOSÉ MORRONE
FACULTAD DE CIENCIAS, UNAM

TUTOR INVITADO:
DRA. CLAUDIA CRISTINA MENDOZA ROSALES
FACULTAD DE INGENIERÍA, UNAM

CIUDAD DE MÉXICO. MARZO, 2023

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COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE ESTUDIOS SUPERIORES ZARAGOZA

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ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **03 de octubre de 2022** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **LOZANO CARMONA DIEGO ENRIQUE** con número de cuent**a 99181840** con la tesis titulada **"ESTUDIO PALEOBOTÁNICO DE LAS BENNETTITALES DEL ÁREA ESTE DEL TERRENO MIXTECO Y REGIONALIZACIÓN FITOGEOGRÁFICA DEL JURÁSICO MEDIO",** realizada bajo la dirección de la **DRA. MARÍA PATRICIA VELASCO DE LEÓN,** quedando integrado de la siguiente manera:

Presidente:	DRA. BLANCA ESTELA BUITRÓN SÁNCHEZ
Vocal:	DR. JOSEP ANTON MORENO BEDMAR
Vocal:	DR. DAVID NAHÚM ESPINOSA ORGANISTA
Vocal:	DRA. UXUE VILLANUEVA AMADOZ
Secretario:	DR. JUAN JOSÉ MORRONE

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 03 de febrero de 2023

COORDINADOR DEL PROGRAMA

COORDINACIÓN

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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Unidad de Posgrado, Edificio D, 1° Piso. Circuito de Posgrados, Ciudad Universitaria
Alcaldía Coyoacán. C. P. 04510 CDMX Tel. (+5255)5623 7002 http://pcbiol.posgrado.unam.mx/

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RESUMEN

El estudio de la flora jurásica del sur de México y en particular la del noroeste de Oaxaca sido intermitente y con un enfoque taxonómico básico (*taxonomía alfa*), poco se ha trabajado integralmente con los datos estratigráficos y sedimentológicos y prácticamente ha sido nulo el análisis fitogeográfico local y/o a nivel mundial. Las Bennettitales fueron el grupo más diverso en esta región, sin embargo, no han escapado a ser estudiadas únicamente bajo un enfoque taxonómico alfa. Esto ha relegado su importancia en estudios locales y mundiales, ya que poco se conoce de esta región a nivel internacional. Por lo tanto, el principal objetivo de esta tesis fue aplicar un estudio sistemático a las Bennettitales que incluya las etapas alfa, beta y gamma, así como, reconocer la regionalización fitogeográfica del Jurásico Medio. Para, de este modo, poder tener un panorama paleobotánico más completo durante el Jurásico en la parte occidente del ecuador de Pangea. Realicé las actividades y análisis que conllevaran a completar el esquema sistemático de un estudio paleobotánico, con ello, se obtuvieron resultados significativos que fueron condensados en cinco capítulos. En el primero de estos se describen integralmente los datos paleobotánicos, incluyendo una nueva especie de *Weltrichia*, y los datos estratigráfico-sedimentológicos de la primera localidad fosilífera de la Formación Tecomazúchil. Con el segundo capítulo se obtiene una modificación a la distribución fitogeográfica de *Anomozamites* hacia el área ecuatorial del occidente de Pangea y se adicionan tres fosiliespecies a la riqueza del área de estudio. En el tercer capítulo se revisa y condensa la riqueza de las Bennettitales, y se presenta la descripción sedimentológica de tres localidades fosilíferas de las formaciones Zorrillo y Zorrillo-Taberna. Con ello, se analizó la distribución fitogeográfica de este grupo en las cuencas sedimentarias del Jurásico en el área de estudio y se obtuvieron evidencias que sugieren áreas de endemismo y seis ensambles fitogeográficos que van del Jurásico Temprano al Medio.

Con esta información, en el cuarto capítulo, se presenta un análisis de trazos que permitió identificar patrones de distribución y las causas posibles de esta, en las tres edades del Jurásico. Con ello, se obtienen resultados que muestran como las Bennettitales fueron disminuyendo en diversidad y distribución hacia el Jurásico Tardío. Proceso que se asocia a la fragmentación de Pangea y la separación de las masas continentales. Por último, en el quinto capítulo, se exploró el reconocimiento de la regionalización fitogeográfica del Jurásico Medio, para ello se empleó el análisis de parsimonia de endemismos. Se presenta un nuevo esquema de regionalización que no es compatible con el esquema tradicional. Esto conlleva a generar interrogantes sobre la naturalidad de las unidades fitogeográficas del Jurásico que tradicionalmente se han utilizado, así como su posible rectificación. La conclusión general es que el esquema sistemático empleado permitió ir complementando el estudio paleobotánico de las Bennettitales y permitió visualizar que es importante aplicarlo a otros grupos paleoflorísticos en el área de estudio y la necesidad de una reevaluación del esquema fitogeográfico tradicional del Jurásico y posiblemente del Mesozoico.

ABSTRACT

The study of the Jurassic flora of southern Mexico and particularly that of northwestern Oaxaca has been intermittent and with a basic taxonomic approach (alpha taxonomy). Little has been done comprehensively with the stratigraphic and sedimentological data and there has been practically no local and/or global phytogeographic analysis. The Bennettitales were the most diverse group in this region, however, they have not escaped being studied solely under an alpha taxonomic approach. This has relegated its importance in local and global studies, since little is known about this region internationally. Therefore, the main objective of this thesis was to apply a systematic study to the Bennettitales that includes the alpha, beta and gamma stages, as well as to recognize the phytogeographic regionalization of the Middle Jurassic. In order, in this way, to be able to have a more complete paleobotanical panorama during the Jurassic in the western part of the equator of Pangea. I carried out the activities and analysis that led to completing the systematic scheme of a paleobotanical study, with this, significant results were obtained that were condensed in five chapters. The first of these fully describes the paleobotanical data, including a new species of Weltrichia, and the stratigraphic-sedimentological data of the first fossiliferous locality of the Tecomazúchil Formation. With the second chapter, a modification to the phytogeographic distribution of Anomozamites is obtained towards the equatorial area of western Pangea and three fossil species are added to the richness of the study area. In the third chapter, the richness of the Bennettitales is reviewed and condensed, and the sedimentological description of three fossiliferous localities of the Zorrillo and Zorrillo-Taberna formations is presented. With this, the phytogeographic distribution of this group in the Jurassic sedimentary basins in the study area was analyzed and evidence was obtained suggesting areas of endemism and six phytogeographic assemblages ranging from the Early to Middle Jurassic.

With this information, in the fourth chapter, a track analysis is presented that allowed to identify distribution patterns and the possible causes of this, in the three Jurassic ages. With this, results are obtained that show how the Bennettitales were decreasing in diversity and distribution towards the Late Jurassic. Process that is associated with the fragmentation of Pangea and the separation of the continental masses. Finally, in the fifth chapter, the recognition of the phytogeographic regionalization of the Middle Jurassic was explored, for this the parsimony analysis of endemisms was used. A new regionalization scheme is presented that is not compatible with the traditional scheme. This leads to questions about the naturalness of the Jurassic phytogeographic units that have traditionally been used, as well as their possible rectification. This leads to questions about the naturalness of the Jurassic phytogeographic units that have traditionally been used, as well as their possible rectification. The general conclusion is that the systematic scheme used allowed us to complement the paleobotanical study of the Bennettitales and allowed us to visualize that it is important to apply it to other paleofloristic groups in the study area and the need for a reassessment of the traditional Jurassic and possibly Mesozoic phytogeographic scheme.

INTRODUCCIÓN

El Terreno Mixteco, en el sur de México, contiene una de las floras mejor conservadas y abundantes del Jurásico en México y Norteamérica. Dicha paleoflora ha sido el objeto de estudio para paleobotánicos nacionales y extranjeros desde principios del siglo XX. Sin embargo, estos trabajos fueron intermitentes, el enfoque principal fue taxonómico y la mayoría carecen de una descripción estratigráfica o sedimentológica detallada (Wieland, 1914; Delevoryas & Gould, 1973; Delevoryas & Person, 1975; Person & Delevoryas, 1982; Silva-Pineda, 1984; Silva-Pineda *et al*., 2011; Velasco-de León *et al*., 2013, entre otros). Históricamente, los afloramientos fosilíferos reportados con dicha flora han sido referidos a la Formación Ayuquila *sensu* Campos-Madrigal *et al.* (2013) y a las unidades litoestratigráficas informales de Rosario, Cualac, Zorrillo, Zorrillo-Taberna y Otlaltepec (estas unidades aún no han sido descritas formalmente con base en el Código Estratigráfico Norteamericano, Artículo 3–16, Barragán *et al*., 2010; *ver* Erben, 1956; Morán-Zenteno *et al*., 1993; Carrasco-Ramírez *et al*., 2016; Martini *et al*., 2016; Zepeda-Martínez *et al.*, 2018, 2021). En todas estas formaciones el elemento principal de la paleoflora es el orden de las Bennettitales. Este es el grupo más diverso y las formaciones Zorrillo y Zorrillo-Taberna registran el mayor número de localidades fosilíferas en el noroeste de Oaxaca (Erben, 1956; Delevoryas & Gould, 1973; Delevoryas & Person, 1975; Silva-Pineda, 1978a, b; Morales-Lara & Silva Pineda, 1996; Aguilar-Arellano, 2004; Jiménez-Rentería, 2004; Velasco-de León *et al.*, 2013; Carrasco-Ramírez *et al.*, 2016; Lozano-Carmona & Velasco-de León, 2016; entre otros).

La revisión de los listados taxonómicos de las Bennettitales reportados en el noroeste de Oaxaca está integrado por 11 fosiligéneros y 41 fosilitaxones, de los cuales 30 fosiliespecies son válidas y 11 fosilitaxones necesitan de revisión taxonómica (Delevoryas & Gould, 1973; Silva-Pineda, 1978a, b; Person & Delevoryas, 1982; Silva-Pineda, 1984; Delevoryas, 1991; Silva-Pineda *et al*., 2011; Lozano-Carmona & Velasco de León, 2016, 2021; Flores-Barragan *et al*., 2017; Lozano-Carmona *et al*., 2019, 2021; Velasco-de León *et al*., 2019). Además, en la mayoría de las contribuciones del siglo XX la ubicación geográfica de las Bennettitales es bien conocida, pero la ubicación estratigráfica exacta se desconoce, esta fue generalmente referida sólo a las unidades litoestratigráficas y no se mencionan detalles sedimentológicos de cada unidad que contiene a dicho registro (Delevoryas & Gould, 1973; Delevoryas & Person, 1975; Silva-Pineda, 1978a, b, 1984; Person & Delevoryas, 1982; Delevoryas, 1991; Morales-Lara & Silva Pineda, 1996; Aguilar-Arellano, 2004; Velasco-de León *et al.*, 2013; Flores-Barragan *et al.*, 2017).

Este enfoque sesgado únicamente a reportar la presencia de los taxones en las unidades litoestratigráficas corresponde a un conocimiento y análisis básico o inicial dentro de un contexto sistemático paleobotánico (Anderson & Anderson, 1989). No obstante, como resultados de décadas de estudio con este enfoque, algunos paleobotánicos sugirieron que el muestreo y conocimiento de los afloramientos fosilíferos de Oaxaca se había completado (Delevoryas & Gould, 1973; Silva-Pineda, 1978a, b; 1984; Person & Delevoryas, 1982; Delevoryas, 1991). Esta concepción fue aceptada y reproducida a nivel nacional e internacional (Anderson *et al*., 2007; Pérez-Crespo, 2011) lo que rezago la elaboración de nuevos proyectos de investigación a finales del siglo XX. Sin embargo, aún no se ha completado el estudio paleobotánico de la flora y en particular de las Bennettitales en la región ya que recientemente la riqueza taxonómica ha estado incrementando con nuevos hallazgos y nuevas especies para la paleobotánica del Jurásico (Silva-Pineda *et al*., 2011; Lozano-Carmona & Velasco de León, 2016, 2021; Flores-Barragan *et al*., 2017; Ortega-Chávez *et al*., 2017, 2021; Lozano-Carmona *et al*., 2019, 2021; Velasco-de León *et al*., 2019; Guzmán-Madrid & Velasco-de León, 2021). Por lo tanto, entre las metas necesarias para concretar el conocimiento paleobotánico y en particular el de las Bennettitales en el sur de México, están revisar y actualizar la validez taxonómica de los fosilitaxones, registrar la ubicación y/o localidad estratigráfica, así como su contexto paleoambiental y reconocer la distribución fitogeográfica local, regional y mundial de los fosilitaxones presentes.

En este sentido, la estrategia adoptada por Anderson & Anderson (1989) para estudios paleobotánicos (basada en los criterios sistemáticos de Mayr, 1969) es ideal para aproximarse a la eliminación de los vacíos y la consolidación de conocimiento paleobotánico del Jurásico en el sur de México. Esta estrategia consiste en realizar el estudio en tres etapas: taxonomía alpha (Taxo-α), beta (Taxo-β) y gamma (Taxo-γ). En particular estas etapas corresponden a la exploración, descripción y reconocimiento de especies y afloramientos fosilíferos (Taxo-α); consolidación taxonómica y monografiado de paleofloras de formaciones particulares (Taxo-β), y afiliación de órganos, análisis poblacionales y fitogeográficos de formaciones representativas (Taxo-γ) (Anderson & Anderson, 1989; Leppe, 2005). Entonces, en esta investigación se realiza un estudio paleobotánico de las Bennettitales del noroeste de Oaxaca y se propone una regionalización fitogeográfica del Jurásico Medio con base en un análisis de parsimonia de endemismos de localidades paleoflorísticas de los reinos de Angara, Gondwana y Laurasia *sensu* Meyen (1987), enfocándose en las Bennettitales y los cinco principales órdenes de gimnospermas de este periodo.

El alcance de este estudio permitirá que el conocimiento de la riqueza taxonómica, su distribución espaciotemporal y la asociación de los diferentes grupos de la paleoflora en el Terreno Mixteco, sean la base para desarrollar los análisis de la diversidad paleoflorística, fundamentar afiliaciones de órganos y reconocer patrones fitogeográficos en esta región. Además, este conocimiento se podrá correlacionar con los procesos geológicos que se desarrollaron durante el Jurásico y que impactaron al occidente de la Pangea ecuatorial para realizar propuestas fundamentadas multidisciplinariamente que reconstruyan las condiciones ambientales, ecológicas y los procesos evolutivos en dicho periodo y región. (Anderson & Anderson, 1989; Weber & Cevallos-Ferriz, 1994; Anderson *et al*., 1999; McLoughlin, 2001; Barbacka, 2011; Ferrusquía-Villafranca, 2013; Barbacka *et al*., 2014; Pott, 2014: Pott & McLoughlin, 2014; Pott *et al*., 2015; Lozano-Carmona & Velasco-de León, 2016; Martini *et al*., 2017; Li *et al*., 2019; Velasco-de León *et al*., 2019).

La estructura de esta tesis resulta de la compilación de cinco contribuciones en donde se fue atendiendo la estrategia sistemática de los criterios alfa, beta y gamma. En el primer capítulo se describe una nueva especie del género *Weltrichia* Braun, el paleoambiente y contenido paleobotánico de la primera localidad paleoflorística de la Formación Tecomazúchil, y se analiza la bioestratigrafía de las especies de *Weltrichia* en el noroeste de Oaxaca (Lozano-Carmona *et al*., 2021). El segundo capítulo es una contribución a la identificación taxonómica de tres fosiliespecies del género *Anomozamites* Schimper, emend. Pott et McLoughlin, registradas en la formación Zorrillo-Taberna, y el análisis de las implicaciones fitogeográficas de la familia Williamsoniaceae (Bennettitales) en el hemisferio

Norte con base en este nuevo reporte (Lozano-Carmona *et al*., 2019). El tercer capítulo aborda la descripción de nuevos hallazgos de órganos reproductivos, entre ellos una nueva especie del género *Williamsonia* Carruthers, emend. Harris, así como la interpretación paleoambiental de tres localidades fosilíferas de las formaciones Zorrillo y Zorrillo-Taberna. Además, se condensa el listado taxonómico de las Bennettitales en el noroeste de Oaxaca y se analiza la distribución fitogeográfica de este grupo en las cuencas sedimentarias del Jurásico en el área de estudio (Lozano-Carmona & Velasco-de León, 2021). El cuarto capítulo trata sobre la identificación de los patrones fitogeográficos, con base en un análisis de trazos, de ocho géneros de la familia Williamsoniaceae durante el Jurásico. Esta metodología permitió obtener cinco trazos generalizados, dos en el Jurásico Temprano y Medio respectivamente, y uno en el Jurásico Tardío, así como dos nodos en el Jurásico Medio. El análisis de estos patrones de distribución muestra la congruencia con la dinámica de la tectónica durante el Jurásico. Esto permite sugerir eventos vicariantes como los causantes de la distribución y una distribución restringida de estos taxones a través del Jurásico. Por último, el quinto capítulo versa sobre el reconocimiento de una regionalización fitogeográfica del Jurásico Medio con base en el análisis de parsimonia de endemismos de seis ordenes de gimnospermas. En este análisis se obtuvo una regionalización sucesivamente anidada, dando pauta a la propuesta de una jerarquización diferente a la realizada por Meyen (1987). Esta propuesta incluye al reino Pangea, la región Laurásica, el dominio Ecuatorial-Eurosiniano y la provincia Paleoecuatorial. Este nuevo esquema permite abrir la posibilidad de reevaluar la propuesta tradicional de regionalización de Meyen (1987) y explorar la integración de otros taxones que complementen el análisis paleobiogeográfico. Al final se sintetiza y concluye, en un epílogo, el trabajo de estas cinco contribuciones.

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PRIMER CAPÍTULO

Weltrichia xochitetlii sp. nov. (Bennettitales) del Jurásico Medio del noroeste de Oaxaca, México: Primer evidencia paleobotánica de la Formación Tecomazúchil.

- **Lozano-Carmona, D. E.** Propuesta y diseño del trabajo; revisión de los ejemplares e identificación taxonómica; recopilación y consulta bibliográfica; análisis e interpretación de datos; toma de fotografías y elaboración de figuras; actividades de campo: recolecta de material, selección de niveles (estratos) de muestreo, medición y descripción sedimentológica de la sección estratigráfica de la localidad de estudio; redacción del manuscrito y registro de material en la Colección de Paleontología de la FESZ-UNAM.
- **Corro-Ortiz, M. G.** Descubridor de localidad; actividades de campo: recolecta de material, apoyo en la medición de la sección estratigráfica de la localidad de estudio, revisión del manuscrito, registro de material en la colección geológica de la Universidad Tecnológica de la Mixteca.
- **Morales, R. L.** Descubridor de localidad; actividades de campo: recolecta de material, revisión del manuscrito.
- **Velasco-de León, M. P.** Dirección de trabajo, revisión de análisis de datos paleontológicos y del manuscrito.

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Weltrichia xochitetlii sp. nov. (Bennettitales) from the Middle Jurassic of northwestern oaxaca, Mexico: First paleobotanical evidence from the Tecomazúchil Formation

Diego E. Lozano-Carmona [a,b,*], Marcos Germán Corro-Ortiz [c], René Luis Morales [d], María Patricia Velasco-de León [b]

[a] *Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Ciudad Universitaria, Universidad Nacional Autónoma de México, Coyoacán. C.P, 04510, Ciudad de México, Mexico*
[b] *Colección de Paleontología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Batalla 5 de mayo, Ejercito de Oriente, Iztapalapa, C.P, 09230, Ciudad de México, Mexico*
[c] *Instituto de Minería, Universidad Tecnológica de la Mixteca, Carretera a Acatlima Km. 2.5, Huajuapan de León, C.P., 69000, Oaxaca, Mexico*
[d] *Instituto de Hidrología, Universidad Tecnológica de la Mixteca, Carretera a Acatlima Km. 2.5, C.P., 69000, Huajuapan de León, Oaxaca, Mexico*

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ABSTRACT

The Jurassic flora of southern Mexico represents a key phytogeographic element in North America, where vegetative organs (leaves) of Bennettitales are the most abundant and best preserved. In this region, valid species of reproductive organs of the genus *Weltrichia* (Williamsoniaceae) have only been recorded in Mexico. These are three species from the Jurassic in northwestern Oaxaca and are restricted to the Ayuquila Formation (Bajocian/Bathonian). Here we present *Weltrichia xochitelii,* a new fossil-species discovered in the Tecomazúchil Formation (Callovian). This new species is established based on diagnostic characters that differ from other species, such as the external outline diameter of the organ, the basal cup diameter, the number of centrifugal rays, and the shape, position, and size of the pollen sacs. *Weltrichia xochitetlii* and *W. microdigitata* comprise the group of smallest reproductive organs of the family Williamsoniaceae (Bennettitales) worldwide. We also provide a stratigraphic and sedimentary description of the first fossiliferous locality of the Tecomazúchil Formation, a comment on its paleobotanical content, and a comparison with records from other localities in southern Mexico. The Ayuquila and Tecomazúchil formations were deposited in the Ayuquila BBasin. This new record broadens the stratigraphic range of *Weltrichia* up to the Callovian in northwestern Oaxaca. In addition, it increases the number of species of this fossil-taxon in the region, which corresponds to the highest richness in North America from the Jurassic.

1. Introduction

The order Bennettitales are a group of extinct gymnosperms with an important morphological, phytogeographic, and evolutionary significance. The innovations in their complex uni- and bisexual reproductive structures are still subject of research. These structures were morphologically like angiosperm flowers but without being homologous to the reproductive structures of this group of seeds plants. Given this morphological similarity, the reproductive organs of Bennettitales have been considered as representative of an evolutionary “test” of reproductive strategies before plants with flowers, or angiosperms, appeared (Harris, 1969; Popa, 2014; Pott, 2014; McLoughlin et al., 2017). Bennettitales were a group with a near worldwide distribution during the Jurassic and were the main element of the vegetation of the Laurasia Kingdom (Anderson et al., 2007; Popa, 2019). There are two families classified in the order Bennettitales: Williamsoniaceae and Cycadeoidaceae. The first one dominated the Late Triassic and all the Jurassic, whereas the second one has been recorded mainly in the Cretaceous (Anderson et al., 2007; Taylor et al., 2009; Popa, 2019).

The unisexual reproductive organs of the family Williamsoniaceae correspond to *Williamsonia* Carruthers and *Weltrichia* (Braun) Harris, which are female and male structures, respectively. Popa (2019) recently reviewed the genus *Weltrichia,* describing the terminology and systematics of the fossil-taxon, and generally commenting the following:

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* Corresponding author. Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Ciudad Universitaria, Universidad Nacional Autónoma de México, Coyoacán. C.P, 04510, Ciudad de México, Mexico

E-mail address: diego.lozano@zaragoza.unam.mx (D.E. Lozano-Carmona).

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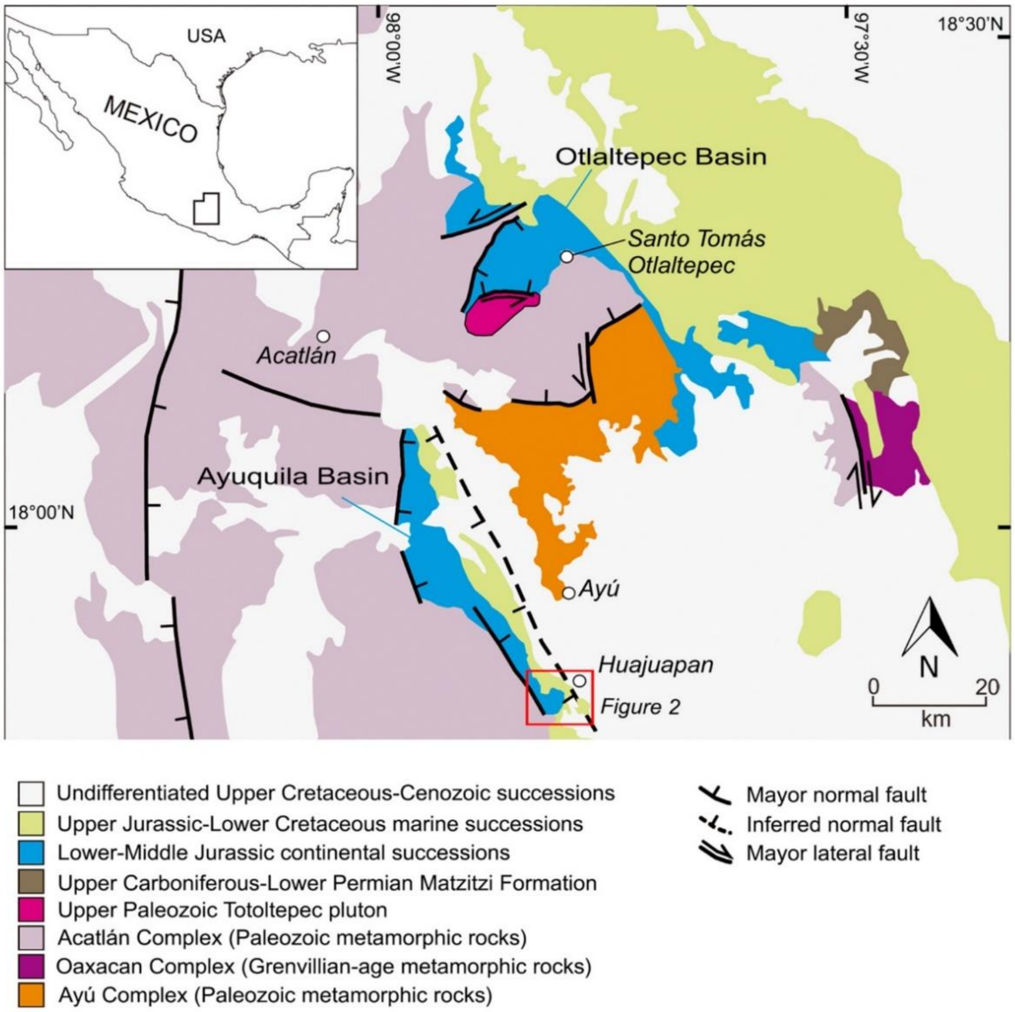

Fig. 1. Schematic geological map showing the Ayuquila Basin location in the northwestern and southwestern of the Huajuapan de León in the northwestern of the state of Oaxaca, southern Mexico. The red square indicates the study locality (Fig. 2). Map constructed based on Morán-Zenteno et al. (1993); Geological-Mining map of E14-9, 1:250,000 scale, (SGM, 2000), Campos-Madrigal et al. (2013), Martini et al. (2016).

its records comprise 25 valid species from Late Triassic to Late Jurassic, distributed in both hemispheres, with radial morphology and heterogeneous size. Popa (2019), also discusses pollination structures and strategies and concludes that *Weltrichia* is a male reproductive structure with peculiar anatomy and high morphological diversity. Finally, Popa (2019) highlights the records from North America, which are restricted to southern Mexico. These records correspond to the Mixteco Terrane in southern Mexico (Delevoryas, 1991; Silva-Pineda et al., 2011).

The sedimentary record of the Mesozoic in the Mixteco Terrane contains the best preserved plant fossils of the Jurassic in Mexico and has a diversity that surpasses 80 fossil-taxa among ferns, Equisetales, Bennettitales, Cycadales, Caytoniales, Coniferales, Podozamitales, Ginkgoales, Czekanowskiales, and Incertae Sedis (Silva-Pineda, 1984; Delevoryas, 1991; Lozano-Carmona and Velasco de León, 2016; Flores-Barragan et al., 2017; Ortega-Chavez et al., 2017; Lozano-Carmona et al., 2019; among others). However, the diversity of *Weltrichia* comprises only three valid fossil-species: *W. ayuquilana* Delevoryas 1991, *W. microdigitata* Delevoryas 1991, and *W. mixtequensis* Silva-Pineda, Arellano-Gil et Grimaldo 2011, and one questionable species, *W. mexicana* (Wieland) Harris 1969. The three valid species were recorded in the Oaxaca state, Ayuquila BBasin, Ayuquila Formation, Bajocian/Bathonian in age, whereas the only specimen of *W. mexicana* was found in the Oaxaca state, Tezoatlán basin, possibly in the lower portion of the Rosario Formation, Toarcian in age (Silva-Pineda, 1984; Delevoryas, 1991; Delevoryas and Gould, 1973; Silva-Pineda et al., 2011; Campos-Madrigal et al., 2013). Even though sampling and studies in Jurassic localities continue to provide both new records and species of foliar and reproductive organs of gymnosperms: *Pseudoctenis lanei* Thomas 1913, *P.* sp., *Williamsoniella* sp., *Agathoxylon* sp., *Anomozamites angustifolium* Pott et McLoughlin 2009, *A.* sp. cf. *A. triangularis* (Nathorst) Pott et McLoughlin 2009 and *A.* sp.1 (Flores-Barragan et al., 2017; Ortega-Chavez et al., 2017; Lozano-Carmona and Velasco de León, 2016, 2019), the case of *Weltrichia* is unusual because there are only a few known specimens of these species and are practically restricted to the Ayuquila Formation (Bajocian–Bathonian). Nevertheless, the recent finding of a new fossiliferous locality in the Tecomazúchil Formation (Callovian) has allowed the discovery of new specimens of *Weltrichia*.

Considering the above, the objective of the present study was to describe both a new species of the genus *Weltrichia* and the first fossiliferous locality of the Tecomazúchil Formation in the Ayuquila Basin (*sensu* Campos-Madrigal et al., 2013). We also comment on the implications of the phytogeographic and biostratigraphic distribution of *Weltrichia* in the Middle Jurassic in southern Mexico and make a first preliminary reference of the paleobotanic content of the locality. The morphological characters of these specimens and their comparison with

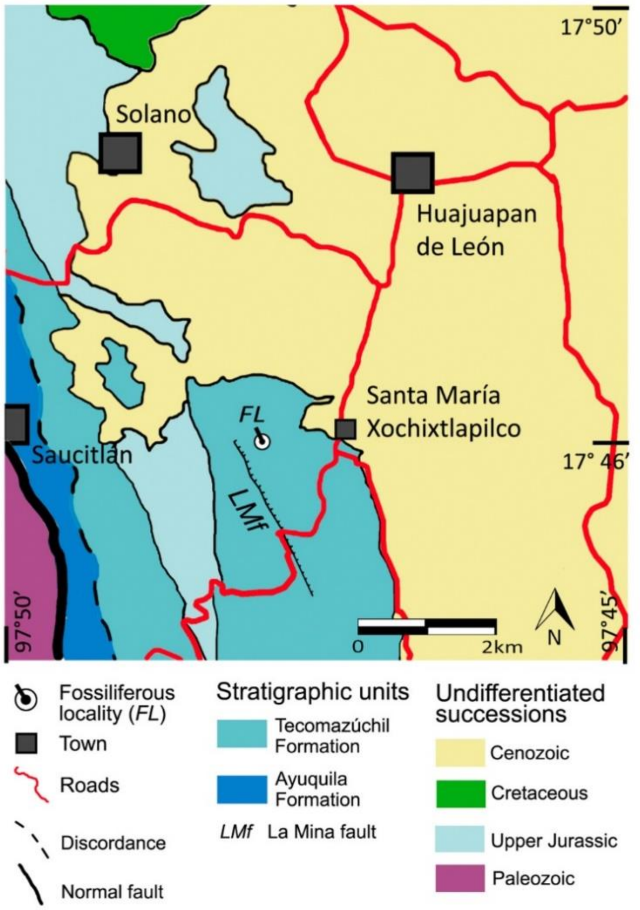

Fig. 2. Schematic geological map including the Santa María Xochixtlapilco locality and showing the distribution of continental units of the Ayuquila Basin: Ayuquila and Tecomazúchil formations, as well as undifferentiated units of the Paleozoic (basement), Upper Jurassic, Cretaceous, and Cenozoic. Map constructed based on SGM (2009) and Campos-Madrigal et al. (2013).

the 25 valid species of *Weltrichia* (*sensu* Popa, 2019) allow to substantiate the occurrence of a new species, named *W. xochitetlii* sp. nov. This new finding broadens the (temporal) stratigraphic distribution of the taxon in southern Mexico up to the Callovian. However, the geographic distribution in the Mixteco Terrane remains almost exclusively within the Ayuquila Basin (Delevoryas and Gould, 1973; Delevoryas, 1991; Silva-Pineda et al., 2011; Campos-Madrigal et al., 2013). This new species is remarkably different from the other species in the Mixteco Terrane, but the size of the organ is similar to *W. microdigitata*, and these two species comprise the group of the smallest species of *Weltrichia*. This allows us to argue that the information on the distribution and diversity of Bennettitales in this region is far from conclusive. Therefore, increasing the knowledge of this taxonomic diversity will allow to determine the phytogeographic patterns that occurred during the fragmentation of Pangea.

2. Geological framework

2.1. *Tecomazúchil Formation (Pérez-Ibargüengoitia et al., 1965 emend. Campos-Madrigal et al., 2013)*

Campos-Madrigal et al. (2013) propose subdividing the Middle Jurassic clastic succession of the Ayuquila Basin into two lithostratigraphic units. They substantiate this based on the major angular unconformity observed in their analysis, as well as on magmatic and detrital zircon dating. They define the Ayuquila Formation as a Bajocian/Bathonian deposit and the Tecomazúchil Formation as corresponding to the Callovian. They also present lithological evidence documenting an environmental change from semiarid to humid for each formation, respectively. The outcrop of the Tecomazúchil Formation extends to the northwestern and southwestern of the Huajuapan de León, Oaxaca, southern Mexico (Fig. 1). Tecomazúchil Formation consists of intercalations of sandstone, siltstone, lutite, and continental conglomerate, and its type locality is the outcrop in the Tecomazúchil river (Pérez-Ibargüengoitia et al., 1965). Campos-Madrigal et al. (2013) recognize 15 fluvial facies, from coarse-grained matrix-supported facies to fine-grained laminated facies and paleosoils. The composition consists of clastic rocks that include monomictic and oligomictic conglomerate, lithic greywacke, sublitharenite, and subarkose.

Based on the lithofacies analysis, Campos-Madrigal et al. (2013) propose that a braided fluvial system occurs above the unconformity, but more evolved than that of the Ayuquila Formation, under a process of siltation and probably as an endorreic Basin with a NW-SE orientation.

The locality that contains the study material is in Santa María Xochixtlapilco in the southwestern of Huajuapan de León (geographic coordinates: 17° 46′ N and 97° 48’ W; Fig. 2).

3. Material and methods

The examined material corresponds to impressions of reproductive organs and leaves of Bennettitales preserved in fine-to medium-grained sandstone. The specimens lack cuticle and the leaves are poorly preserved. The collected material was catalogued with the acronym UTMSMX and a consecutive number from 1 to 17. Specimens of *Weltrichia* were deposited in the Paleontology Collection of the Zaragoza Faculty of Higher Studies (FESZ) of the Universidad Nacional Autónoma de México (UNAM), while leaf specimens were deposited in the collection of the Institute of Mining of the Universidad Tecnológica de la Mixteca. In cases when a hand sample contained more than one fossil-taxon of the same genus, species, or another fossil-taxon, we used a combination of numbers; for example, UTMSMX 4(1), where 4 is the hand sample and (1) the fossil-taxon number in the sample. The stratigraphic data of the collected specimens were recorded through standardized sampling (Lozano-Carmona and Velasco-de León, 2016).

In order to verify that the specimens UTMSMX 4(1) and 12 corresponded to a reproductive organ of the fossil-genus *Weltrichia*, we first performed a series of observations and obtained morphometric data and compared them with the description of *Weltrichia* by Harris (1969) and Popa (2014, 2019). Morphometric data were obtained using a Nikon SMZ-10A stereoscope and quantitative macroscopic characters were measured with a Vernier caliper. Each examined specimen was photographed with a Sony Cibershot DSC-H10 (Carl Zeiss Lens: 3,5- 4,4/6,3-63) camera applying the techniques proposed by Kerp and Bomfleur (2001). We then obtained millimetric measurements whit ImageJ 1.48v software. Once we verified that the specimens UTMSMX 4(1) and 12 corresponded to *Weltrichia*, we compared them with the valid species (Table 1) of this fossil-genus (*sensu* Popa, 2019) to corroborate either a new record of a previously described species or the presence of a new species (Saporta, 1891; Wieland, 1914; Krasser, 1922; Harris, 1969; Pal and Ghosh, 1985; Bose and Banerji, 1984; Kimura and Ohana 1989; Delevoryas, 1991; Popa, 2001, 2014, 2019; Sun et al., 2001; Li et al., 2004; Silva-Pineda et al., 2011). Reconstructive illustrations of the new species were made based on the methodology described by Popa (2019) and the general reconstructions of the genus *Weltrichia* presented by Anderson et al. (2007) and Rothwell et al. (2009). Later, the leaf organs were determined based on the paleobotanical literature of the region (Person and Delevoryas, 1982; Silva-Pineda, 1969, 1978, 1984, 1990; Silva-Pineda and González-Gallardo, 1988; Morales-Lara and Silva-Pineda, 1996; Lozano-Carmona and Velasco-de León, 2016).

During survey visits to the Santa María Xochixtlapilco locality, we

Table 1
List of *Weltrichia* fossil-species and their principal characters compared with *Weltrichia xochitetlii* sp. nov.

Taxon	D	Bcd	Cfr	Crl	Crw	Cpr	Ps	Ps(l, w)	Pss	Reference
Weltrichia alfredii (Krasser) Popa	120	55	13–14	30–32	10–12	?	?	?	?	Krasser (1922); Popa (2014), 2019
Weltrichia alpina Krasser	54	?	14	10 d	17 d	?	?	?	?	Popa, (2019)
Weltrichia antonii Popa	100	52	9–10	25	13	?	?	?	?	Popa, (2014)
Weltrichia ayuquilana Delevoryas	60	30	10	15	?	no	many	6, 2	Elliptic–elongated	Delevoryas, (1991)
Weltrichia daohugouensis Li et al.	98–100	48–50	22–23	20–25	4–5	?	many	2, 1–1.5	Elliptic	Li et al. (2004)
Weltrichia fabrei Saporta	?	?	?	50–60	8–10	?	?	3–4, 1	Elongated	Saporta (1891); Popa (2019)
Weltrichia givulescui Popa	100	30–40	16	40–50	7–10	16	?	?	?	Popa, (2001)
Weltrichia harrisiana Bose et Banerji	120–150	20	12–14	25–35	5–8	?	5	7–9, 1.5	Elongated	Bose and Banerji (1984); Popa (2019)
Weltrichia hirsuta Schweitzer	130–140	?	46	?	?	?	?	?	Elongated– elliptic	Popa, (2019)
Weltrichia huangbanjingouensis Sun et al.	?	35	?	?	?	?	?	?	?	Sun et al., (2001); Popa (2019)
Weltrichia johannae Popa	70	15	12	25–27	5–6	12	?	?	?	Popa, (2014)
Weltrichia maldaensis Pal et Ghosh	70 d	20	8 (16 d)	25	5	?	12?	?	Circular	Pal and Ghosh (1985); Popa (2019)
Weltrichia microdigitata Delevoryas	30	15	14	7–8	?	no	20–30	?	Elongated–tubular	Delevoryas, (1991)
Weltrichia mirabilis Braun	100	50	10–11	30–40	?	?	20	3–5, ?	Elliptical–elongated	Popa, (2019)
Weltrichia mixtequensis Silva Pineda et al.	160	20	14	75–80	7–9	?	7–9	1.6–5.5, 0.3–1.3	Elongated–drop-shaped	Silva-Pineda et al. (2011)
Weltrichia oolithica Saporta	80 d	40	9?	30–40	?	?	?	?	?	Popa, (2019)
Weltrichia pecten (Leckenby) Harris	100–120	30–50	10–12	30	5–10	no	?	3, 1	semicircular	Harris, (1969)
Weltrichia primaeva Schweitzer et Kirchner	?	?	?	60	9	?	8–10	?	Elliptic	Popa, (2019)
Weltrichia santalensis (Sitholey et Bose) Harris	220–230	28–45	20	?	?	?	?	?	Elongated	Harris (1969); Popa (2019)
Weltrichia setosa (Nathorst) Harris	120	40	20	40–60	10–16	40	12?	3–7, ?	Flattened,	Harris, (1969)
Weltrichia sol Harris	170–200	100	30	50–60	10	no	4–5	4, 2.5	Semicircular	Harris, (1969)
Weltrichia sp. (sp. nov.?)	100	27	15–16	37	10	?	?	?	?	Kimura and Ohana (1989)
Weltrichia spectabilis (Nathorst) Harris	?	40	13	30–50	10	no	1–3	1–1.5, ?	Semicircular-elongated	Harris, (1969)
Weltrichia steierdorfensis Popa	105–120	40–45	12	25	13	?	?	?	?	Popa, (2014)
Weltrichia whitbiensis (Nathorst) Harris	120–130	40–50	13–16	40	10	no	7–8	2–3, ?	Elliptic	Harris, (1969)
***Weltrichia xochitetlii* sp. nov.**	**32–45.2**	**11**	**8**	**14.1–22.5**	**3.1**	**?**	**6**	**1.2, 1**	**Oval–elliptical**	**This study**

AbbreviationsD: External outline diameter; Bcd: Basal cup diameter; Cfr: centrifugal rays; Crl: Centrifugal ray length; Crw: Centrifugal ray width; Cpr: Centripetal rays; Ps: Pollen sacs; Ps(l, w): Pollen sacs (length, width); Pss: Pollen sac shape; ? unknown data; d: character deduced based on reference. All metric data is in millimeters.

measured a stratigraphic section containing the fossil strata using a Jacob's staff and made a lithological and sedimentary description of each stratigraphic unit. We also made a description of the facies based on Miall (2000, 2006). The stratigraphic section was plotted in SedLog ver. 3.1 (Zervas et al., 2009) and edited in Photoshop CC 2017 for its representation in the present study. We used photo-mosaics to represent the measured lithostratigraphic units (Miall, 2000, 2006). Facies and stratigraphic, lithological, and sedimentary characteristics were compared with those mentioned by Campos-Madrigal et al. (2013) in order to corroborate the correspondence to the Tecomazúchil Formation.

4. Results and discussion

4.1. Systematic palaeobotany

Weltrichia is a cup-shaped male reproductive organ with basally fused centrifugal rays, occasionally with sterile bracts or centripetal rays in a single row. Inner side of centrifugal rays bearing pollen sacs, also called synangia, which can be arranged in one or several rows, the whole structure has radial symmetry (see Harris, 1969; Popa, 2014, 2019).

Order: **Bennettitales** Engler, 1892.

Family: **Williamsoniaceae** (Carruthers) .

Genus: ***Weltrichia*** Braun, 1847 emend. Harris (1969).

Type species: Weltrichia mirabilis Braun (1847), from Jurassic of Veitlahm (Bavaria), Germany.

Weltrichia xochitetlii sp. nov. Lozano-Carmona et Velasco-de León.

Etymology: The specific epithet means "stone flower" (xochitetl) in Nahuatl language and refers to the flower-like morphology of the fossil.

Holotype: UTMSMX-12, deposited in the Paleontology Collection of the FESZ, UNAM.

Paratype: UTMSMX-4(1), deposited in the Paleontology Collection of the FESZ, UNAM. *Type locality:* Santa María Xochixtlapilco, Huajuapan de León, Oaxaca. Tecomazúchil Formation. Callovian age. Coordinates: 17° 46′ N and 97° 48' W.

Fig. 3.

Studied material: UTMSMX 4(1) and 12, two specimens.

Diagnosis: Male reproductive structure, small, composed of at least eight centrifugal rays basally fused to form a central cup, semicircular to oval pollen sacs on each side of the centrifugal rays forming up to three rows; centrifugal ray are filiform in appearance with a strong median ridge on each one; without centripetal rays and resin bodies.

Description: Adaxial and abaxial views of an open star-shaped male reproductive structure, with at least eight centrifugal rays basally fused to form a cup-shaped structure with pollen sacs in each side of the centrifugal rays. The structure has a diameter of 32 mm preserved. Most rays are fragmented of the apex, ray number one is the best preserved (Figure, 3A; 4A).

Dimensions of centrifugal rays are up to 22.5 mm in length (from the fusion of the basal cup), 3.1 mm wide (at the base). Centrifugal rays are filiform with a straight margin and without hairs or trichomes. Central cup diameter is of 8–13.2 mm (average 11 mm). The adaxial surface of

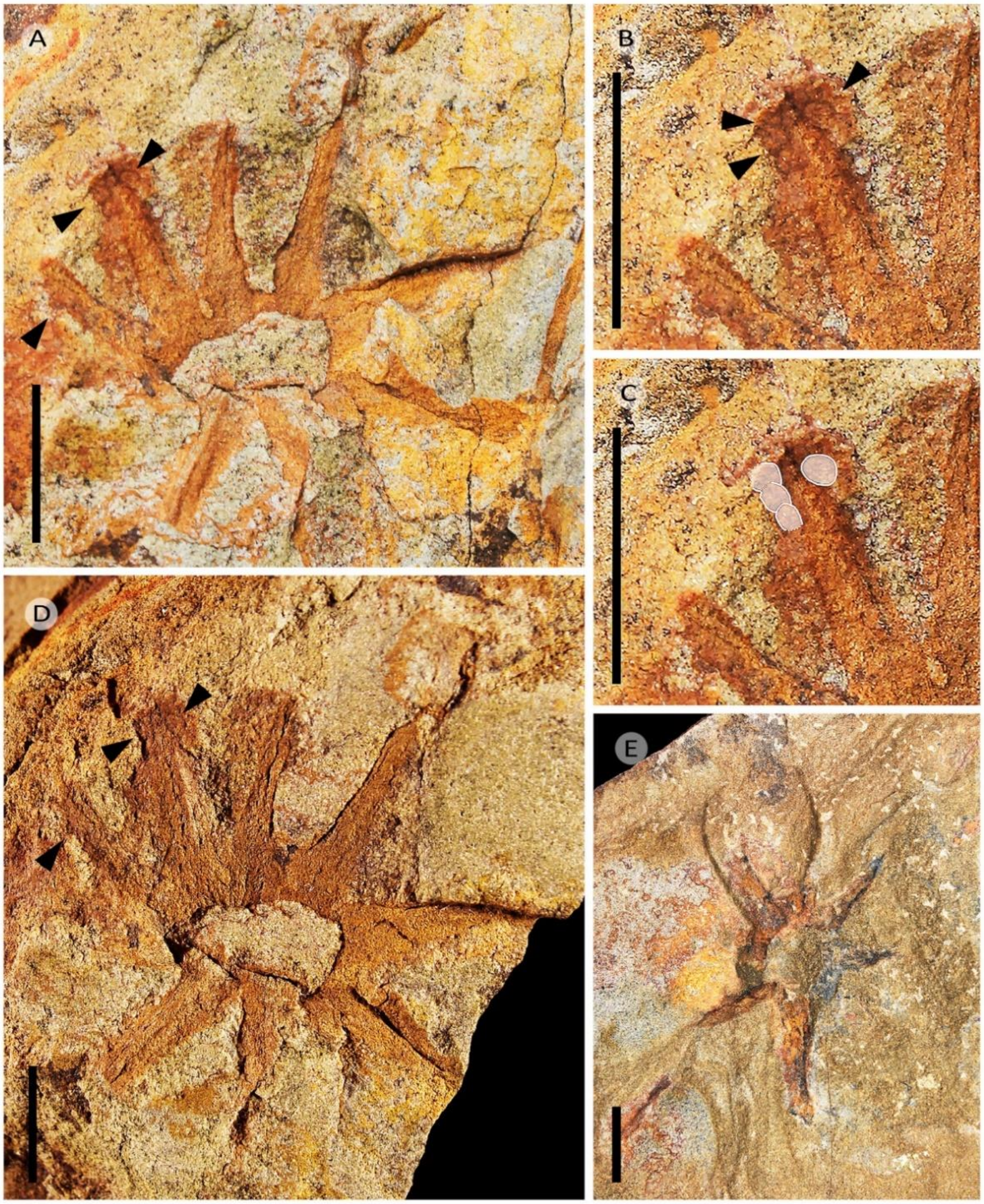

Fig. 3. Flora of Santa María Xochixtlapilco locality, Tecomazúchil Formation. A–D. *Weltrichia xochitetlii* sp. nov., Holotype UTMSMX-12, E. Paratype UTMSMX-4(1). Adaxial (A, photograph *in situ*; D, photograph in lab) and abaxial (E) views of the star-shaped cone. Black arrows indicate the presence of three rows of a single pollen sac on each side of the centrifugal rays. B and C. Close-up of a centrifugal ray with pollen sacs. C. Highlighted in white indicate the oval to semicircular shape of the pollen sacs. D. Photograph prepared in the laboratory where the ornamentation of the centrifugal rays, as well as the pollen sacks, can be observed. *Scale bars in all images*= 1 cm.

the cone is ornamented with longitudinal median ridge diverging from the center of the cup and continuing along the centrifugal rays up to the most distal part. Median ridge on the central part of each ray are notably more robust than adjacent fibrous strands (Fig. 3A). At least three rows of microsporangia can be observed. These are located on the median distal part of rays six, seven, and eight, and are more visible on ray seven (Fig. 3A–C; 4A). On each side of each centrifugal ray there is only one pollen sac of oval to elliptical shape and with a diameter of 1–1.2 mm (Fig. 3A–C). No centripetal rays or sterile scales are observed at the center of the cup (Table 2).

Comments and interpretation: Weltrichia is a fossil-genus distributed mainly in Laurasia with a stratigraphic range from Late Triassic to Late Jurassic (Saporta, 1891; Wieland, 1914; Krasser, 1922; Harris, 1969; Pal and Ghosh, 1985; Bose and Banerji, 1984; Kimura and Ohana 1989; Delevoryas, 1991; Popa, 2001, 2014, 2019; Sun et al., 2001; Li et al., 2004; Silva-Pineda et al., 2011). Records during the Triassic are scarce and generally incomplete, whereas records from the Jurassic are mostly of well-preserved material (Kimura and Ohana 1989; Popa, 2014, 2019). Most of *Weltrichia* species are notably larger in both, external outline diameter and basal cup diameter, and have a larger number of centrifugal rays compared to *Weltrichia xochitetlii* (Table 1). In addition, the morphology of pollen sacs differs with most species as shown in Table 1. In the region of the Mixteco Terrane, four fossil-species have been reported: *W. ayuquilana*, *W. microdigitata*, *W. mixtequensis* and

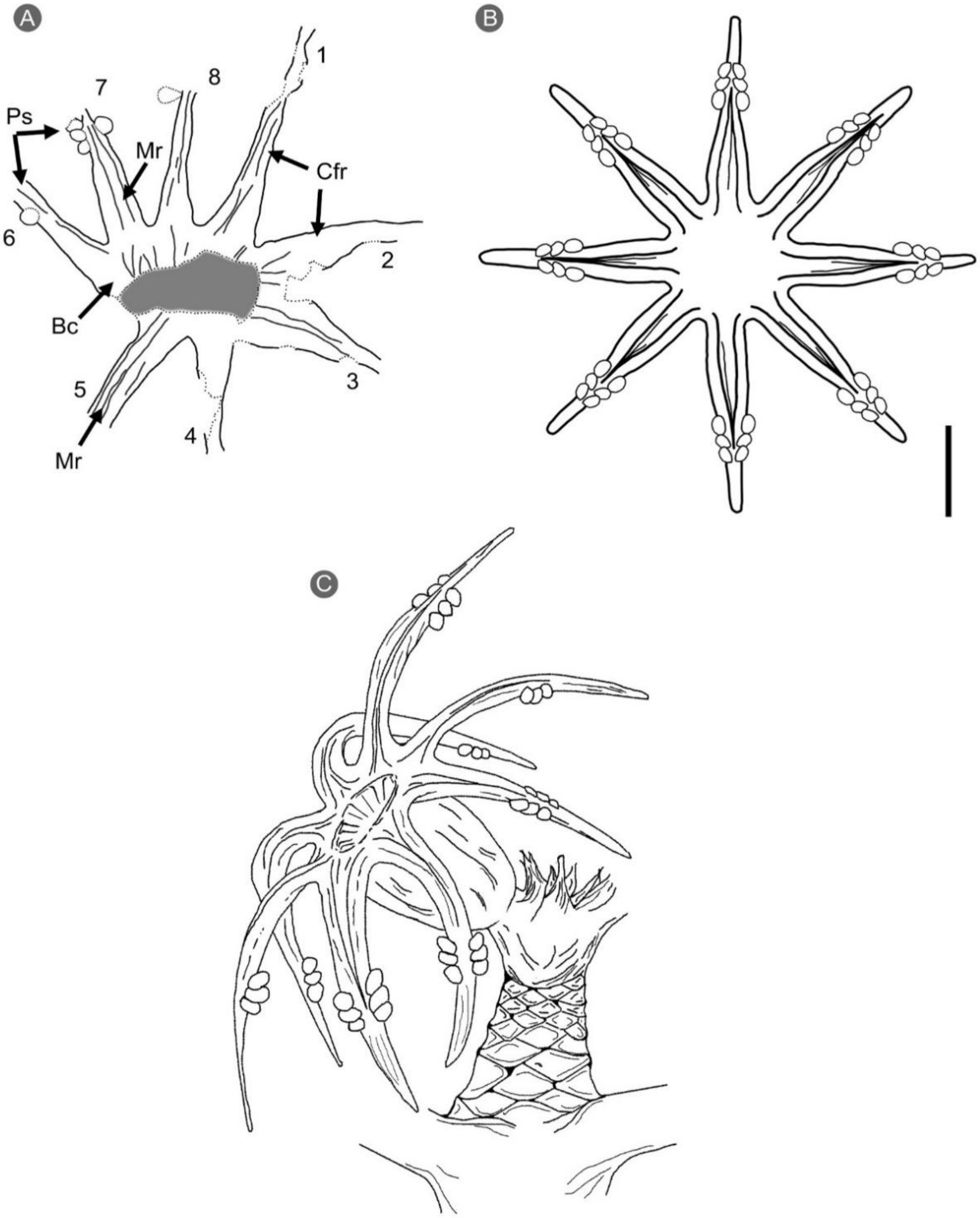

Fig. 4. Illustrations of *Weltrichia xochitetlii* sp. nov. A. Interpretative drawing based on the holotype, specimen UTMSMX-12. Abbreviations: **Ps,** pollen sacs, **Bc,** basal cup, **Cfr:** centrifugal rays, **Mr:** median ridge. B. Reconstruction of *W. xochitetlii* made by Diego E. Lozano-Carmona with the technical propose by Popa (2019). This reconstruction represents the dimensions and positions of the morphological characters in adaxial view. C. Hypothetical restoration of *W. xochitetlii* corresponds to a flower with extended centrifugal rays. The basal cup is reconstructed based on the general shape of the genus (see Anderson et al., 2007; Rothwell et al., 2009),. drawing by Diego E. Lozano-Carmona. Hypothetically, the flower would be attached to a short bud at the base of a forked branch, based on the interpretation of the growth habit of the Williamsoniaceae family (see Pott, 2014; Pott and McLoughlin, 2014). *Scale bar in A, B* = 1 cm.

W. mexicana? all from Jurassic distribution (Wieland, 1914; Delevoryas, 1991; Silva-Pineda et al., 2011). *W. xochitetlii* differs from species described from the Jurassic of Mexico in almost all characters, mainly the basal cup diameter, which is smaller, the number of centrifugal rays and pollen sacs, which is lower, and the shape and dimensions of the pollen sacs, which are oval–semicircular and smaller in *W. xochitetlii* (Table 2, Fig. 3A–C, 4). The only similar character between *W. xochitetlii* and *W. microdigitata* is the diameter total and the central cup diameter (Table 2) these characters do not exceed 50 mm. These characters of both species could be a result of the environmental conditions of the region, since both correspond to the same basin, albeit to a different lithostratigraphic unit.

The diversity of *Weltrichia* includes 25 species in its stratigraphic range (*sensu* Popa, 2019), most of them recorded in Europe (Table 3). In North America, the reports with identifications to species level correspond to those mentioned from the Jurassic of Mexico: *W. ayuquilana*, *W. microdigitata* and *W. mixtequensis* (Table 3). The specimens from the Santa Clara Formation, from the Triassic of Sonora, and the Morrison Formation, from the Upper Jurassic of the USA, have been identified only to genus level (Weber et al., 1980; Chure et al., 2006; Behrensmeyer

Table 2
Comparison of morphological characters of *Weltrichia* fossil-species of the Mixteco Terrane, southern Mexico.

	Mc	*Weltrichia xochitetlii* sp. nov.	*W. mixtequensis*	*W. ayuquilana*	*W. microdigitata*	*W. mexicana?*
1	D	32 p. (45.2 d)	75–80	60	30	? (35 d)
2	Bcd	9.5–14 (a.11)	20	30	15	20
3	Cfr	8	14	10	14	?
4	Crl	14.1–22.5 p.	76	15	7–8	12–15
5	Crw	3.1	7–9	?	?	?
6	Cro	Longitudinal ridge	Striae and hairs	?	?	?
7	Cpr	?	?	no	no	?
8	Ps	6	7–9	Various	20–30	?(10 d)
9	Psl	1.2	1.65–5.54	6	?	1.5 –2
10	Psw	1	0.39–1.37	<2	?	2–2.5
11	Psr	2	7–9	?	10–15	5–6
12	Rps	3–4	1	2	2	2
13	Pss	Oval–elliptical	Elongated–drop-shaped	Elongated	Elongated–tubular	Oval
	Fm	Tecomazúchil	Ayuquila	Ayuquila	Ayuquila	Rosario?

Abbreviations. 1 **D:** External outline diameter, **p**: preserved, **d**: character deduced. 2 **Bcd:** Basal cup diameter, **a**: average. 3 **Cfr:** centrifugal rays. 4 **Crl:** Centrifugal ray length. 5 **Crw:** Centrifugal ray width. 6 **Cro:** Centrifugal ray ornamentation. 7 **Cpr:** Centripetal rays. 8 **Ps:** Pollen sacs. 9 **Psl:** Pollen sacs length. 10 **Psw:** Pollen sacs width. 11 **Psr:** Pollen sacs per row. 12 **Rps:** Rows of pollen sacs. 13 **Pss:** Pollen sac shape. **Mc:** Morphological character. **Fm:** formation. All metric data is in millimeters. Grey rows indicate the main taxonomic characters for the differentiation of *Weltrichia* fossil-species according to Harris (1969) and Popa (2014, 2019).

Table 3
List of fossil-species compared with *Weltichia xochitetlii* sp. nov., ordinated by age, locality and formation.

Taxon	Age	Locality	Formation	Reference
Weltrichia huangbanjingouensis Sun et al.	Late Jurassic–Early Cretaceous	Liaoning Province, China	Yixian Fm.	Sun et al., (2001); Popa (2019)
Weltrichia maldaensis Pal et Ghosh	Late Jurassic	Malda región, India	Unknown	Pal and Ghosh (1985); Popa (2019)
Weltrichia oolithica Saporta	Late Jurassic	Venetian Alps	Unknown	Popa, (2019)
Weltrichia santalensis (Sitholey et Bose) Harris	Middle to Late Jurassic	Rajmahal Hills, India	Unknown	Harris (1969); Popa (2019)
Weltrichia daohugouensis Li et al.	Middle Jurassic	Daohugou village, China	Haifanggou Fm.	Li et al. (2004)
Weltrichia pecten (Leckenby) Harris	Middle Jurassic	Yorkshire, United Kingdom	Lower–Middle Deltaic Series	Harris, (1969)
Weltrichia setosa (Nathorst) Harris	Middle Jurassic	Yorkshire, United Kingdom	Middle Deltaic Series	Harris, (1969)
Weltrichia sol Harris	Middle Jurassic	Yorkshire, United Kingdom	Middle Deltaic Series	Harris, (1969)
Weltrichia spectabillis (Nathorst) Harris	Middle Jurassic	Yorkshire, United Kingdom	Lower Deltaic Series	Harris, (1969)
Weltrichia whitbiensis (Nathorst) Harris	Middle Jurassic	Yorkshire, United Kingdom	Lower Deltaic Series	Harris, (1969)
***Weltrichia xochitetlii* sp. nov.**	**Calloviano**	**Oaxaca, Mexico**	**Tecomazúchil Fm.**	**This study**
Weltrichia ayuquilana Delevoryas	Bajocian–Bathonian	Oaxaca, Mexico	Ayuquila Fm.	Delevoryas, (1991)
Weltrichia microdigitata Delevoryas	Bajocian–Bathonian	Oaxaca, Mexico	Ayuquila Fm.	Delevoryas, (1991)
Weltrichia mixtequensis Silva Pineda et al.	Bajocian–Bathonian	Oaxaca, Mexico	Ayuquila Fm.	Silva-Pineda et al. (2011).
Weltrichia harrisiana Bose et Banerji	Early to Middle Jurassic	Kachchh region, India	Unknown	Bose and Banerji (1984); Popa (2019)
Weltrichia mirabilis Braun	Early Jurassic	Veitlahm, Germany	Unknown	Popa, (2019)
Weltrichia fabrei Saporta	Early Jurassic?	Lozere área, Mende, France	Unknown	Saporta (1891); Popa (2019)
Weltrichia primaeva Schweitzer et Kirchner	Pliensbachian–Toarcian	Alborz Mountains, Iran	Shemshak Group	Popa, (2019)
Weltrichia hirsuta Schweitzer	Sinemurian–Toarcian	Alborz Mountains, Iran	Shemshak Group	Popa, (2019)
Weltrichia alfredii (Krasser) Popa	Sinemurian	South Carpathians, Romania	Steierdorf Fm.	Krasser (1922); Popa (2014), 2019
Weltrichia antonii Popa	Sinemurian	South Carpathians, Romania	Steierdorf Fm.	Popa, (2014)
Weltrichia givulescui Popa	Sinemurian	Anina, Romania	Steierdorf Fm.	Popa, (2001)
Weltrichia johannae Popa	Sinemurian	South Carpathians, Romania	Steierdorf Fm.	Popa, (2014)
Weltrichia steierdorfensis Popa	Sinemurian	Anina, Romania	Steierdorf Fm.	Popa, (2014)
Weltrichia alpina Krasser	Late Triassic	Southern Tirol, Germany	Cassian Beds	Popa, (2019)
Weltrichia sp. (sp. nov.?)	Late Jurassic	Outer Zone, NE Japan	Oginohama Formation	Kimura and Ohana (1989)

and Turner, 2019) or have even been reassigned to another fossil-taxon, as is the case of the specimens from the Santa Clara Formation (Weber et al., 1980). Therefore, thus far, the best diversity of *Weltrichia* in North America is that of Mixteco Terrane in southern Mexico. When comparing this to records of species from the Jurassic of the closest localities in Eurasia (Tables 1 and 3), we obtain results showing that the specimens UTMSMX 4(1) and 12, studied here, clearly correspond to a different species.

Comparisons with species from the Jurassic locality of Yorkshire, England show that the species with highest similarity with *Weltrichia xochitetlii* is *W. pecten* (Leckenby) Harris (Harris, 1969; Popa, 2019). *W. pecten* are similar in the shape and arrangement of pollen sacs, which are semicircular and are arranged in two parallel rows along the centrifugal rays up to the middle part. However, they differ in diameter, central cup diameter, number of centrifugal rays, and the size of the pollen sacs, these characters being smaller in *W. xochitetlii* (Table 1). When comparing with the whole of Sinemurian species from Romania (Tables 1 and 3), only similarities are observed with *W. antonii*. These similarities are the number and length of the centrifugal rays. But, the difference in size is notable since *W. xochitetlii* is up to 70 mm smaller in diameter (Table 1). In summary, the main difference between *W. xochitetlii* and the 25 valid species is clearly the size of the organ (external outline diameter and central cup diameter), the number of centrifugal rays, and the size and shape of the pollen sacs (Tables 1 and 2).

The distribution of male reproductive organs in the Jurassic of Mexico is almost restricted to the Ayuquila Basin, except for *Weltrichia mexicana*? which is considered to have been found in the lower part of the Rosario Formation (Person and Delevoryas, 1982; Silva-Pineda, 1984; Delevoryas, 1991; Silva-Pineda et al., 2011). Previous reports of the Ayuquila Basin correspond to the Ayuquila Formation (Campos--Madrigal et al., 2013). Thus, this is the first record of the Tecomazúchil

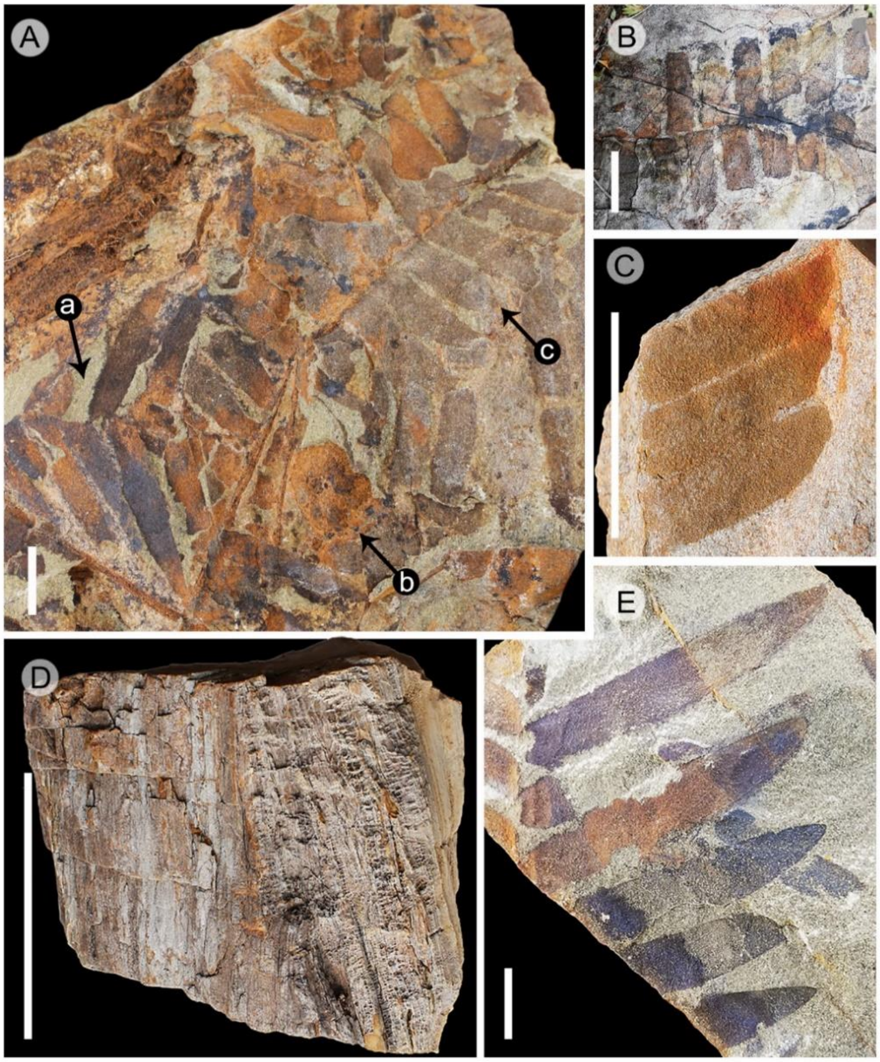

Fig. 5. Plant fossils recorded in Santa María Xochixtlapilco locality. A. Leaves of *Zamites tribulosus* (a) UTMSMX 5(1), female cone *Williamsonia oaxacensis* (b) UTMSMX 5(2) and *Pterophyllum* sp. (c) UTMSMX 5(3). B. cf. *Zamites* sample i*n situ.* C. *Z. lucerensis* fragment (three leaflets) UTMSMX 15. D. Permineralized trunk fragment UTMSMX 16. E. *Zamites feneonis* UTMSMX 14. *Scale bars: A, C, E= 1 cm; B=2 cm; D= 10 cm.*

Formation within the basin. This would broaden the stratigraphic range of *Weltrichia* in the region, from the Bajocian to the Callovian, but not its geographic range.

4.2. Palaeobotanic content of the locality of Santa María Xochixtlapilco

Given that the previously reported fossiliferous localities for the Tecomazúchil Formation are now considered within the Ayuquila Formation (Delevoryas, 1991; Silva-Pineda et al., 2011; Campos-Madrigal et al., 2013), the locality presented in this study and its paleoflora correspond to the first confirmed for the Tecomazúchil Formation. During survey visits and stratigraphic measurements, we collected 13 hand specimens with 17 plant fossils, from which we made the following determinations, Bennettitales: *Zamites lucerensis* (Wieland) Person et Delevoryas 1982, *Z. tribulosus* (Wieland) Person et Delevoryas 1982, *Z. feneonis* Brongniart 1828, *Z.* sp., *Pterophyllum* Brongniart, *Williamsonia oaxacenis* Delevoryas et Gould 1973, and *Weltrichia xochitetlii sp. nov.*, Coniferales: *Pelourdea* Seward, and Ginkgoales: *Allicospermum* Harris. This paleofloristic richness is mostly composed of Bennettitales, and a few Coniferales and Ginkgoales, and there are also records of permineralized woods that have not been studied thus far (Fig. 5). When comparing this to records from other localities in the region, we presently qualitatively recognize a higher abundance of leaves of *Zamites tribulosus* and *Z. feneonis*, and a lower abundance of *Z. lucerensis*, the latter being notably more abundant in other localities of the Mixteco Terrane (Silva-Pineda, 1984; Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Velasco-de León, 2019). The leaf area of *Zamites tribulosus* and *Z. feneonis* is larger than that of *Z. lucerensis.* This variation in leaf area and abundance of the mentioned fossil-taxa is probably due to conditions of higher humidity during the deposition of the Tecomazúchil Formation (Campos-Madrigal et al., 2013) and a continental location far from marine influxes of the Bajocian/Callovian with respect to the other Jurassic localities of the same region (Morán-Zenteno et al., 1993).

In this new locality the association between foliar and reproductive organs of the Bennettitales is still not very relatable. Although there is considerable accumulation of leaves at several sites, at none of these sites is there evidence of a connection between the reproductive and foliar organs (Figs. 3D, 5 and 6E). The closest that can be estimated is the proximity between *Williamsonia oaxacensis* and the leaves of *Zamites tribulosus* and *Pterophyllum* sp., (Fig. 3D). These taxa were found close together in the same hand sample (UTMSMX5(1–3). However, the

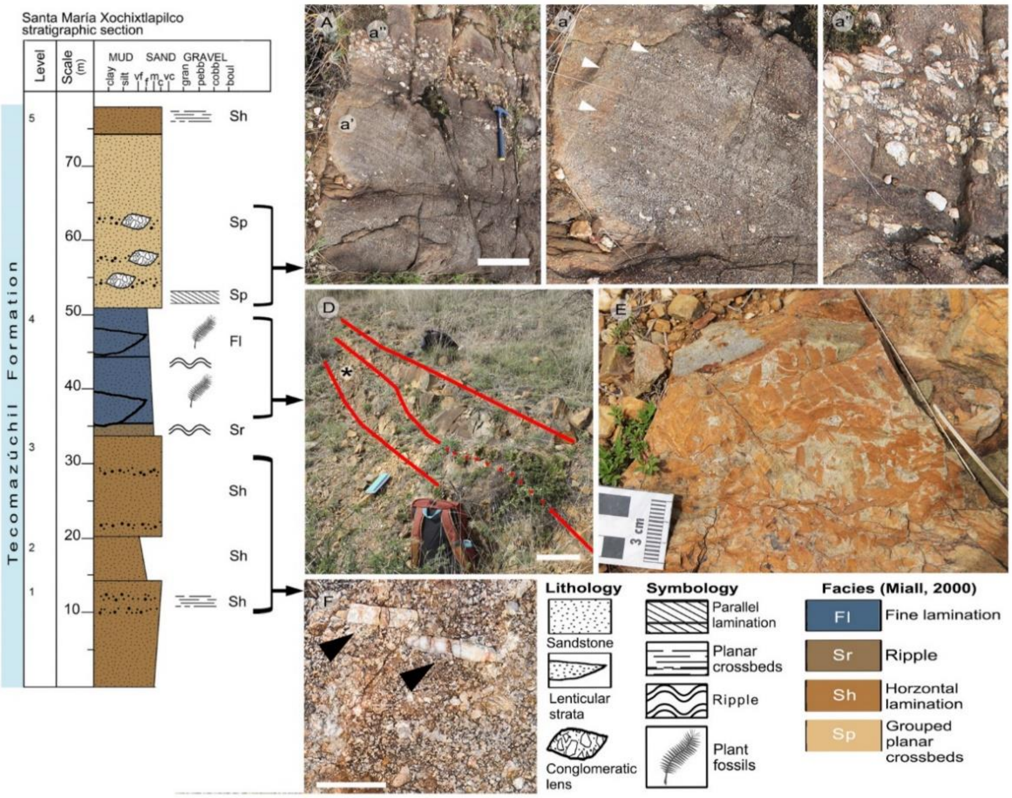

Fig. 6. Stratigraphic section of María Xochixtlapilco locality, Tecomazúchil Formation, Oaxaca state. Lithology and symbology of the stratigraphic section see in. A. Planar cross-lamination associated to a conglomeratic lens. a'. Close-up to planar cross-lamination in A. a''. Close-up to conglomeratic lens in A. D. Overview of fossiliferous strata, red lines indicate irregular stratigraphic surfaces and (*) indicate plant fossils in situ. E. *In situ* plant fossils of the fossiliferous strata (*). F and G. Discontinuous parallel laminations with presence of tabular and irregular gravel (black arrows indicate the tabular gravels). *Scale bars: A*= 35 cm*; D*= 30 cm*; F*= 2 cm.

specimen of *W. oaxacensis* shows signs of fragmentation, possibly due to transport in the river system. Unlike, the leaves are hinged and disordered position, indicating a lower transport. In the case of *Weltrichia xochitetlii* the specimens were found isolated and far from the leaf samples, this makes it difficult to estimate any relationship between these taxa.

4.3. Stratigraphic and sedimentary description of the locality of Santa María Xochixtlapilco, first fossiliferous locality of the Tecomazúchil Formation

The fossiliferous locality of Santa María Xochixtlapilco is located within the Ayuquila Basin. In order to provide a geographic and stratigraphic framework of this locality, we measured and described the stratigraphic section.

The stratigraphic section was measured to the northeast of La Mina fault at the southwestern of Huajuapan de León, Oaxaca (Fig. 2). We measured approximately 30 m above and below the fossiliferous zone, with a total of 78 m in thickness. This section is characterized by thin lutite beds, thin and medium beds of fine to medium sandstone with parallel laminations and ripples (fossiliferous zone), which are encased by intercalations of thick beds of coarse to very coarse sandstone that present laminations of pebbles, conglomeratic lenses, and planar cross-stratification (Fig. 6). The fossiliferous zone is located on level 4 and corresponds to a series of thin to medium beds of fine to medium sandstone (Figure D, E). The horizontal extension of this zone covers approximately 250 m and the beds structure changes from tabular, in the thickest region, to wedge-shaped, on both sides of the zone, which gradually disappear between the lower and upper levels 3 and 5, respectively. The beds of coarse-to very coarse-sand that comprise levels 1–3 and 5 are semitabular-to irregular-shaped and are mostly supported by clasts and, in some cases, with a sandy matrix. Clasts of larger size are gravel (pebbles to cobbles), tabular, discoidal, and some are equidimensional, with low sphericity, and from semicircular to subangular. These clasts mainly constitute the conglomeratic lenses and some parallel laminations (Fig. 6).

According to Miall (2000; 2006), the identified lithofacies are Sh, Sp, and Fl (Table 4 and Fig. 6). These are recognized and interpreted within the associations of facies SB and FF for the Tecomazúchil Formation. Each facies association was described by Campos-Madrigal et al. (2013) based on Miall (2006). Facies associations result from grouping facies related by their origin; thus, associations of facies SB and FF of the Tecomazúchil Formation are described as follows: (SB), this association is composed of sandy facies, in this case Sp, Sr, and Sh. According to Campos-Madrigal et al. (2013), "the combination of sandy lithofacies and their primary structures allows to interpret them as channel and bar fills, product of moderate to critical flow, the thickness and arrangement of layers indicate frequent changes in the flow regime, which can represent seasonal fluctuations or sudden flooding" (Campos-Madrigal et al., 2013, pp. 31). (FF), fine sediment facies are grouped in this association, which in this case correspond to Fl. According to Campos-Madrigal et al. (2013), this association allows to propose that "the vertical sedimentation is discontinuous and represents flooding events of diverse temporal extension, varying from plains to small reservoirs, depending on its thickness, extension, and fossil content" (Campos-Madrigal et al., 2013, pp. 31).

Based on the association facies SB and FF identified, we can conclude that the fossiliferous beds corresponded to a small reservoir. The

Table 4
Summary of facies present in the Santa María Xochixtlapilco locality, based on Miall (2000; 2006).

Facies code	Description	Primary structures	Interpretation
Sp	Coarse to very coarse sand with gravel and cobbles, subtabular to irregular beds, with parallel conglomeratic lenses, circular to subangular quartz clasts.	Solitary planar cross-stratification. Gravel conglomerate lenses. Isolated parallel lamination.	Transversal bedforms deposited by moderate to critical flow regime.
Sr	Medium sand, medium undulate non- parallel beds.	Fine ripples, coarsening downwards.	Deposited by lower flow regime.
Sh	Mainly coarse sand, occasionally medium sand, subtabular to irregular beds with medium to very large widths (30–220 cm). High content of siliceous clasts, the largest (gravel) are tabular, discoidal, and some are equidimensional and from semicircular to subangular. Moderately classified.	Horizontal parallel lamination.	Deposited by upper or critical flow regime.
Fl	Fine to medium sandstone in fine to medium beds (7–30 cm), intercalated with lutite lenses with fine widths of less than 10 cm. Association of discontinuous layers wedged towards the edges. High content of plant fossils in some sections.	Fine horizontal discontinuous lamination, very small asymmetric ripples. Coarsening downwards.	Waning flood deposits.

characteristics that allow to propose this type of sedimentary body are a moderate thickness of 17 m, composed of thin beds of fine-medium sand and lutite, with fine parallel lamination and small asymmetric ripples. These beds are discontinuous and are wedged in a length of *ca.* 250 m and are associated with overflow sedimentation from sandy bars (upper, lower, and lateral beds). This small reservoir allowed the accumulation of leaf and reproductive organs of Bennettitales (Fig. 3D), among other groups, mainly at the top of each bed. Given the low amount of energy during the deposit of this reservoir, a great number of leaves were able to be preserved (Figs. 3D and 6C). Furthermore, based on the aforementioned facies, in addition to the clear presence of coarse sandstone beds supported by clasts with conglomeratic lenses (Table 3 and Fig. 6) and the low presence of a sandy matrix, we are able to recognize the correspondence to the Tecomazúchil Formation. It also differs from the Ayuquila Formation because the latter consists of "abundant sandstone and schist lithics" … among others, and a fine-grained matrix (Campos-Madrigal et al., 2013, pp. 28), which are characteristics not observed in the study locality.

4.4. Final comments

The Weltrichia species described from the Jurassic in southern Mexico show a variety of forms. These variations can be visualized mainly in the morphology and the number of the centrifugal rays. Each of the five species has a different morphology and number of centrifugal rays (Table 2). However, they are slightly similar in the basal cup diameter. Where *W. xochitetlii* and *W. microdigitata* have a smaller basal diameter (11–15 mm), while in *W. mixtequensis*, *W. ayuquilana* and *W. mexicana* it is greater (20–30 mm). The shape and position of the pollen sacs also show similarities. In this character two groups can be formed: elongated pollen sacs (*W. mixtequensis*, *W. ayuquilana*, *W. microdigitata*) and oval pollen sacs (*W. xochitetlii*, *W. mexicana*). This allows observing a morphological diversity in the reproductive organs of Bennettitales in this region of Pangea. However, the low number of specimens for each species limits the observation of intraspecific variability.Based on the data set (Table 1), it is observed that *W. xochitetlii* and *W. microdigitata* have the smallest size recorded for Weltrichia species worldwide. Although this would allow the generation of hypotheses about the ecological and evolutionary conditions that could influence the reduction in size of these organs, it is still necessary to register a greater number of specimens to be able to base such analyzes. However, due to the robust and fibrous characteristics of the centrifugal rays that are present in Weltrichia (Harris, 1969; Delevoryas, 1991; Silva-Pineda et al., 2011; Popa, 2019) it can be considered that the organs (*W. xochitetlii* and *W. microdigitata*) were in a mature stage when they were deposited. This statement is supported by considering the pollination strategy. Possible pollination strategies in Weltrichia are by wind and / or interactions with insects (Popa, 2019). Morphological characteristics such as the projection of the pollen sacs and the opening of the centrifugal rays allow us to interpret that the specimens of *W. xochitetlii* and *W. microdigitata* must have been in a mature stage to be able to disperse the pollen by air streams and / or interaction with insects. Therefore, *W. xochitetlii* and *W. microdigitata* are the smallest Jurassic species described worldwide.On the other hand, the woody characteristics of Weltrichia and especially of *W. xochitetlii* were those that allowed the transport, deposit and fossilization in the small reservoir that gave rise to the fossiliferous locality (see section 4.3 of this study). However, the less coriaceous texture of the Bennettitales leaves did not allow a good fossilization process. This small reservoir is associated with overflow sedimentation of the sandy bars of the main channel in the Ayuquila Basin. Therefore, the dynamics in the deposit environment influenced the preservation of leaves and reproductive organs of Bennettitales. Thus, the identification of this locality and its interpretation of the sedimentation conditions and fossil content will allow the identification of other possible sites within the Ayuquila Basin. In this way, strategies can be designed for future prospecting in the Tecomazúchil Formation.

5. Conclusions

Two specimens corresponding to reproductive organs were found in a first fossiliferous locality of the Tecomazúchil Formation. The examination and analysis of these specimens provided substantial evidence to propose the existence of a new species: *Weltrichia xochitetlii*. The characters that support this are the diameter of the organ (32–45.2 mm), the basal cup diameter (average 11 mm), eight centrifugal rays, and the shape, position, and size of the pollen sacs on centrifugal rays. Moreover, this new record of reproductive organs broadens the stratigraphic range of *Weltrichia* form the Bajocian/Bathonian to the Callovian in southern Mexico. We can assert that the highest diversity described for this genus in North America is found in southern Mexico. In addition, records of Bennettitales are still contributing with new species, which demonstrates that the Jurassic flora of this region represents an element of high value for Mexican palaeontology. In this sense, the Jurassic species *Weltrichia xochitetlii* and *W. microdigitata* comprise the group of smallest reproductive organs recorded for this genus worldwide. This will allow to generate new lines of research as well as hypotheses related to the paleoecological and paleogeographic conditions that could have influenced the occurrence of a possible reduction in size in the reproductive organs of Bennettitales in this region of Pangea.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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SEGUNDO CAPÍTULO

Flora jurásica en el sur de México: *Anomozamites* Schimper, 1870 Emend. Pott et McLoughlin, 2009, del Terreno Mixteco, implicaciones fitogeográficas de la familia Williamsoniaceae (Bennettitales).

- **Lozano-Carmona, D. E.** Propuesta y diseño del trabajo; revisión de los ejemplares e identificación taxonómica; recopilación y consulta bibliográfica; análisis e interpretación de datos; toma de fotografías y elaboración de figuras; actividades de campo: recolecta de material y selección de niveles (estratos) de muestreo; redacción del manuscrito.
- **Velasco-de León, M. P.** Dirección, revisión del trabajo y manuscrito; actividades de campo: selección de localidad y niveles (estratos) de muestreo, recolecta de material.
- **Flores-Barragan, M. A.** Actividades de campo: recolecta de material y selección de niveles (estratos) de muestreo, descripción de localidad; curaduría y registro de material en la Colección de Paleontología de la FESZ; apoyo en toma de fotografías; revisión del manuscrito.

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Jurassic Flora in Southern Mexico: *Anomozamites* Schimper, 1870 Emend. Pott et McLoughlin, 2009 from Mixteco Terrane, Phytogeographical Implications of Williamsoniaceae Family (Bennettitales)

Diego Enrique Lozano-Carmona[1,2], **María Patricia Velasco-de León**[2], **Miguel Angel Flores-Barragan**[2]

[1]Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Mexico City, Mexico
[2]Colección de Paleontología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Mexico City, Mexico
Email: coralillo8@gmail.com, pativel@unam.mx, 08.mike.angel@gmail.com

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Abstract

Anomozamites is a fossil-genus of leaf attributed to the Bennettitales, with a distribution mainly in the Kingdom of Laurasia and a stratigraphic range of the Upper Triassic to the Lower Cretaceous. In Mexico there were only reports of some specimens until the 1980s and later of four fossil-species at the beginning of the 21st century, all of them from the Jurassic in the Mixteco Terrane. In this review, three fossil-species of *Anomozamites* are identified: *A. angustifolium* is the first of them, which is a fossil-taxon with a range of the Rhaetian to Bajocian and Euramerican distribution; the second one is *A.* cf. *triangularis*, of which the geographic and stratigraphic extension of fossil-taxon is proposed; finally, we propose the existence of the *A.* sp.1, informally named, but with morphological characters that do not match the descriptions of Triassic/Jurassic fossil-taxa. These identifications were made based on macromorphology of the foliar organs and on the review of the diagnostic characters of both the fossil-genus and the fossil-species of taxonomic validity. Then, with this study, the taxonomic and phytogeographic knowledge of *Anomozamites* during the Jurassic period is increased and this allows reconsidering the amplitude of the *Wielandiella* distribution, a fossil-genus related to *Anomozamites* due to the existence of two fossil-taxa in organic connection.

Keywords

Phytogeography, Bennettitales, *Wielandiella*, North America, Oaxaca

1. Introduction

The Jurassic flora, in the Paleofloristic kingdom of Laurasia, were dominated by gymnosperms and among them, the Bennettitales stood out for their abundance and their wide distribution. The Bennettitales resided primarily in the kingdom of Laurasia, but there were records of their distribution in the kingdoms of Gondwana to the south and Angara to the northeast. They were the main elements in the vegetation of Laurasia along with Ginkgoales, Pinales, Cheirolepidiales and ferns [1] [2] [3] [4] [5]. In several Jurassic localities of the Mixteco Terrane in southern Mexico, the abundance of *Zamites* Brongniart and *Otozamites* Braun (Bennettitales) is outstanding. When citing an example, in the Río Ñumí locality of the undifferentiated Zorrillo-Taberna formation (Zorrillo-Taberna), the abundance of these fossil-genera reaches 43.5% of the registered paleoflora, which consists of 415 specimens [6] [7] [8] [9]. Therefore, some studies have proposed that the Bennettitales are distributed among the autochthonous, allochthonous and parautochthonous communities in lowland and floodplains environments of the Mixteco Terrane, a distribution that has been based on the taphonomic analysis [10] [11]. Based on these studies, we know that leaves of *Anomozamites* Schimper emend. Pott et McLoughlin are exclusive bennettitals of the parautochthonous community in the Zorrillo-Taberna formation [10]. However, *Anomozamites* has not been studied in Mixteco Terrane [6] [12].

The reports of *Anomozamites* in the Mixteco Terrane have been rare. Only references [12] [13] reported a specimen collected during their work in the Mixteca Alta, respectively. This situation causes a deficit in the knowledge of the richness and distribution of *Anomozamites* within the Mixteco Terrane and the adjacent regions. In addition, having specifically the presence of *Anomozamites* in the Mixteco Terrane would imply changes in their distribution within the Kingdom of Laurasia during the Jurassic and the Mesozoic.

To achieve an advance in the knowledge of the richness and distribution of *Anomozamites* within the Mixteco Terrane, we have worked with the paleobotanical set protected in the Paleontological Collection of the Faculty of Higher Studies Zaragoza (FESZ) of the National Autonomous University of Mexico (UNAM). This collection contains more than 3 thousand specimens of macrofossils from the Mixteco Terrane and is widely representative due to its diversity and abundance [7] [8] [9] [11] [14] [15] [16]. Then, to identify the material, we carried out the search and compilation of the morphological diagnostic characters of *Anomozamites* and the valid fossil-species of the Mesozoic [17] [18] [19] [20]. Therefore, we followed the diagnostic characters for the identification of *Anomozamites*, and his characters were applied to 400 hand specimens with plant fossils of the Cañada Alejandro locality, Zorrillo-Taberna formation in Mixteco Terrane, to separate the corresponding specimens. In this way, we obtained results demonstrating the presence of several fossil-species of *Anomozamites* in Mexico.

In this work, we identify three fossil-species of *Anomozamites* based only on the macromorphological characters because even though the material is fragmented and is not abundant (parautochthonous), the morphological characters are visible, and they allow supporting the identifications. Therefore, the present review has constituted a significant advance in the knowledge of the diversity of *Anomozamites* and the Williamsoniaceae family in the Mixteco Terrane, and this allows us to incorporate information on the distribution of these fossil-taxa in the kingdom of Laurasia. Information may be used in subsequent phytogeographic analyzes of the Jurassic.

2. Material and Methods

To carry out the identification and classification of the plant fossils of Cañada Alejandro deposited in the Paleontological Collection of the FESZ-UNAM, firstly, a bibliographic review of the taxonomic status of *Anomozamites* and its fossil-species valid worldwide was carried out. Subsequently, the different diagnostic characters mentioned in the historical and recent documents were collected [6] [13] [17]-[27]. These characters were compared with 400 hand specimens with plant fossils, and the specimens compatible with the description of *Anomozamites* were selected. In the second step, to carry out a detailed review of these specimens and to determine the number of fossil-species a Nikon SMZ-10A stereoscope was used. The use of this instrument allowed to observe in detail the morphological characters of the specimens in question. Each specimen was reviewed and classified based on the diagnostic characters (qualitative and quantitative) that are mentioned in the literature (**Figure 1**). These characters are the following: the general morphology of the leaf and leaflets, see [19]; the length and width of leaflets, length/width ratio (typically as long as wide, but up to twice as long as wide); the type of base and type of apex of the leaflets; the number of veins and presence-location of dichotomies; the attachment angles and position of the leaflets on both sides of the rachis; the width and characteristics of the rachis; the length and width of the segmented (pinnate) leaf. To measure the macroscopic quantitative characters, a Vernier and 360˚ transporter was used. To measure millimeter details, the ImageJ 1.48v program was used, which allows obtaining precise measurements. Each specimen worked was photographed with the use of a Sony Cybershot DSC-H10 camera (Carl Zeiss Lens: 3.5 - 4.4/6.3 - 63) applying the techniques proposed in [28].

Also, an analysis of the distribution within the Mixteco Terrane was made and compared with the *Anomozamites* world records based on the Fossilworks.org registry [29] and the published records to interpret the taxonomic and phytogeographic implications with the records of *Anomozamites* in the Mixteco Terrane

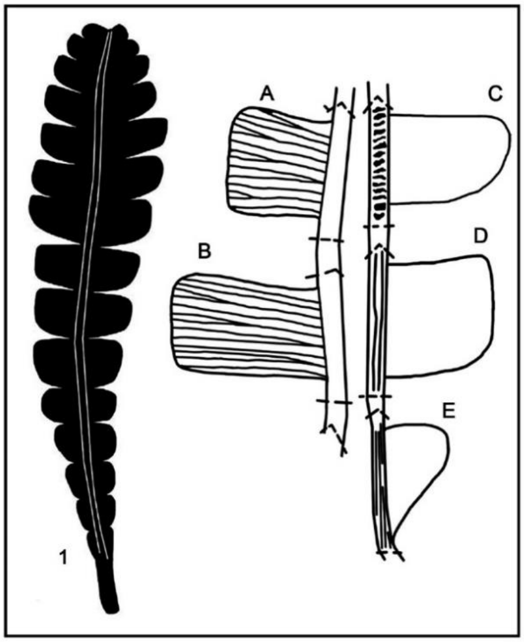

Figure 1. Diagnostic morphological characters of *Anomozamites*. (1). Leaf petiolate, lanceolate and elongated, lamina divided into leaflets, apically paripinnate. Leaflets typically as long as wide, maximum twice as long as wide (B) and laterally inserted into the rachis (A)-(E). The venation is dichotomous, and parallels arranged perpendicular to the rachis. Dichotomies from the basal portion to the apex (A) (B). Leaflets trapezoidal, semi-square to triangular in form. Rachis striated transverse- and longitudinally by several stretch marks. Apex from round to truncated (C)-(E). Prepared based on Reference [19].

and its relationship with *Wielandiella* Nathorst emend. Pott (Bennettitales: Williamsoniaceae) [24] [26].

3. Geological Framework

The study locality from which the revised material comes is called Cañada Alejandro and is located in the municipality of Tlaxiaco, Oaxaca, southern Mexico (**Figure 2**). This locality has been referred to as the Zorrillo-Taberna formation [15]. The general lithological composition of Zorrillo-Taberna consists of interlayers strata of coal, shale, and sandstone [30] [31]. Specifically, in the locality of study, it has been reported that it is composed of "sandy and shale, in irregular and continuous strata of a thickness of 20 cm, which thin up to 10 cm, with a high percentage of clay matrix, with fine clasts to very fine and sub-angular quartz" ([15], p. 60). Characteristics allowed the fossilization of an abundant association of the leaves, mainly Bennettitales [15]. The accumulation of Zorrillo-Taberna was under constant subsidence of the paleobasin of Tlaxiaco. This process is associated with the fragmentation of Pangea during the Middle Jurassic [30] [31]. The inference of the age of the deposit has been proposed based on its stratigraphic position, which underlies the Taberna formation. The deposit of the Taberna formation was made during the Bajocian inferred age based on the content of the Ammonites [32].

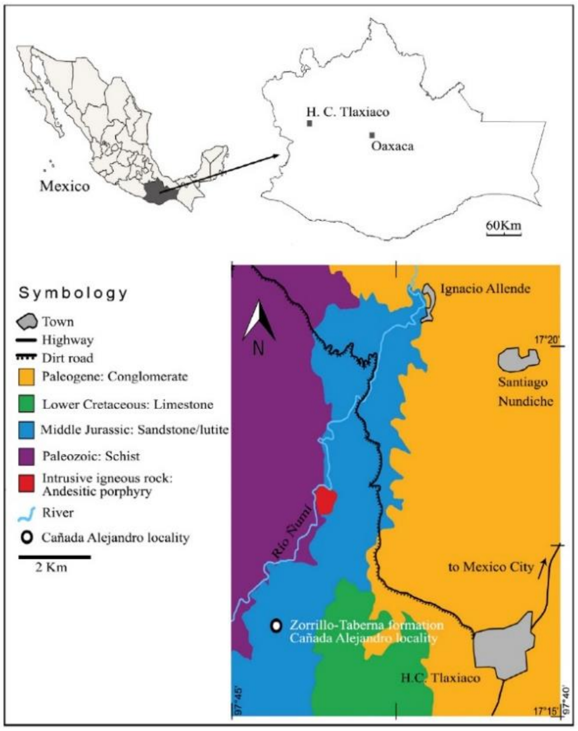

Figure 2. Simplified geologic map showing the location of the Cañada Alejandro locality to the west of the H. Tlaxiaco City in the northwest Oaxaca. The map is based on the Tlaxiaco Geological Chart-Mine E14-D34 Oaxaca [33] and the references [15] [30].

4. Results and Discussion

We reviewed 400 hand specimens from Cañada Alejandro (Ca), which corresponds to the Zorrillo-Taberna formation [15]. Of these specimens, 20 correspond to *Anomozamites* based on the morphological characteristics of the leaf and its leaflets [19].

4.1. Paleobotanical Systematics

Order **Bennettitales** Engler, 1892

Family **Williamsoniaceae** (Carruthers, 1870) Nathorst, 1913

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

Species Type: *Anomozamites nilssonii* (Phillips, 1829) Harris, 1969, from the Jurassic of Yorkshire, UK.

Anomozamites angustifolium Pott et McLoughlin, 2009

Figure 3(a), Figure 3(d) and Figure 3(e)

Material studied. CFZ-Ca 11, 51 (1), 115 (1), 208; 210, 224, 205, 304, 306, 319, 354, of Cañada Alejandro, Tlaxiaco, Oaxaca. Undifferentiated Zorrillo-Taberna formation.

Description. Narrow and regularly segmented leaves. Incomplete specimens with a conserved length of up to 6.1 cm and 1.5 to 3 cm in width. The leaflets of a square to semi-trapezoidal shape, subopposed and laterally inserted into rachis. The leaflet with a length of 0.7 to 1.8 cm and a width of 0.9 to 1.3 cm, in the

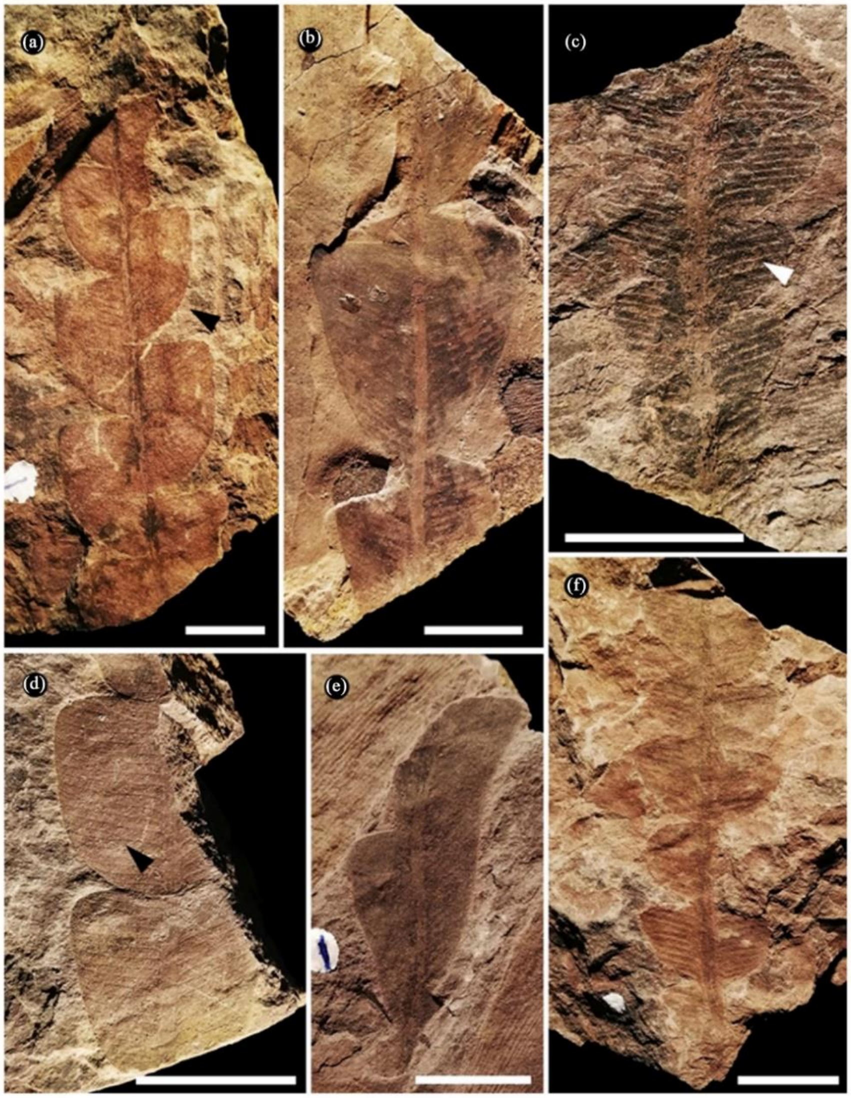

Figure 3. Leaves of *Anomozamites* of the Cañada Alejandro locality, Zorrillo-Taberna formation. (a), (d) and (e) *A. angustifolium*, leaf is regularly segmented from the middle region of the leaf, strongly convex basiscopic margin; (d) the venation of the leaflet is observed, and the dichotomy of the veins is indicated by a black arrow; (e) basal region of a leaf where the leaflets are wider than their length; (b) *A.* cf. *triangularis*, the leaflets with triangular morphology and the slightly convex basiscopic margin; (c) and (f) *A.* sp.1, in (c), the basal portion of the leaf is observed, and the leaflets decrease in length toward the anterior portion, with a white arrow indicating the venation parallel; (f) corresponds to the middle region of a leaf regularly segmented and with the opposite leaflets; (c) and (f) the falcate form and obtuse apex of the species are noted. Graphic scale = 1 centimeter.

basal portion the width of the leaflet reaches 2.5 cm; a length/width ratio of 1:>1, the acroscopic angle is straight 90˚, while the basiscopic angle goes from 60˚ to 90˚; truncated apex and straight base. Thin veins that pass through the leaflets and are arranged perpendicular to the rachis in a range of 15 to 25 per leaflet, bifurcating at least once at the base very close to the rachis. Rachis width is 0.1 cm, without a preserved petiole. The acroscopic margin of the leaflets is straight, but the basiscopic margin can be strongly convex.

Comments and interpretation: *Anomozamites angustifolium* is a species with a wide stratigraphic range that goes from the Upper Triassic (Rhaetian) to the Middle Jurassic (Bajocian) with records mainly in Euroamerica. It is a species of a foliar organ with morphological variations in its foliar architecture which has been recognized based on a large collection [19]. The reviewed specimens of the Mixteco Terrane share most of the morphological characters, only with some minimal variations. Characters that match and are diagnostic of the fossil-species are the following: the length/width ratio of the leaflets, which is less than twice the length with respect to the width, the number of veins greater than 15 per leaflet, the truncated to round apex, and the square shape of leaflets. Characters with slight variations are the width of the leaflets that is greater in the samples of the Mixteco Terrane. This could indicate that some fragmented samples would correspond to the base part of the leaves. However, other specimens are regularly segmented indicating that they correspond to the middle or even apical region of the leaf. In this case, 10 specimens are considered to be from the middle region mainly because of the width of the leaflets, since if they corresponded to the apical part the leaflets should decrease in proportional size. Only the CFZ-Ca 306 specimen corresponds to the base portion of a leaf because it is clearly the portion that is not segmented as in the rest of the leaf, a feature commented in the reference [19].

The studied specimens that correspond to *Anomozamites angustifolium* differ from other species with general morphology of the similar leaf in several characters, especially in the morphology and size of the leaflets, number of veins and location of dichotomies. *A. angustifolium* differs from *A. minor* (Brongniart) Nathorst (Rhaetian), *A. thomasi* Harris (Middle Jurassic), *A. sanjiaocunensis* Miao *et al.* (Middle Jurassic), *A. villosus* Pott *et al.* (Middle Jurassic) and *A. sinensis* (Zhang et Zheng) Pott (Callovian/Kimmeridgian) since this has leaflets of square to semi-trapezoidal morphology, they are arranged in a subopposite way on each side of the rachis and contain more than 15 veins with dichotomies in the base of each leaflet. In addition, the length/width relation of the leaflets in the middle region of the leaf is up to 1:>1 and does not present hairs [19] [20] [21] [23] [27].

Anomozamites cf. *triangularis*

Figure 3(b)

Material studied. CFZ-Ca 226 and 262 of Cañada Alejandro, Tlaxiaco, Oaxaca. Undifferentiated Zorrillo-Taberna formation.

Description. Leaves regularly segmented, narrow and incomplete, with a conserved length of up to 6.8 cm and 2.5 cm wide. The leaflets of triangular form, opposite to semi-opposite, inserted laterally into the rachis with a length of 1 - 1.3 cm and a width of 2.1 - 2.6 cm, with a length/width ratio of 1:2, the acroscopic margin is straight (90˚), while the basiscopic is acute (35˚ - 40˚), apex rounded, straight base, with 22 - 25 fine veins that pass through the leaflets and arranged perpendicular to the rachis, few dichotomies at the base and at the middle portion of the leaflet. The rachis width is 0.1cm with several longitudinal grooves, without preserved petiole.

Comments and interpretation: The reviewed specimens correspond to incomplete leaves, so their total length is unknown, and it is impossible to estimate it since the fragments are small. The region to which they would correspond is the middle portion of the leaf because the segmentation is regular, and the leaflets are well defined. The apex and petiole are unknown. The rachis is remarkably narrow and has several very fine longitudinal grooves; this characteristic is present and is observable in all the previous records of *Anomozamites* in the Mixteco Terrane [9]. The rachis is notably different from that of the Triassic species of Scania and Greenland [19] [24] and with other records from the Jurassic of Asia and South America [21] [22] [23] endowing the leaf with a light and fragile but not rigid appearance. The leaflets are triangular in shape (scalene triangle) and the length/width ratio is 1:2.

The characteristic shape of the leaflets of the specimens studied is clearly comparable with the *Anomozamites triangularis* (Nathorst) Pott et McLoughlin from Scania, Sweden, and *A.* sp., from Daohugou, China, which correspond to the only reports with a triangular morphology of the leaflets outside the Mixteco Terrane [19] [27]. However, there are several qualitative to quantitative differences with *A. triangularis*, on the one hand, the general shape, although it is triangular in Mexican specimens, the apical part is noticeably more rounded and the basiscopic margin is more convex in Swedish specimens. In addition, the dimensions are incompatible, in the revised specimens the leaflets are double the width with respect to *A. triangularis* which has leaflets with a width of 1.3 cm and 1 cm in length; therefore, the length/width ratio is also incompatible, seen as 1:2 in the specimens studied, while in *A. triangularis* it is <1:1 [19]. On the other hand, compared to the Daohugou specimen, the differences are with the width and number of leaflet veins that is greater in the Mexican specimens. The morphology proposed in the reconstruction of the Chinese specimen differs when presenting a greater acroscopic margin length [27].

The comparison with the previous records of *Anomozamites* in the Mixteco Terrane denotes differences and similarities. The shape and arrangement of stretch marks in the rachis is a compatible character among all records, including this one. The reference to the report of *A. triangularis*, made in [9], denotes the same differences mentioned as with those reported for the Scania, Sweden. Regarding the stratigraphic scope of *Anomozamites triangularis*, reports from Sweden correspond to the Upper Triassic, with exclusivity to the Rhaetian age [19]. A second report corresponds to the one made for the Zorrillo-Taberna formation, in the Río Ñumí locality [9], 6 kilometers away from the town of Cañada Alejandro. However, a stratigraphic correlation between both locations has not been made.

Anomozamites sp.1

Figure 3(c) and Figure 3(f)

Material studied. CFZ-Ca 11, 167, 168, 326 (2), 328, 329, 375 of Cañada

Alejandro, Tlaxiaco, Oaxaca. Undifferentiated Zorrillo-Taberna formation.

Description. Thin leaves regularly segmented, the apex, the base and the petiole of the leaves are unknown. They are up to 7.7 cm long and between 1.3 and 2 cm wide. The leaflets are falcate in form, with a length of 0.6 to 0.9 cm and a width of 0.6 to 1 cm, consequently a length/width ratio of 1:1. The number of veins per leaflet is 9 to 12, they are parallel and dichotomous at the base and occasionally in the middle region, and they pass through the leaflets perpendicular to the rachis. The apex is obtuse to subround and they are united by all the base to the rachis in the opposite position and sometimes they are subopposed. The rachis is thin with a thickness of 0.1 cm with a longitudinal groove.

Comments and interpretation: The reviewed specimens are thin leaves, segmented regularly, and the size and morphology of leaflets are homogeneous. However, the apex and the base of the leaves are unknown, so it is not possible to estimate the total length of the leaves. The morphology, both of the leaf and of the leaflets, is remarkably different from the species previously registered in the Mixteco Terrane region, with the exception of the *Anomozamites* cf. *angustifolium* [6] [9]. The morphological data reported in reference [9] corresponding to the size, number of veins and shape of the leaflets are fully compatible with *A.* sp.1 and since *A. angustifolium* consists of the leaflets of the square to semi-trapezoidal shape with a round apex and more than 15 veins per leaflet, we consider that the previous report of *A.* cf. *angustifolium* made in [9] must be included in this new identification. Another report that presents high morphological similarities with *A.* sp.1 is that of *A. minor* from the Upper Jurassic of Colombia [21]. However, the latter has a poor morphological description, and the distinguishing characteristics do not allow the classification with *A. minor* because, as comments in [19], the inadequate classification of several reports in this species was generally done when in fact they corresponded to some other.

In this case, we consider, according to the characteristics shown in references [21] that the report of *A. minor* of the Jurassic of Colombia, could correspond to the identification presented here of *A.* sp.1. The basis of this interpretation is the compatibility of the following characters: falcate shape, obtuse apex, number of veins of the leaflets and the size and presence of a single longitudinal groove in the rachis.

Anomozamites sp.1 differs from species such as *A. baegunsaensis* Kim (Upper Triassic), *A. minor* (Rhaetian), *A. lindleyanus* Schimper (Middle Jurassic), *A. nilssonii* (Phillips) Harris (Middle Jurassic), *A. sanjiaocunensis* (Jurassic Middle), *A. thomasi* (Middle Jurassic), *A. villosus* (Middle Jurassic) and *A. sinensis* (Callovian/Kimmeridgian), because it has small leaflets with a 1:1 length/width ratio, has a falcate shape, obtuse apex and they are attached to the rachis in the opposite position, and have no hairs, dentate margin, rectangular shape or longitudinal groove in the rachis [17] [19] [20] [23] [27]. Therefore, the proposal that the revised specimens correspond to a new species is based on their unique characteristics for the geographic region and stratigraphic range.

4.2. Comments on the Phytogeographic Distribution of *Anomozamites* (Leaf) and Its Relationship with *Wielandiella* ("Flower") (Bennettitales: Williamsoniaceae)

Anomozamites is a foliar fossil-genus included in the order of the Bennettitales which has a stratigraphic range from the Upper Triassic to the Lower Cretaceous and distributed mainly in the Kingdom of Laurasia and in the Euro-American region. The greatest diversity recorded has been in the Greenland and Sweden, with some reports from the Jurassic of the United Kingdom [2] [17] [19]. However, there are recent findings in the regions of Asia, mainly from the Middle Jurassic in China [20] [22] [23] [26] [27]. Other reports come from North America (E.U.A) and South America (Colombia) (**Figure 4**); however, in the first case only the presence of the fossil-genus is reported in the Morrison Formation (Upper Jurassic) and in the second case, the description is remarkably shallow and we even consider that the specimens correspond to the fossil-species *A.* sp.1 reported in this study [21] [34].

Within the Mixteco Terrane (southern Mexico) the first reports were made in reference [13], here mentions that only collected a hand specimen of the Middle Jurassic and assigned it to *A.* cf. *lindleyanus*, subsequently this issue is reviewed in [12] and when adding a sample, they consider keeping specimens only at genus level, mainly because they are few and small fragments; later in reference [6] was agrees with this determination. The last reports of *Anomozamites* in the Mixteco Terrane correspond to *A. triangularis*, *A.* cf. *angustifolium*, *A.* cf. *intermedium* and *A.* sp., from the Middle Jurassic of the Tlaxiaco region, Oaxaca

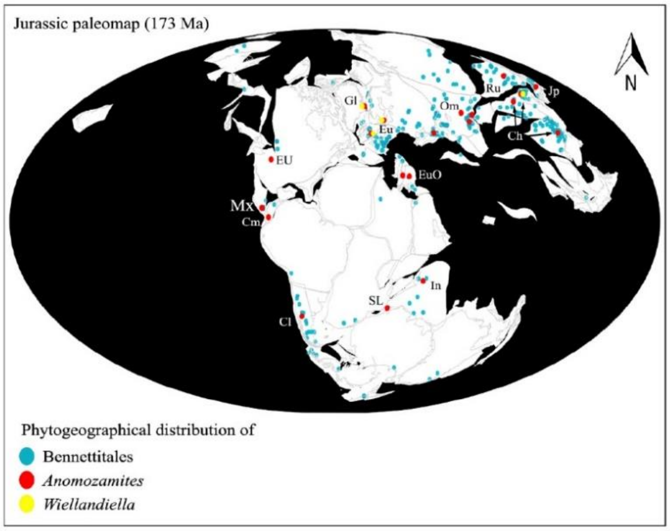

Figure 4. Map of the Jurassic (173 Ma) showing the phytogeographical distribution of the Bennettitales order (blue dots), *Anomozamites* (red dots) and *Wielandiella* (yellow dots). Mx: Mexico, Cm: Colombia, Cl: Chile, EU: United States, SL: Sri Lanka, Gl: Greenland, Eu: Europe (Sweden and the United Kingdom), EuO: Eastern Europe (Romania and Georgia), In: India, Om: Middle East (Kazakstan, Tajikistan and Uzbekistan), Ru: Russia (Siberia), Ch: China, and Jp: Japan. Map obtained from Paleobiology Database (https://paleobiodb.org/navigator/).

[9]. We consider *A.* cf. *angustifolium* would also correspond to *A.* sp.1 (see above) based on clear morphological details. We agree with the proposal in [9] regarding its report of *A.* sp., as compatible with the copy described in [6], that is, both correspond to the same fossil-species. However, a systematic review of the specimens is necessary for the establishment of a new fossil-species.

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We consider *A.* cf. *angustifolium* would also correspond to *A.* sp.1 (see above) based on clear morphological details. We agree with the proposal in [9] regarding its report of *A.* sp., as compatible with the copy described in [6], that is, both correspond to the same fossil-species. However, a systematic review of the specimens is necessary for the establishment of a new fossil-species.

The records obtained from the website Fossilworks.org and Paleobiology Database indicates that there is a distribution of *Anomozamites* during the Jurassic which includes, in addition to the areas already mentioned, Chile, Georgia, India, Japan, Kazakhstan, Romania, Russian Federation, Sri Lanka, Tajikistan and Uzbekistan (**Figure 4**). Then, with the corroborated records we can observe a dominant Laurasia distribution of *Anomozamites* and the outcroppings of the Middle Jurassic of the Mixteco Terrane conserve a diversity composed possibility of up to five fossil-species. Comparing with the five registries of the Rhaetian/Bajocian of Europe, the Mixteco Terrane would be at the same level of diversity, sharing with certainty two fossil species: *A. angustifolium* and *A. triangularis*, and possibly *A. intermedium* Antevs.

The stratigraphic range of the *Anomozamites angustifolium* is from the Rhaetian to Bajocian [19], therefore, the distribution to the Bajocian in the Mixteco Terrane is considerable. In the case of *A. triangularis* it would correspond to an extension of the geographical and stratigraphic distribution, because this fossil-species have only been registered in the Rhaetian of Scania, Sweden. Finally, the probable identification of *A.* cf. *intermedium* in the Middle Jurassic of Mexico would also broaden the geographic and stratigraphic distribution, however, since it is not completely safe to identify such speculation, it would be overestimating both distributions.

On the other hand, the recent revision, finding and description of the organic connection between leaves, stems, and cones of the Williamsoniaceae family extends the understanding of the relationship of the *Anomozamites*-type leaves and the *Wielandiella* flower-type reproductive structures. It also represents the confirmation of a bifurcated growth in the habit of this family of Bennettitales. These findings have allowed us to propose two species within the *Wielandiella* fossil-taxon: *W. Angustifolia* (Nathorst) emend. Pott and *W. villosa* Pott, McLoughlin, Wu et Friss, with a stratigraphic and geographical range from the Rhaetian of Europe to the Middle Jurassic of China [24] [25] [26].

In the first case, the revision of specimens of the Rhaetian/Hettangian from Sweden and Greenland allowed understanding the relationship between the foliar organs of *Anomozamites angustifolius* Pott et McLoughlin and the cones ("flowers") of *Wielandiella angustifolia* (Nathorst) Nathorst emend. Pott. In addition, it clarifies the unisexual nature of *Wielandiella* and constitutes a fossil-genus distinct from *Williamsoniella* Thomas and *Williamsonia* (Carruthers) Harris [24]. The second case corresponds to the first finding of isolated *Anomozamites*-type leaves with the distinctive feature of presenting hairs (trichomes) along the rachis and at the base of the leaflets. This characteristic is mainly the one that distinguishes fossil-species *A. villosus* from others [20]. Later, when discovering leaves linked to bifurcated stems and with the presence of possible "flowers" (type *Wielandiella*) at the base of these bifurcations, *A. villosus* is reassigned and amended to *W. villosa* (Pott, McLoughlin, Wu et Friis) Pott. In addition, this second taxonomic assignment to *Wielandiella* broadens the knowledge of leaf architecture, habit and the various ecological strategies of the Williamsoniaceae family [25] [26]. Therefore, since the correlation between the *Anomozamites*-type leaves and the unisexual flower-type reproductive organs of *Wielandiella* has been verified by organic connection in the two cases mentioned, it is highly possible that the presence of up to five species of *Anomozamites* in the Mixteco Terrane are linked to the existence of some fossil-species of *Wielandiella* in the region. In this way the diversity of reproductive organs of the Bennettitales and specifically of the Williamsoniaceae family would be represented by the fossil-genera confirmed *Williamsonia*, *Weltrichia* Braun emend. Harris and *Williamsoniella* [15] [35] [36] [37], while, the possible existence of *Wielandiella*, in light of the discovery of their fossils in the outcrops of the Mixteco Terrane, it would be verified.

5. Conclusions

The identification of three fossil-species of *Anomozamites* extends the richness of the Williamsoniaceae family in the Mixteco Terrane, confirms the distribution of *Anomozamites* in this region within the kingdom of Laurasia and allows estimating the possible existence of fossil-genus *Wielandiella* in the same area during the Middle Jurassic.

We consider, according to the analysis of our results, that a systematic review of the specimens attributes to *Anomozamites* cf. *lindleyanus* in Reference [13] and *A*. sp. [6] [9] [12] to clarify their taxonomic identification and complement the systematic knowledge of the Bennettitales of the Mixteco Terrane. In addition, these findings may be incorporated in future paleobotanical analyzes that incorporate the study area. This will provide knowledge that may support paleoecological, phytogeographic and evolutionary studies of palaeobiodiversity in the Middle Jurassic, in both North America and Laurasia.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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TERCER CAPÍTULO

Bennettitales del Jurásico Medio del noroeste de Oaxaca, México: Diversidad, ambientes sedimentarios y fitogeografía

- **Lozano-Carmona, D. E.** Propuesta y diseño del trabajo; revisión de los ejemplares e identificación taxonómica; recopilación y consulta bibliográfica; análisis e interpretación de datos taxonómicos, sedimentarios y fitogeográficos; toma de fotografías y elaboración de figuras; actividades de campo: recolecta de material y selección de niveles (estratos) de muestreo; redacción del manuscrito.
- **Velasco-de León, M. P.** Dirección, revisión del trabajo y del manuscrito; actividades de campo: selección de localidad y niveles (estratos) de muestreo, recolecta de material.

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Bennettitales from the Middle Jurassic of northwestern Oaxaca, Mexico: Diversity, sedimentary environments, and phytogeography

Diego Enrique Lozano-Carmona[a,b,*], María Patricia Velasco-de León[b]

[a] *Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Ciudad Universitaria, Universidad Nacional Autónoma de México, Coyoacán, C.P, 04510, Ciudad de México, Mexico*

[b] *Colección de Paleontología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Batalla 5 de Mayo, Ejercito de Oriente, Iztapalapa, C.P, 09230, Ciudad de México, Mexico*

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ABSTRACT

The Jurassic flora of Mexico represents a key element for the knowledge of the paleoflora on the western margin of equatorial Pangea because of its abundance and diversity. Bennettitales were the dominant group and are represented by leaves and reproductive organs in Jurassic outcrops from southern Mexico. This group has been historically recorded in seven lithostratigraphic units in southern Mexico in a range from the Toarcian to the Callovian. These reports have focused on morphological and taxonomical aspects for the obtention of paleofloristic listings by locality but do not provide environmental data or have any impact on biostratigraphic or phytogeographic analyses. The highest number of localities in Mexico has been reported in the state of Oaxaca, where plant fossils are more abundant and better preserved in comparison with localities of Guerrero, Puebla, Veracruz, and Hidalgo states. Therefore, in order to reinforce the paleofloristic knowledge of southern Mexico, the present study documents the diversity of Bennettitales in northwestern Oaxaca region, which is composed of 11 fossil-genera and 41 fossil-taxa, included 30 valid species and 11 species that need taxonomic revision. We provide the description of a new species, ***Williamsonia sanjuanensis*** sp. nov., new findings of ***Williamsonia nathorstii,*** and the first record of *Bennetticarpus* for southern Mexico. We also describe fossiliferous outcrops of the Zorrillo and Zorrillo/Taberna undifferentiated formations and propose their sedimentary environments. In addition, we provide a proposal of one biozone based on Bennettitales. Finally, we recognize six spatio-temporal distribution patterns for this plant group in northwestern Oaxaca. These new data add to a growing set of information on the Jurassic flora of Mexico and allow to substantiate the paleobotanic importance of southern Mexico within the region of North America.

1. Introduction

Bennettitales are a group of extinct gymnosperms with an important botanical significance, mainly due to their evolutionary relationships and morphological innovations in the complex uni- and bisexual reproductive structures they presented, as well as their phytogeographic patterns (Harris, 1969; Bose et al., 1984; Bardoni and Linder-Dutra, 2013; Popa, 2014; Pott, 2014; Pott and McLoughlin, 2014; Pott and Axsmith, 2015; Pott et al., 2015; McLoughlin et al., 2018). From an evolutionary perspective, their phylogenetic position remains a subject of debate, since they were considered the sister group of angiosperms (Crane, 1985; Watson and Sincock, 1992; Friis et al., 2011), and, on the other hand, they were proposed as an independent clade within spermatophytes (Rothwell et al., 2009). Nevertheless, due to the morphological and anatomical characteristics of their reproductive organs, Bennettitales have been considered as representatives of an experiment in plant architecture before the appearance and dominance of flowering plants (Harris, 1969; Popa, 2014; Pott, 2014; McLoughlin et al., 2018). This is because the reproductive organs of the *Williamsonia* Carruthers, emend. Harris, *Weltrichia* Braun, emend. Harris, *Williamsoniella* Thomas, and *Wielandiella* Nathorst, emend. Pott are morphologically flower-like (Pott, 2014; Popa, 2019). Bennettitales had a near worldwide distribution during the Jurassic and were the main element of the vegetation of the floristic kingdom of Laurasia (Anderson et al., 2007; Taylor et al.,

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* Corresponding author. Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrados, Ciudad Universitaria, Universidad Nacional Autónoma de México, Coyoacán, C.P, 04510, Ciudad de México, Mexico.

E-mail address: diego.lozano@zaragoza.unam.mx (D.E. Lozano-Carmona).

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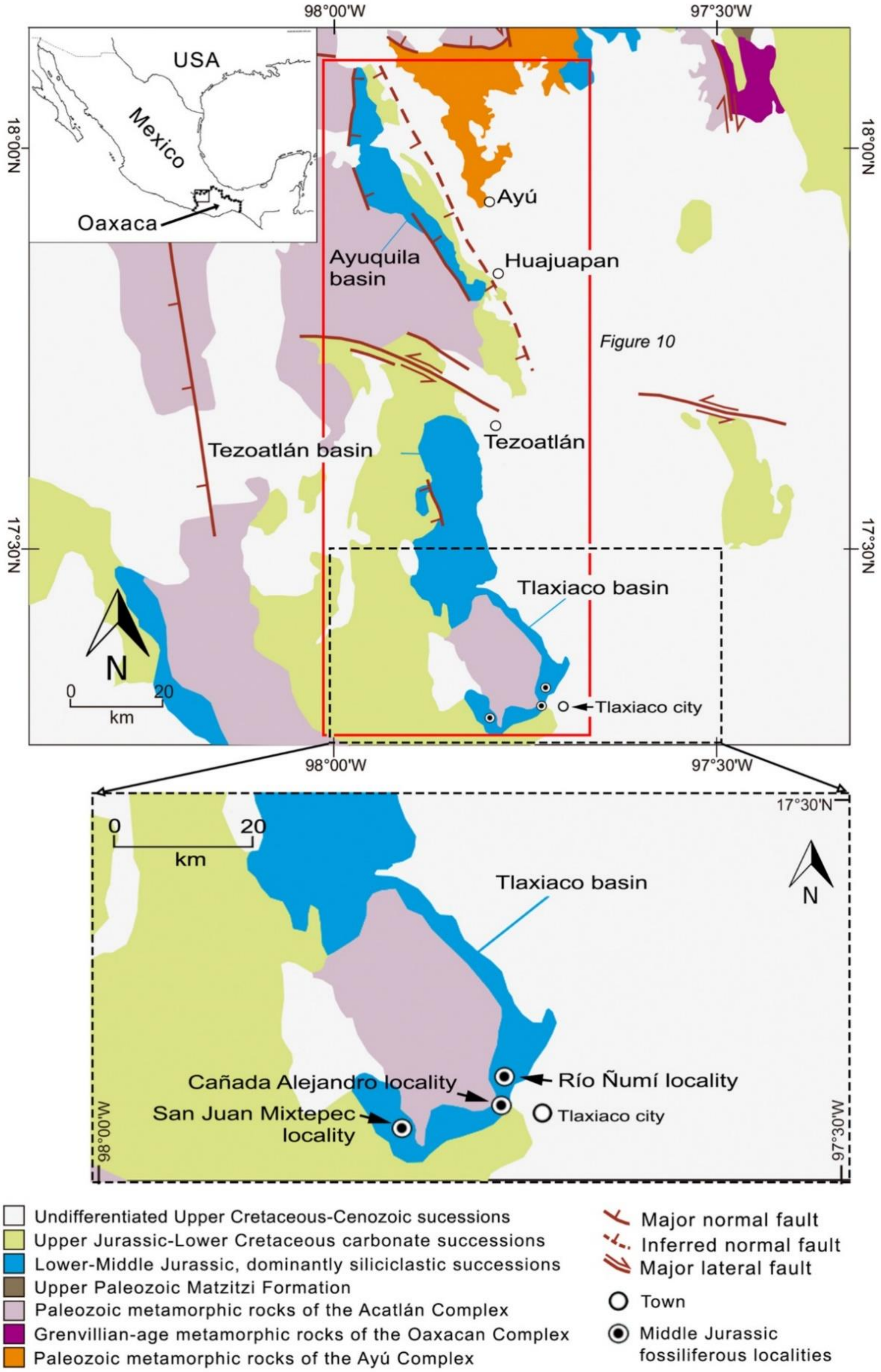


Fig. 1. Schematic geological map of southern Mexico. It shows the location of the Jurassic sedimentary basins of Ayuquila, Tezoatlán and Tlaxiaco, as well as the study localities. The red box is Fig. 10, area used for section 4.4 *Phytogeography of Bennettitales in northwestern Oaxaca*. Map taken and modified from Martini et al. (2017); and the Oaxaca E14-9 Geological-Mining Chart, scale 1:250,000 from the Mexican Geological Service (SGM, 2000). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2009; Popa, 2019). Outcrops with Bennettitales in the Northern Hemisphere, mainly in Europe and Asia, are the best studied of this kingdom. In the region of North America, the most studied Jurassic are those of the Upper Jurassic Morrison Formation (Parrish et al., 2004; Chure et al., 1998, 2006, 2006; Anderson et al., 2007) which is notable for dinosaur records, but it also has a diverse paleoflora (Tidwell and Medlyn, 1992; Parrish et al., 2004; Chure et al., 1998, 2006), although the diversity of Bennettitales is low (Parrish et al., 2004). Nevertheless, there are outcrops in the southern Mexico with the presence of flora from the Lower–Middle Jurassic (Toarcian–Callovian) with a high diversity of Bennettitales (Erben, 1956a, 1956b; Delevoryas and Gould, 1973; Delevoryas and Person, 1975; Silva-Pineda, 1984; Delevoryas, 1991; Anderson et al., 2007; Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019, 2021).

Some of the best preserved and most abundant floras, composed by Bennettitales, Caytoniales, Ginkgoales, Coniferales, Cycadales, Filicales, Equisetales and incertae sedis, from the Jurassic of North America are found in southern Mexico (Silva-Pineda, 1969, 1978; 1984; Delevoryas and Gould, 1971, 1973; Delevoryas and Person, 1975; Silva-Pineda and González-Gallardo, 1988; Velasco-de León, 1990; Delevoryas, 1991; Corona Esquivel et al., 1995; Silva-Pineda et al., 2011; Velasco-de León et al., 2014, 2019; Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Ortega-Chavez et al., 2017; Lozano-Carmona et al., 2019, 2021). However, the study of this paleoflora has not had an impact on biostratigraphc or phytogeographic studies, since they have been limited to morphological, taxonomic, floristic and paleoecological aspects (Silva-Pineda, 1984; Weber and Cevallos-Ferriz, 1994: Pérez-Crespo, 2011; Velasco-de León et al., 2013, 2014; Ortiz-Martínez et al., 2013; Lozano-Carmona and Velasco-de León, 2016). Historically the paleoflora has been reported from the Rosario, Cualac, Zorrillo, Zorrillo/Taberna undifferentiated, Otlaltepec, Ayuquila, and Tecomazúchil formations. However, studies on these records have focused on the description of morphological and taxonomical aspects for the obtention of floristic listings. These studies provide little detail about their stratigraphic location or sedimentology. Bennettitales are the most abundant group in all these formations, and the Zorrillo/Taberna undifferentiated Formation (Bajocian) has the highest number of records with 24 species (Erben, 1956a, 1956b; Delevoryas and Gould, 1973; Delevoryas and Person, 1975; Silva-Pineda, 1978; Velasco-de León et al., 2013; Carrasco-Ramírez et al., 2016; Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019). This has resulted in biased information and analyses of Bennettitales, in aspects such as their specific diversity, biostratigraphy, and taphonomic processes, as well as the paleoenvironmental and paleogeographic correlations between lithostratigraphic units. Thus, with the purpose of filling some of the gaps and consolidating the paleobotanical knowledge of the Jurassic of southern Mexico, the objectives of the present study were: (1) describe new fossil findings and their outcrops from the Zorrillo and Zorrillo/Taberna undifferentiated formations; (2) establish the Bennettitales diversity and biostratigraphy and (3) analyze the phytogeographic distribution of this group in the Middle Jurassic of northwestern Oaxaca.

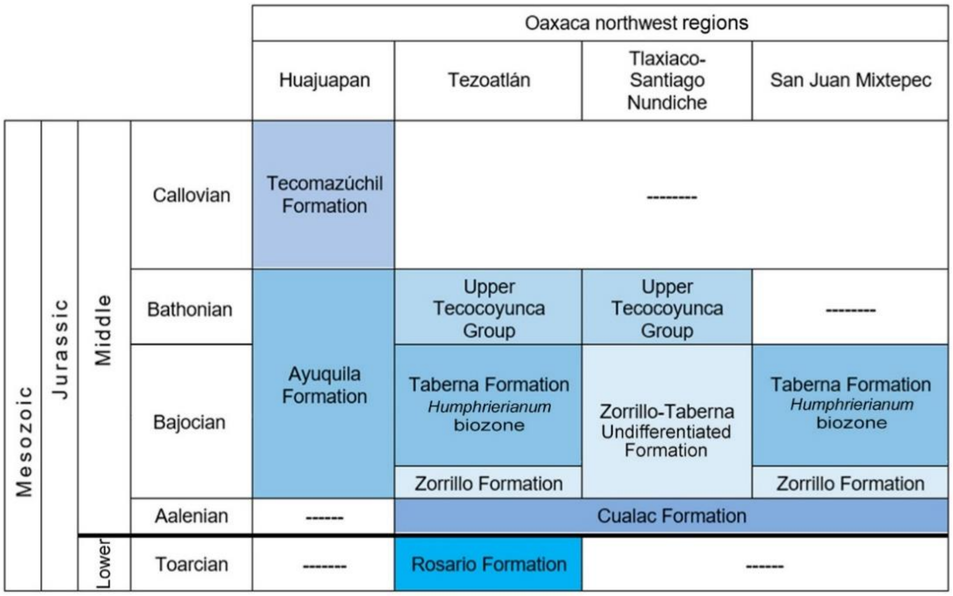
In order to achieve these objectives, we studied the specimens collected and curated between 2008 and 2019, and we also surveyed and described the fossiliferous localities during 2018–2019. We obtain results that show a clear record of the diversity, biostratigraphy, and phytogeographic distribution of Bennettitales in the study area (Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019, 2021). This diversity consists of 30 valid species and 11 species that need taxonomic revision, in total 41 fossil-taxa, shows a biostratigraphic record from the Toarcian to the Callovian, and allows to complete previously reported distribution patterns of Bennettitales. Therefore, our results contribute to knowledge on the Jurassic flora of Mexico, which represents a key element for the understanding of the paleobiota of North America during the Jurassic since in the region there are few formations with a flora record for this period.

2. Geological setting

The material studied was collected from the Zorrillo and Zorrillo/Taberna undifferentiated formations (Fig. 1–2) and correspond to the Middle Jurassic, Bajocian in age (Erben, 1956a, 1956b; Sandoval and Westermann, 1986; Morán-Zenteno et al., 1993; Carrasco-Ramírez et al., 2016).

2.1. *Zorrillo Formation sensu Erben (1956a, 1956b)*

Outcrops of this formation have been recorded in the southwest of Tezoatlán and the south of San Juan Mixtepec in Oaxaca. The Zorrillo



				Oaxaca northwest regions			
				Huajuapan	Tezoatlán	Tlaxiaco-Santiago Nundiche	San Juan Mixtepec
Mesozoic	Jurassic	Middle	Callovian	Tecomazúchil Formation	--------		
			Bathonian	Ayuquila Formation	Upper Tecocoyunca Group	Upper Tecocoyunca Group	--------
			Bajocian		Taberna Formation *Humphrierianum* biozone	Zorrillo-Taberna Undifferentiated Formation	Taberna Formation *Humphrierianum* biozone
					Zorrillo Formation		Zorrillo Formation
			Aalenian	------	Cualac Formation		
		Lower	Toarcian	-------	Rosario Formation	------	

Fig. 2. Summary of formations that outcrop northwestern Oaxaca and age range of the deposit according to: Erben (1956), Sandoval and Westermann (1986), Morán-Zenteno et al. (1993), Campos-Madrigal et al. (2013), Carrasco-Ramírez et al. (2016), and Zepeda-Martínez et al. (2018).

Formation is mainly composed of fine-to medium-grained sandstone and siltstone, occasionally with cross-stratification. It exhibits thin stratification with a thickness ranging between 20 and 80 m. Grey-yellowish siltstone contain terrestrial plant fossils, as well as carbonaceous lutite and coal seams. It overlies the Cualac Formation and transitionally underlies the Taberna Formation. Based on its stratigraphic position, it has been dated to the Bajocian (Erben, 1956a, 1956b; Sandoval and Westermann, 1986). Its environment has been generally interpreted as continental floodplains with local swamps (Morán-Zenteno et al., 1993). The paleofloristic content of this formation is mainly composed of Bennettitales and ferns, as well as Ginkgoales, Czekanowskiales and Incertae sedis (Delevoryas and Gould, 1971, 1973, 1973; Delevoryas and Person, 1975; Lozano-Carmona et al., 2015).

2.2. *Zorrillo/Taberna undifferentiated formation sensu Carrasco-Ramírez et al. (2016)*

The Zorrillo and Taberna formations are considered in conjunction due to their high lithological similarity and poorly differentiated transitional limit. This complicates the distinction between the two formations outside of their type localities. The differentiation is particularly difficult in the outcrops of the Ñumí riverbank, Tlaxiaco, Oaxaca (Carrasco-Ramírez et al., 2016). The column has a thickness of 325 m from the transitional contact with the Cualac Formation (Lozano-Carmona and Velasco-de León, 2016). It is composed of sandstone strata intercalated with lutite and lenticular coal beds. The age proposed for this undifferentiated formation corresponds to the Bajocian based on its stratigraphic relationships and fossil content that indicated the *Humphriesrianum* Biozone (Erben, 1956a, 1956b; Sandoval and Westermann, 1986; Carrasco-Ramírez et al., 2016). The upper portion of the unit contains the highest paleofloristic diversity, composed of Bennettitales, Cycadales, Filicales, Equisetales, Coniferales, Caytoniales, Ginkgoales, *Podozamites* Braun 1843 and Incertae sedis (Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019).

Sediment deposition resulted from continuous subsidence, with swamp areas protected by sandy bars and islets, and low fluvial energy. These processes allowed a homogeneous sedimentation. Thus, the sedimentary environment has been interpreted as two scenarios: (1) coastal swampy and (2) a fluvial system; both scenarios comprising a delta system (Carrasco-Ramírez et al., 2016).

3. Material and methods

The studied material corresponded to leaves and reproductive organs of Bennettitales collected in localities of the Zorrillo (loc. San Juan Mixtepec) and Zorrillo/Taberna undifferentiated (loc. Río Ñumí and Cañada Alejandro) formations during paleontological campaigns from 2008 to 2019. They are a total of 117 hand samples deposited in the Paleontological Collection of the Facultad de Estudios Superiores Zaragoza (FESZ) of the Universidad Nacional Autónoma de México. The inventory is labelled with the acronyms CFZM and CFZZt, CFZCa. Where CFZ is the reference from Paleontologicall Collection of the FESZ, M from San Juan Mixtepec locality, Zt from Zorrillo/Taberna-Río Ñumí locality and Ca from Cañada Alejandro locality. In cases when a hand sample contained more than one fossil-taxon of the same genus, species, or another fossil-taxon, we used a combination of numbers; for example, CFZM 55(8), where 55 is the hand sample and (8) the fossil-taxon number in the sample. The stratigraphic data of the collected specimens were recorded through a standardized sampling according to Lozano-Carmona and Velasco-de León (2016).

The specimens are adpressions fossils without cuticle. The material is well preserved and allowed the observation of morphological characters of the reproductive organs of Bennettitales. In this study we follow the morphological terminology for Bennettitales used and described by Watson and Sincock (1992), Pott et al. (2010), Pott (2014) and McLoughlin et al. (2018). The term "flower" refers to the whole reproductive structures of Bennettitales. The term "perianth" refers to the ring of bracts arranged in rows that form the outer part of reproductive structures. The term "receptacle" is used for the central tissue on which the ovules are inserted. Finally, we refer to "gynoecium" when the receptacle and the interseminal scales and ovules are attached. However, like McLoughlin et al. (2018), we do not intend to indicate homology of these structures with the reproductive organs of other seed plants.

Plant fossils were examined with a Nikon SMZ-10 A stereomicroscope. The photographic record was carried out with a Sony Cyber-shot DSC-H10 (Carl Zeiss lens: 3,5–4,4/6,3–63) camera and whit a set for oblique lighting. We used ImageJ 1.48v software to obtain microscopic data of the specimens. Based on the listings of Bennettitales in northwestern Oaxaca, we established the diversity and stratigraphic ranges of the species and explored the biostratigraphic definition of the study area based on the criteria of the North American Stratigraphic Code (Barragán et al., 2010). We also carried out a phytogeographic analysis of Bennettitales of northwestern Oaxaca based on the identification of their spatio-temporal consistency (Espinosa-Organista et al., 2001, 2002; Morrone and Escalante, 2016).

Additionally, during the period of 2018–2019, we surveyed and described the fossiliferous localities of the Zorrillo and Zorrillo/Taberna undifferentiated formations. For the stratigraphic-sedimentological contribution of the localities, we used the topographic and geological-mining map E14-D34 Tlaxiaco 1:50,000 scale and the geological-mining map E14-9 Oaxaca 1:250,000 scale by Mexican Geological Service (SGM, 2000). Based on the detailed description of each column, we used Miall's facies classification (Miall, 2000, 2006) to identify each of the facies present. Graphs of the measured lithostratigraphic columns were made in SedLog ver. 3.1 (Zervas et al., 2009) and edited in Photoshop CC 2017 software.

4. Results and discussion

We only provide descriptions of new taxonomical records for the study area, for a detailed revision of previous records see the original publications.

4.1. *Systematic Paleobotany*

Order: Bennettitales Engler, 1892

Family: Williamsoniaceae Carruthers, 1870

Genus: *Williamsonia* Carruthers, emend. Harris (1969).

Type species: *Williamsonia gigas* (Lindley et Hutton) Carruthers, 1870, Bajocian of Yorkshire, UK (according to Harris, 1969).

Williamsonia sanjuanensis sp. nov. Lozano-Carmona et Velasco-de León.

Syntypes: CFZM8(27), 8(35), 8(41), 66(6), 75(2).

Fig. 3. *Repository*: Paleontological Collection of the Facultad de Estudios Superiores Zaragoza (FESZ) of the Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico.

Paratypes: CFZM6(3), 8(5), 8(11), 8(15), 8(17), 8(21), 8(29), 8(44), 8 (55), 24, 46, 53(6), 66(1), 66(2), 66(4), 66(5), 78(4), 79(2), 81(1), 83, 88. Repository: Paleontological Collection of the Facultad de Estudios Superiores Zaragoza (FESZ) of the Universidad Nacional Autónoma de México (UNAM), Mexico City, Mexico.

Type locality: San Juan Mixtepec, Oaxaca, Mexico (17°17′N, 97°48′W).

Type horizon and age: *Zamites lucerensis* bed, Zorrillo Formation; Bajocian, Middle Jurassic.

Etymology: Refers to the name of the locality of San Juan Mixtepec, the only area where this species has been found in the southern Mexico.

Diagnosis: Small *Williamsonia* composed of a perianth with up to three rows of 8–10 linear to slightly lanceolate and entire-margined bracts, with fine longitudinal striae. Bracts arranged radially. Small, ovoid

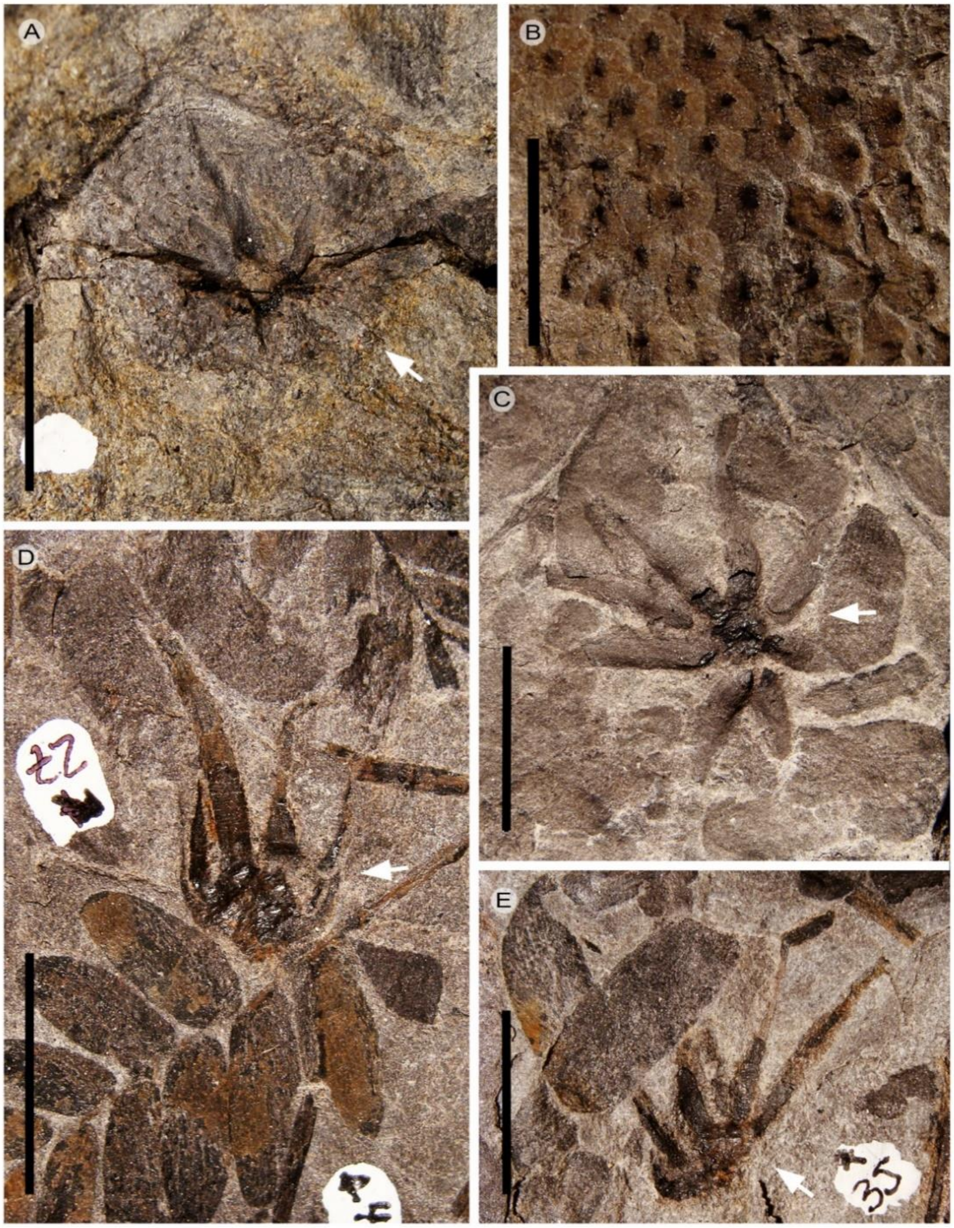


Fig. 3. *Williamsonia sanjuanensis* sp. nov., from the Zorrillo Formation in the San Juan Mixtepec locality. A. Specimen showing the organic connection between the perianth and the mature gynoecium, specimen M66 (6). B. Detail of the seminal scales, specimen M24. D. Association between *Williamsonia sanjuanensis,* specimen M8(27) and *Zamites lucerensis*, specimen M8(4). C. Abaxial view of the perianth where up to eight bracts and three rows are observed, specimen M75(2). E. *Williamsonia sanjuanensis* in cross-section view, where can observe the immature gynoecium (on as in imagen D) and only part of the perianth, specimen M8(35). The white arrows indicate the specimens. Scale bars = 5 mm in B, 10 mm in A, C–E.

immature gynoecium and semi-circular mature gynoecium with densely packed hexagonal seminal and interseminal scales, attached scar of a proportionally robust peduncle.

Description: Impressions of female reproductive organs (flowers) composed of perianth and gynoecium (immature and mature) (Figs. 3 and 4). Perianth composed of up to three rows of linear bracts (Fig. 3C, 4B–C). The apex of the bracts is possibly acute, as there is a marked decrease in width towards the apex (Fig. 3C–D, 4B–D). Several specimens were preserved in cross-section showing longitudinally five–six bracts in general (Fig. 3D–E, 4C–D). Up to four bracts can be seen in the first row, two–three bracts in the second row, and two–three bracts in the third row. We thus estimate about 8–10 bracts, because in the three rows of the perianth could accommodate at up to 10 bracts (Fig. 5). The most complete bracts are 14.9 mm long, with a maximum width of 1.8 mm. Bracts are ornamented with fine longitudinal striae. The immature gynoecium is oval to semi-circular, of 2.7 to 4.5 mm in external outline diameter, attached to the central part of the structure and surrounded by the perianth in a protective position (Figs. 3 and 4). The mature gynoecium is semi-circular with a diameter of up to 15.6 mm, with densely packed seminal and interseminal scales. The seminal and interseminal scales are hexagonal in form and have 0.9 mm length and 0.8 mm of width (Fig. 3B). Two specimens are connected to the perianth, which surrounds the gynoecium in an opening position (Fig. 3A).

Remarks and discussion: The preservation of the specimens (Fig. 3) allows us to observe and interpreted an organic connection of the perianth and gynoecium; the latter in both immature and mature stages (Figs. 4 and 5). We can distinguish the immature stage of the gynoecium because some specimens have a smaller size, an oval shape, undifferentiated or not visible scales and are still surrounded by the perianth. If the perianth is surrounding the gynoecium, it could be interpreted as a protective condition, allowing the gynoecium to mature for the fertilization stage (Fig. 3D – E, 4C – D). While in the specimens M66(6) and M8(41) a gynoecium of greater size is observed, a semi-circular shape and surrounded by an open perianth, which indicates a mature stage. Similar conditions of gynoecium development have been evaluated and analyzed by Pott and Axsmith (2015). The connection between the parts

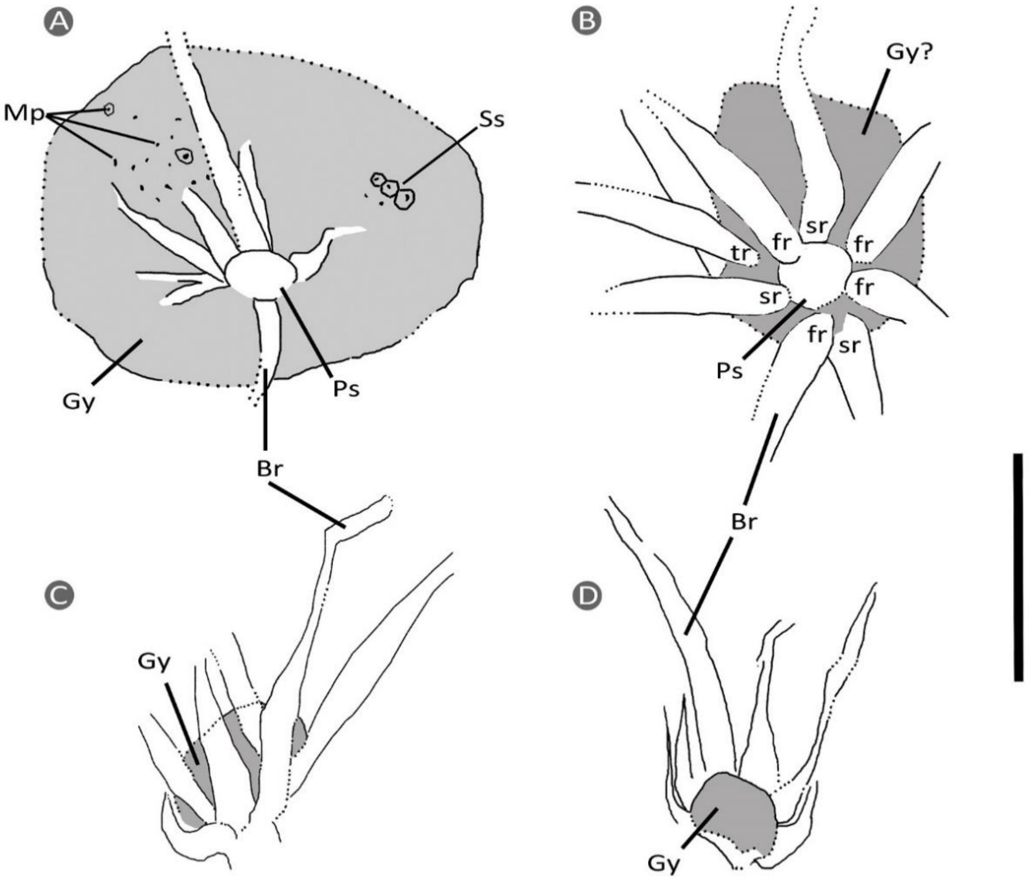


Fig. 4. Interpretative drawing based on the syntypes of *Williamsonia sanjuanensis* sp. nov., see Fig. 3 to compare the specimens. Abbreviations: **Mp**, micropyles; **Ss**, seminal scales; **Gy**, gynoecium; **Br**, bracts; **Ps**, peduncle scar; **fr**, first row of bracts; **sr**, second row of bracts; **tr**, third row of bracts. A. Flower in the mature gynoecium stage; there are up to three rows of bracts attached basally to the peduncle scar and a semi-circular mature gynoecium (in grey) with some seminal scales, specimen M66(6). B. Up to three rows of bracts related to the peduncle scar, each of the rows is indicated: first row (fr), second row (sr), third row (tr); in the specimen the possible gynoecium perimeter (Gy?) was observed. C and D. Ovoid immature gynoecium protected by the perianth in cross section, in C the view allows observing the bracts on the gynoecium, in D the frontal bracts were not preserved allowing the gynoecium to be seen. *Scale bar* = 10 mm.

that make up the flower that can be seen in *Williamsonia sanjuanensis* has been documented in other Bennettitales, for example: *Williamsonia gigas* Harris, *W. potyporanae* Bardoni et Linder-Dutra, *Wielandiella angustifolia* (Nathorst) emend. Pott, and the mature and immature state of the gynoecium in *Williamsonia carolinensis* Pott et Axsmith (Harris, 1969; Bardoni and Linder-Dutra, 2013; Pott, 2014; Pott and Axsmith, 2015). However, it is not common to find this type of preservation and the different stages of development in the williamsonias of southern Mexico (Silva-Pineda, 1984; Delevoryas and Gould, 1973; Delevoryas, 1991).

The perianth consists of three rows of bracts arranged until four bracts per row (Fig. 4B). In some cases, the perianth surrounds the immature gynoecium, which appears to indicate that the bracts protected the gynoecium until it maturated and was receptive to pollination (Fig. 3–5). However, micropyles were not exposed in the two preserved specimens with mature gynoecia. This condition is analyzed by Pott and Axsmith (2015), who propose that if the organ was mature and receptive, micropyles should be exposed, although they can retract during seed maturation. Thus, it is possible that the ovules had already been fertilized or the micropyles were eroded or were not preserved by fossilization. Consequently, the addition of this species to the diversity of the Middle Jurassic of southern Mexico shows that this group presents a wide variety of forms.

The specimens of *Williamsonia sanjuanensis* have a distinctive morphology that is not observed in *Williamsonia* species of southern Mexico (Delevoryas and Gould, 1973; Silva-Pineda, 1984; Delevoryas, 1991). The species *W. huitzilopochtlii* Wieland and *W. cuauhtemoci* Wieland, which are described based on the perianth (bracts), differ from *W. sanjuanensis* in all characters: length, width, and number of bracts (Table 1). In the case of *W. netzahualcoyotlii* Wieland, *W. oaxacensis* Delevoryas et Gould, and *W. nathorstii* Wieland, described based on adpressions on the external surface of the gynoecium, the main difference is the gynoecium diameter, which is smaller in *W. sanjuanensis*. *Williamsonia oaxacensis* is the most similar in size, since it is only 5 mm larger. However, the two species differ in the type of scales, since scales in *W. sanjuanensis* are hexagonal, whereas they are pentagonal in *W. oaxacensis* (Table 1). *Williamsonia diquiyui* Delevoryas et Gould is the only species preserved as a calcified petrifaction, which allowed to observe anatomical details of the ovules, interseminal scales, and receptacle. However, comparable characters were incompatible with *W. sanjuanensis*; for example, the diameter of the mature gynoecium is larger in *W. diquiyui* (Table 1). Finally, *Williamsonia oligosperma* Delevoryas is a species described based on a single specimen and its fossilization does not allow to observe many details. Only the diameter of this species could be corroborated, and it is almost twice the size of that of *W. sanjuanensis* (Table 1). *Williamsonia oligosperma* could even be reassigned to *Bennetticarpus* Harris (see below) according to the characters presented by Delevoryas (1991).

Williamsonia sanjuanensis differs from other Middle Jurassic species (Table 2) by the combination of characters such as the smaller williamsonian size, number and shape of the slightly lanceolate bracts, and

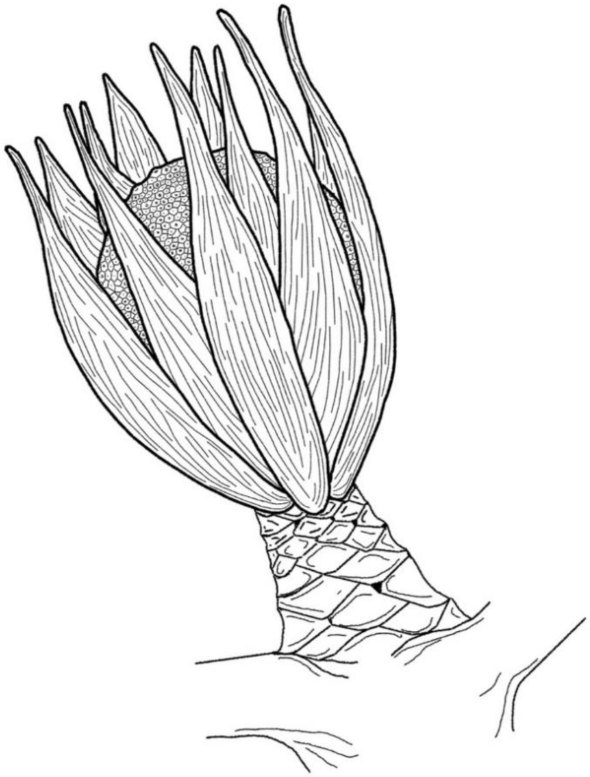


Fig. 5. Hypothetical restoration of *Williamsonia sanjuanensis* sp. nov. Small flower with perianth (bracts) surrounding a semi-developed semi-circular gynoecium; the bracts have longitudinal striae and the gynoecium has densely packed seminal and interseminal scales. Hypothetically, the flower would be attached to a short bud at the base of a forked branch, based on the interpretation of the growth habit of the Williamsoniaceae family (Pott, 2014; Pott and McLoughlin, 2014).

shape and size of the gynoecium (Harris, 1969; Delevoryas and Gould, 1973; Dragastan and Băbulescu, 1980; Silva-Pineda, 1984; Delevoryas, 1991; Schweitzer and Kichner, 2003; Vaez-Javadi, 2013). Therefore, based on the characters present in the series of reviewed specimens and their comparison with the Jurassic species of southern Mexico and other regions, it allows us to support the erection of *W. sanjuanensis* as a species with peculiar and unique characteristics.

On the other hand, the type locality contains several leaves of Bennettitales, mainly of the genus *Zamites* Brongniart (Lozano-Carmona et al., 2015). *Zamites lucerensis* (Wieland) Person et Delevoryas was the dominant species, found in over 50% of the 90 collected hand samples. Other leaf elements correspond to *Z. tribulosus* (Wieland) Person et Delevoryas, *Z. oaxacensis* (Wieland) Person et Delevoryas, *Otozamites hespera* Wieland, and *Anomozamites* sp. However, they are notably less abundant in the locality. Therefore, the association of leaves of *Zamites lucerensis* with flowers of *Williamsonia sanjuanensis*, which were found in very close proximity in most of the hand samples (Fig. 3B, D), suggests that these organs could have belonged to the same plant. Nevertheless, *Z. lucerensis* is the most common species in all localities of the Middle Jurassic of southern Mexico (Silva-Pineda, 1984; Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Velasco-de León et al., 2019) and *W. sanjuanensis* has only been found in San Juan Mixtepec locality. Thus, their organic relationship cannot be corroborated outside of this locality.

Williamsonia nathorstii Wieland, 1914

Fig. 6

Studied material: CFZCa56, Ca303.

Locality: Cañada Alejandro, Zorrillo/Taberna undifferentiated Formation

Description: Impressions of two gynoecium with well-defined seminal and interseminal scale heads (external character). The preserved structure is 46–49 mm in diameter and the peduncle scar is 12 mm in diameter. Receptacle at least 19 mm in diameter at the base. Interseminal scales are hexagonal and, occasionally pentagonal in front view, oval and elongated at the base near the peduncle scar. Diameter of scale heads is 0.7–2 mm and diameter of micropyle is 0.3–0.5 mm. Cuticle and bracts are not preserved.

Remarks and discussion: In both specimens, some micropyles can be observed in the upper left section, as well as seminal and interseminal scales arranged in rosettes (Fig. 6B and C). This indicates a mature cone in a receptive stage for fertilization (Pott and Axsmith, 2015). Scales are elongated or rectangular towards the base and then become hexagonal, occasionally pentagonal but arranged in rosettes (Fig. 6). The mostly hexagonal scales are densely agglomerated, forming rosettes of six to seven scales surrounding a central scale that presents a micropyle (Fig. 6). Silva-Pineda (1984) reports in the Rosario Formation only one specimen whose morphological description agrees with the specimens Ca56 and Ca303. The main difference of *Williamsonia nathorstii* with other *Williamsonia* species in southern Mexico is the arrangement (rosettes), shape, and size of the interseminal scales (Delevoryas and Gould, 1973), and it is the same case with other species of the Middle Jurassic (Harris, 1969; McLoughlin et al., 2018). *Willamsonia durikaiensis* McLoughlin et al. (McLoughlin et al., 2018), presents interseminal scales arranged in rosettes surrounding a micropyle, which is the character most like *W. nathorstii*. However, the arrangement in *W. durikaiensis* consists of four to seven (generally six) triangular interseminal scales surrounding a micropyle (McLoughlin et al., 2018), which is inconsistent with *W. nathorstii*.

Specimen Ca303 shows an impression of the basal part of the gynoecium preserving most of the external or superficial part of the interseminal scales. It also shows a convex impression of the receptacle, the bases of the scales attached very close to the peduncle scar, and the scars of the scales-ovules attached to the receptacle (Fig. 6D and E). These characters are not visible or preserved in the specimen collected by Wieland (1914) and revised by Silva-Pineda (1984).

We did not observe a possible relation between the reproductive organ of *Williamsonia nathorstii* and leaves of Bennettitales in the association of flora of the Cañada Alejandro locality. Even though *Zamites lucerensis* is the most abundant leaf species, as mentioned above, it would be more closely related to *Williamsonia sanjuanensis*. Furthermore, the low representativeness of *W. nathorstii* in the Cañada Alejandro locality, with only two specimens of the 400 collected, could indicate an allochthonous origin of this species.

Williamsonia sp. 1

*Fig. 7*A–C

Studied material: CFZCa342

Locality: Cañada Alejandro, Zorrillo/Taberna undifferentiated Formation.

Description: Specimen of a flower with gynoecium adpression, external and internal partial views, bracts, and peduncle present. The total diameter of the preserved gynoecium is 35 mm. The receptacle is approximately 23 mm in diameter with no preserved crown. Interseminal scales are hexagonal with heads 0.6–1.2 mm in diameter on the surface. Micropyle is 0.25 mm wide and 1 mm long, not exposed to the external surface of the gynoecium. The internal or transversal view of the gynoecium allows to observe the immature ovules, 1.1 mm wide and 5 mm long, and the interseminal scales, 1.5 mm wide and 6 mm long. Two rows of bracts are attached to the peduncle and are arranged surrounding the gynoecium; the most complete bract is 42 mm long and only five bracts are visible.

Remarks and discussion: The *Williamsonia* sp.1 (specimen Ca342) consist of peduncle, perianth and gynoecium in organic connection (Fig. 7B). The preservation of this specimen is the second of its type, since only one species where all the parts are joined has been found in

Table 1

Comparison of morphological characters of *Williamsonia* fossil-species of southern Mexico.

		Gynoecium (external mold)				Perianth		Gynoecium (cross-section)	Gynoecium, Perianth	
		W. netzahualcoyotlii	*W. oaxacensis*	*W. diquiyuii*	*W. nathorstii*	*W. huitzilopochtlii*	*W. cuauhtemoci*	*W. oligosperma*	*W. sanjuanensis* sp. nov.	*W.* sp.1
	C									
1	D	(5.9) 20–45	20	(23) 34	(55) 110	35–40	100	30	2.7–4.5 immature 15.6 mature	35 p. (70 d)
2	Ps	3–6 (8)	4	?	(5) 15	?	?	?	2.5–3.2	?
3	R	(3) 5–12	?	14–15 conical shape	?	6–8 'small cone'?	?	?	?	23 Semi-circular?
4	S-Is	poly, hexa, penta, elongated, fuse	poly, penta	poly	penta-hexa, to rounded	?	?	?	hexa	hexa
5	Ds-i	1–1.7 (3)	0.8–2	0.5–1	2	?	?	?	0.9–0.8	0.6–1.2
6	Md	0.5–1.8	<0.1–0.2	?	0.5	?	?	?	0.1	0.25
7	S/Ow	?	?	1.13	?	?	?	6	?	1.5 scale 1.1 ovule
8	S/Ol	?	?	6–10	?	?	?	12	?	6 scale 5 ovule 1 micropyle
9	Br	?	?	?	?	6–8	16	?	10–12	5 (11)
10	Bl	?	?	?	?	12–25	70–90	?	14.9	42
11	Bw	?	?	?	?	3–6	10–12	?	1.8	?
13	Bm	?	?	?	?	lanceolate	lanceolate	?	linear to lanceolate	?
	Fm	Ay, Tg, Ot, R? Z, Zt	Ay, Z, Zt	Z	Ay, R?	R? Z	R?	Ay	Z	Zt

Table 1. Abbreviations. **C:** character; 1. **D:** External outline diameter, **p:** preserved, **d:** character deduced; 2. **Ps:** diameter of peduncle scar; 3. **R:** receptacle; 4. **S-Is:** Seminal and interseminal scale shape; 5. **Ds-i:** diameter of the head of the seminal and interseminal scales on the surface; 6. **Md:** micropyle diameter; 7. S/**Ow:** seed/ovule width; 8. **S/Ol:** seed/ovule length; 9. **Br:** bracts; 10. **Bl:** Bracts length; 11. **Bw:** Bracts width; 13. **Bm:** Bracts morphology; **Fm:** Formation; **Ay:** Ayuquila; **Tg:** Tecocoyunca group; **Ot:** Otlaltepec; **R:** Rosario; **Z:** Zorrillo; **Zt:** Zorrillo/Taberna undifferentiated; **poly:** Polygonal; **hexa:** Hexagonal; **penta:** Pentagonal. Data in parentheses are exceptional cases, variations or deduced from the specimens. Characters taken from Delevoryas and Gould (1973); Silva-Pineda (1984); Velasco-de León (1990); Delevoryas (1991).

the whole southern Mexico, which is *Williamsonia sanjuanensis* (Table 1), described here (see above). *Williamsonia* sp.1 differs from *W. sanjuanensis* in external outline diameter, number, and length of the bracts, and micropyle diameter. In general *W.* sp.1 is larger in dimensions than *W. sanjuanensis* (Table 1).

In *Williamsonia* sp.1 we can observe the attachment, shape, and arrangement of the ovules and interseminal scales attached to the receptacle (Fig. 7A, C). The morphology of the ovules and interseminal scales, in non-petrified specimens, has been observed in the species *W. carolinensis* Pott et Axsmith from the Upper Triassic of North America (Pott and Axsmith, 2015), where the preservation of a gynoecium in cross section shows the shape of mature and immature ovules. When comparing the morphological characters of *Williamsonia carolinensis* with the specimen Ca342 this exhibits possibly immature ovules, since the micropyle was not yet exposed to the external surface of the gynoecium (Fig. 7C) and appears to have just started "anthesis". Furthermore, the bracts are observed surrounding the gynoecium (Fig. 7B), which could be related to its immature stage prior to "anthesis".

In this case, the gynoecium is partially incomplete, but its visible characters allow to propose a general morphology. Based on the preserved portion, the shape could be spherical with up to ~70 mm in diameter. Even though there are no traces of a crown, this characteristic is absent in all *Williamsonia* species in southern Mexico and could also be absent in the present case. The receptacle is partly visible and appears to be damaged in the central basal part (Fig. 7A–B). The damage could have been caused by degradation processes or even herbivory. The union between the receptacle, the scales, and the ovules is visible in the upper right part, and they are projected outwards (Fig. 7A, C). The bracts are observed surrounding the gynoecium (Fig. 7B). The visible number of bracts is five, arranged in two rows attached to the peduncle. It is possible that the total number of bracts is between 9 and 11, since the specimen is preserved in cross section. Moreover, the symmetry of several species of *Williamsonia* does not always have an even number of bracts (Popa, 2014; McLoughlin et al., 2018). The length of one of the best-preserved bracts is of 42 mm, but it could have been longer.

This is the second female flower of Bennettitales discovered and described in outcrops of the Middle Jurassic of northwestern Oaxaca, which increases the value of these outcrops according to paleontological criteria and the knowledge of the paleobotanic diversity of Bennettitales.

Genus: *Bennetticarpus* Harris, 1932

Bennetticarpus sp.1

Fig. 7D, E

Studied material: Zt17, 50, 65, 78.

Locality: Río Ñumí, Zorrillo/Taberna undifferentiated Formation.

Description: Adpressions of gynoecia of oval to semicircular shape in cross section, with an external outline diameter of ~36 mm. The receptacle is dome-shaped with 15–22 mm in diameter and up to 1 mm in height. The ovules and interseminal scales surround the receptacle. Scales are hexagonal with 1.5 mm in diameter and ~6–14 mm in length.

Remarks and discussion: Specimens CFZZt17, 50, 65, and 78 are preserved in cross section of the gynoecium. These specimens show characters like those described by Pott and Axsmith (2015) in *Williamsonia carolinensis* who have demonstrated a correspondence between adpressions and molds of the internal view (transversal and longitudinal) of several gynoecia (progressive stages of gynoecium development). However, Popa (2014) mentions that when characters are not sufficiently clear in order to accurately assign a genus of Bennettitales, the non-committal name *Bennetticarpus* is used. This genus was established by Harris (1932). Thus, we follow this nomenclature in order to determinate the studied specimens, since the characters, albeit visible, are few or incomplete. This prevents a comparison with the species proposed by Pott and Ashmith (2015) or any other species of reproductive organs of Bennettitales from southern Mexico (Silva-Pineda, 1984; Delevoryas and Gould, 1973; Delevoryas, 1991; Silva-Pineda et al., 2011) because the characters are not sufficiently clear in the studied

Table 2
List of fossil-species of *Williamsonia* from Middle Jurassic compared with *W. sanjuanensis* sp. Nov., and *W.* sp.1.

Taxon	Age	Occurrence	Reference
Williamsonia cuauhtemoci Wieland	Early–Middle Jurassic	Mexico	Silva-Pineda (1984)
Williamsonia danubii Dragastan et Băbulescu	Middle Jurassic	Romania	Dragastan and Băbulescu (1980)
Williamsonia diquiyui Delevoryas et Gould	Middle Jurassic	Mexico	Delevoryas and Gould (1973)
Williamsonia gigas Carruthers	Middle Jurassic	United Kingdom	Harris (1969)
Williamsonia hildae Harris	Middle Jurassic	United Kingdom	Harris (1969)
Williamsonia himas Harris	Middle Jurassic	United Kingdom	Harris (1969)
Williamsonia huitzilopochtlii Wieland	Middle Jurassic	Mexico	Silva-Pineda (1984)
Williamsonia iranica Vaez-Javadi	Middle Jurassic	Iran	Vaez-Javadi (2013)
Williamsonia leckenbyi Nathorst	Middle Jurassic	United Kingdom	Harris (1969)
Williamsonia netzahualcoyotlii Wieland	Middle Jurassic	Mexico	Silva-Pineda (1984); Delevoryas and Gould (1973)
Williamsonia nathorstii Wieland	Middle Jurassic	Mexico	Silva-Pineda (1984)
Williamsonia oaxacencis Delevoryas et Gould	Middle Jurassic	Mexico	Delevoryas and Gould (1973)
Williamsonia oligosperma Delevoryas	Middle Jurassic	Mexico	Delevoryas (1991)
Williamsonia parvula Schweitzer et Kichner	Middle Jurassic	Iran	Schweitzer and Kichner (2003)
Williamsonia sanjuanensis sp. nov.	Middle Jurassic	Mexico	This study
Williamsonia sp.1	Middle Jurassic	Mexico	This study

specimens.

On the other hand, *Williamsonia oligosperma* is a species established based on a single specimen (Delevoryas, 1991). This specimen is preserved in cross section and shows morphological similarity to specimens here assigned to *Bennetticarpus*. The only data provided by Delevoryas (1991) are the diameter (30 mm) and width and length of the seeds (6 mm and 12 mm, respectively), without further details. The author discussed the proportion of seeds present in *Williamsonia* species but did not mention the number present in *W. oligosperma*. Based on the data provided by Delevoryas (1991) and the poorly preservation of the single specimen, we consider that it should be reassigned to *Bennetticarpus*.

Table 3
Synthesis of the lithofacies identified in the stratigraphic columns measured in the Zorrillo and Zorrillo/Taberna formations, based on Miall (2000, 2006).

Lithofacies code	Description	Sedimentary structures	Interpretation
Sr	Sand, medium to v. coarse, wavy and parallel strata from 4 to 65 cm.	Ripples and cross and parallel laminations, both fine occasionally decreasing grain gradation.	Lower flow regimen deposits.
Sh	Coarse sand mostly, medium and fine sand sometimes, coarse strata from 40 to 80 cm, lenticular discontinuous to irregular. High content of coarse quartz.	Horizontal lamination, occasionally gradation decreasing grain.	Deposit with subcritical or critical flow.
Ss	Sand coarse, strata with erosive base, mainly contained in quartz clasts.	Shallow scours.	Shallow erosive cavities.
Sm	Fine to very coarse sand, medium to very coarse strata from 30 to 150 cm. Occasional wedged strata. Fossilized plant fragments.	Massive, with occasional faint parallel laminations, occasionally decreasing grain gradation.	Small channels, collapse of sandbanks.
Fl	Siltstone and carbonaceous lutite in medium and very coarse tabular strata from 10 to 110 cm. Fine sandstone in medium tabular strata from 9 to 30 cm. Some wave surfaces and abundant content of plant fossils.	Fine lamination and discontinuous. Decreasing grain gradation.	Floodplain deposits.
Fm	Carbonaceous lutite strata medium rare plant fossils.	Massive.	Distal floodplain, or overflow reservoirs.
Fr	Fine sandstone in coarse to v. coarse tabular strata, 30–150 cm. Some plant fossils.	Roots, bioturbation.	Incipient soils, periods of no deposit in floodplains with vegetation.
C	Coal (Kerosene) and carbonaceous lutite.	Plants (leaves, reproductive organs, barks, roots).	swamp deposits with abundant surrounding vegetation.

4.2. Lithological description and sedimentary environment of the studied localities

The sedimentary environments of the Rosario, Otlaltepec, Ayuquila, and Tecomazúchil formations have been recently proposed based on facies analysis (Campos-Madrigal et al., 2013; Martini et al., 2017; Zepeda-Martínez et al., 2018). Therefore, we only provide an analysis of data from the study localities: San Juan Mixtepec, Cañada Alejandro, and Río Ñumí.

4.2.1. San Juan Mixtepec locality, Zorrillo Formation

The San Juan Mixtepec locality is in the south of the municipality of the same name, in northwestern Oaxaca. It is part of the sedimentary basin of Tlaxiaco (Fig. 1). The partial stratigraphic column A (Fig. 8) is 5.40 m in thickness and has the following identified facies: Fm, Fl, Sm, and Sh (Table 3; Fig. 8). This section essentially corresponds to the whole fossil zone, since, due to the nature of the outcrop, the adjacent portions are covered by landslide deposits and/or vegetation. Strata are fine to coarse, lenticular discontinues, subparallel, and are composed of carbonaceous lutite and very fine to coarse sandstone. Some strata present parallel to ripple lamination. The column consists of 12 differentiated levels, and fossils were found in 2, 6, 7, and 10 levels (Fig. 8). The levels 1 and 2 present a fining-upward granulometry of medium to fine sandstone and parallel lamination, which is weak in some cases (Sm and Sh lithofacies; Fig. 8). There are records of well-preserved plant fossils in the upper part of 2 level. The level 3 presents wedged coarse strata of fine sandstone with parallel lamination. Level 4 consists of carbonaceous lutite at the top of the strata with plant fragments that are taxonomically unidentifiable (Fm lithofacies; Fig. 8). The 5 level is a coarse stratum of medium sandstone without structures or fossils. The area between levels 6 and 7 contains the main richness of plant fossils, including the here described new species *Williamsonia sanjuanensis.* These levels consist of an intercalation of fine to coarse strata of very fine, fine, and medium sandstone. The level 6 is composed of an intercalation of 4–9 cm strata of very fine-to medium-grained- sandstone with discontinuous, parallel, semi-ripple lamination (Lithofacies Fl;

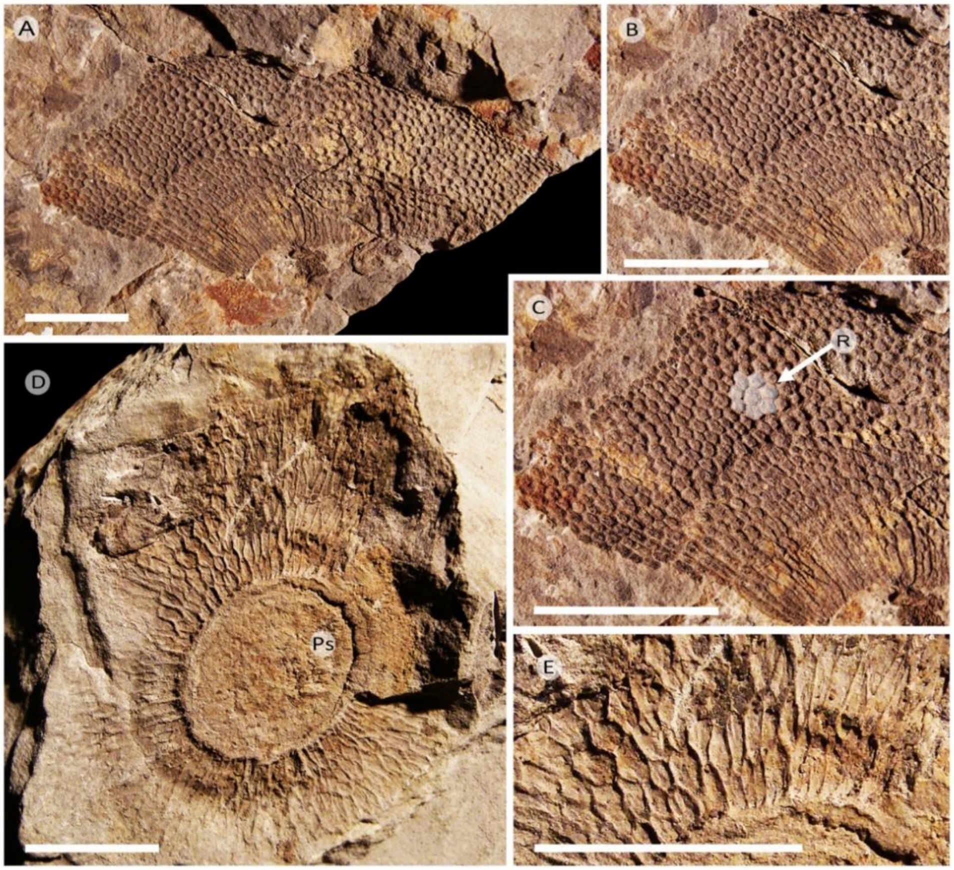


Fig. 6. *Williamsonia nathorstii* from Zorrillo/Taberna undifferentiated Formation in the Cañada Alejandro locality. B and C. Close-up of image A, where rosettes (R) of 6–7 scales are observed, specimen Ca56. D. The peduncle scar (Ps) and the interseminal scales surrounding it are observed, specimen Ca303. E. Close-up where the rosettes formed by seminal and interseminal scales are observed, specimen Ca303. Scale bars = 10 mm in all imagens.

Fig. 8). This is the level with the highest abundance of fossil material. Level 7 is composed of a wedged stratum with few fossils. The subsequent levels (8–12) consist of intercalations of fine-to medium-grained sandstone and carbonaceous lutite with occasional plant fossils, corresponding mainly to ferns.

If we consider the macroscopic characteristics of the strata, the facies, and the state of preservation of the fossils described here, San Juan Mixtepec locality would correspond to an area in the floodplain of a fluvial environment of the Tlaxiaco basin. Morán-Zenteno et al. (1993), infer a floodplain environment with swampy zones, and coal strata in the vicinity of the locality would indicate the presence of swamps in the floodplain (Miall, 2000, 2006). However, thus far, the location of these strata has not been correlated with the fossiliferous locality, but the facies association shows a clear cyclicality in the deposit. Sandy facies indicate overflows resulting from the collapse of the banks of the main channel with occasional critical flow (Miall, 2000, 2006). Fine sediments were deposited when these overflows reduced their energy during lower flow regime conditions (Fm, Fl lithofacies), which favored a higher concentration of leaves and reproductive organs. Fm lithofacies strata represent distal deposits in the floodplain (Miall, 2006). This could indicate that the zone was relatively distant from the main channel or related to an abandoned channel that reactivated during the events of highest energy (Sm, Sh lithofacies).

The stratigraphic location within the whole column of the Zorrillo Formation is difficult to establish, since the contact with the basal unit (Cualac Formation) could not be identified due to the influence of regional and local faults that complicate making correlations between stratigraphic units.

4.2.2. *Río Ñumí locality, Zorrillo/Taberna undifferentiated Formation*

The Río Ñumí locality contains three fossil zones, ZtA, ZtB, and ZtC (where Zt is the abbreviation of Zorrillo/Taberna and A, B, C, are de sets of fossiliferous levels) and is in the sedimentary basin of Tlaxiaco. Zone ZtC is located between 290 and 305 m and is characterized by a high content of plant fossils (leaves, flowers, branches, and roots) in coal, carbonaceous lutite, and fine sandstone strata (Lozano-Carmona and Velasco-de León, 2016). In zone ZtC, we measured the partial stratigraphic column B of 6 m (Fig. 8) and established the levels of the study flora. The lithofacies identified in this section were C, Fr, and Fl (Table 3; Fig. 8). The section consists of intercalations of tabular strata with 30–150 m of fine sandstone with poorly visible sedimentary structures and roots (Fr lithofacies; Fig. 8) and lenticular strata of siltstone and carbonaceous lutite with fine, continuous-discontinuous, planar-parallel lamination (Fl lithofacies; Fig. 8) of 20–100 cm in thickness. The limit of levels 9 and 10 exhibits an exposed surface of ±23 m^2 with borings of the ichnospecies *Gastrochaenolites* cf. *ornatus* (Lozano-Carmona et al., 2016). Levels 2, 4, 6, and 8 are composed of fine to very fine sandstone and present tube-type bioturbation by an undefined ichnotaxon.

The reproductive organs described in the present study were found between levels 5 and 6. Level 3 only contained leaves of *Zamites* and *Otozamites*. Roots were observed to perpendicularly run along up to three stratigraphic levels between levels 2 and 7. Fossils of level 8 consist of poorly preserved impressions of leaves and barks. Coal strata (C lithofacies; Fig. 8) are located towards the base of this section. A recent

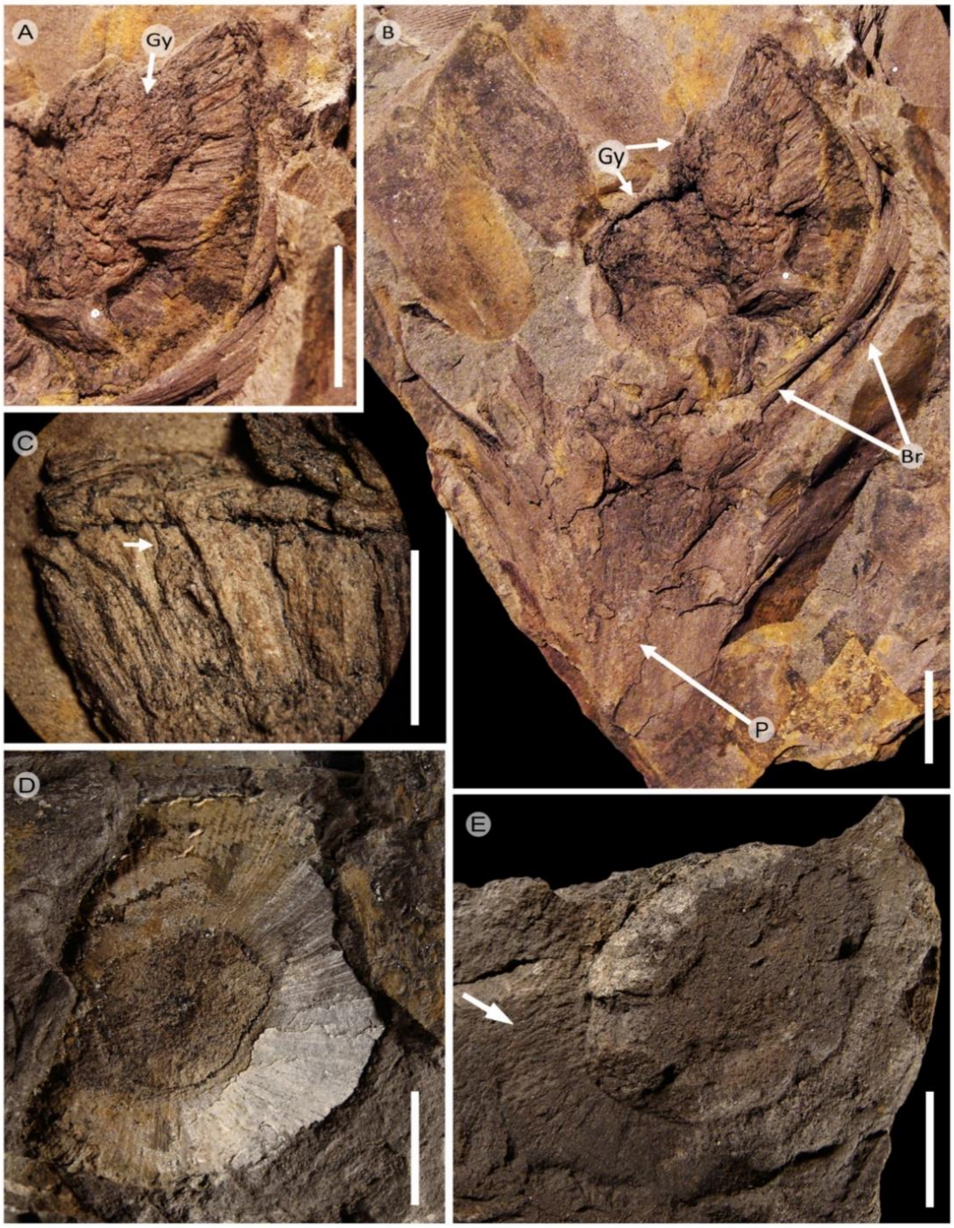


Fig. 7. *Williamsonia* sp.1 from Zorrillo/Taberna undifferentiated Formation in the Cañada Alejandro locality, specimen Ca342. A. Close-up to the gynoecium, where the interseminal and seminal scales attached to the receptacle (R) are observed. B. The entire specimen is observed in organic connection: gynoecium (Gy), bracts (B) and peduncle (P); here the gynoecium is observed whit a possible damage of herbivory or degradation processes. C. Close-up where the micropyle and an undeveloped ovule (arrowhead) are observed. D–E. *Bennetticarpus* sp.1 from Zorrillo/Taberna undifferentiated Formation in the Río Ñumí locality. D. The peduncle scar and slightly preserved scales are seen surrounding it, specimen Zt65. E. The receptacle is seen surrounded by some interseminal or seminal scales (arrowhead), specimen Zt50. *Scale bars* = 10 mm in A, B, D, E; 5 mm in C.

analysis of these coal strata indicates that vitrinite is their main component, which is a type 3 kerogen. Type 3 kerogen is manly derived from tissues of leaves, stems, roots, and woods of medium maturity (Piedad-Sánchez, 2016 com. pers.).

Therefore, based on the facies analysis, type of strata, and fossil content, we can infer sedimentation conditions that correspond to a floodplain with swampy zones and an abundant vegetation cover (Miall, 2006). Carrasco-Ramírez et al. (2016), proposed that the deposit of the Zorrillo/Taberna undifferentiated Formation resulted from a continuous subsidence of the basin. These authors interpreted the environment of the deposit as two scenarios: (1) coastal swampy and (2) a fluvial system; both comprising a delta system. The association of facies identified in the Río Ñumí locality presents evidence that allows to define zone ZtC as an area relatively distant from overflow areas of the main fluvial system and with weak traction currents. Plant organs were buried mainly as a result of mild contributions of fine sediments. In this area, the floodplain had an abundant vegetation cover and incipient soil development was possible when low flow regimes were absent. Level 10 contained records of abundant *Gastrochaenolites* cf. *ornatus* (Lozano-Carmona et al., 2021), which leads to the assumption that the environment was invaded by marine transgressions. Thus, it is possible to ascertain that zone ZtC corresponds to the sedimentary environment proposed by Carrasco-Ramírez et al. (2016), as the two scenarios associated with a delta system.

4.2.3. *Cañada Alejandro locality, Zorrillo/Taberna undifferentiated Formation*

The Cañada Alejandro locality is part of the sedimentary basin of Tlaxiaco (Fig. 1). This locality is characterized by a high content of plant fossils (Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019), mainly in fine to medium sand strata. In the site "Las Mesas", we measured the partial stratigraphic column C of 10.45 m (Fig. 8) and

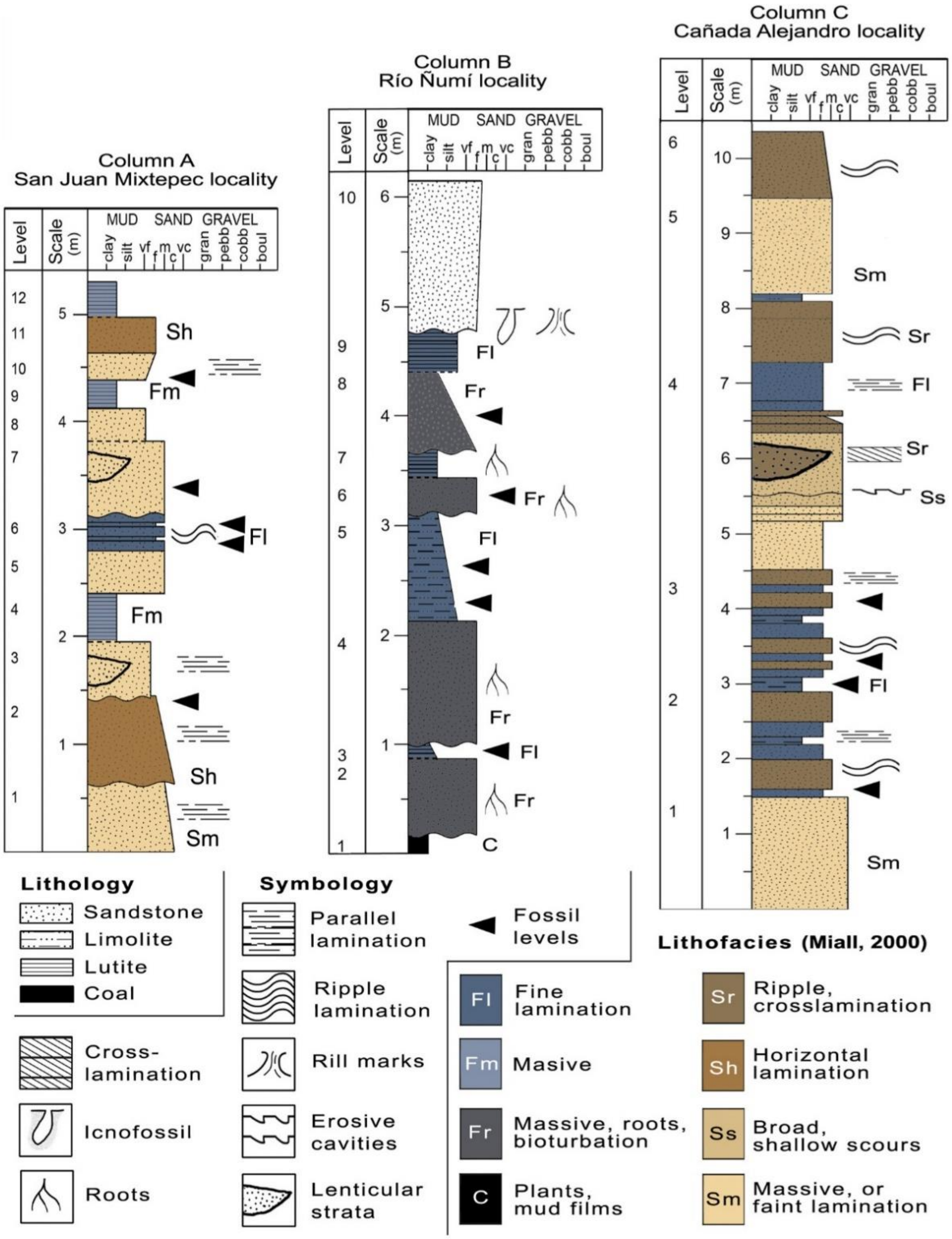


Fig. 8. Partial stratigraphic columns of the San Juan Mixtepec locality, Zorrillo Formation (column A), Río Ñumí locality (column B) and Cañada Alejandro locality (column C) both from Zorrillo/Taberna undifferentiated Formation. For detailed descriptions of lithofacies refer to Table 3.

identified the lithofacies Sm, Ss, Sr, and Fl (Table 3; Fig. 8).

This column is composed of very fine and coarse strata, primarily of fine, medium, and coarse sandstone, with a few intercalations of fine strata of siltstone (Fig. 8). The first level consists of 1.5 m of very coarse-grained sandstone without visible sedimentary structures (Sm lithofacies, Fig. 8). The fossiliferous zone begins on the second level, which is 3 m in thickness and is composed of intercalations of very fine -to medium grain-sandstone and fine strata of siltstone. The thicknesses of the strata range between 1 and 4 cm and occasionally exceed 10 cm. Strata are semitabular, parallel, and with ripple lamination (ripples in transversal view) and occasionally with fine, parallel lamination (Fl and Sr lithofacies; Fig. 8). Level 4 is composed of intercalations of strata of fine to coarse sandstone. Thin to medium strata (between 6.5 and 9 cm) can be observed in the basal part, and a 92 cm set of coarse sandstone is observed above these strata, which is characterized by an erosive base (Ss lithofacies, Fig. 8) and wedged strata with cross-lamination (Sr lithofacies, Fig. 8). The end of this level and the contiguous levels 5 and 6 consist of 3 m of intercalations of discontinuous strata of fine-to medium grain-sandstone with a linear base and, ripple lamination discontinuous and weak.

Based on the facies association and the structure of the strata, we can infer a floodplain environment with overflow deposits resulting from the breaking of the lateral banks of the central channels of the basin (Miall, 2000, 2006). In this zone, the deposit dynamics showed intercalations of

Table 4
Bennettitales registered in basins and lithostratigraphic units from Jurassic in northwestern Oaxaca (see also Figs. 1 and 2).

	Tezoatlán basin	Tlaxiaco basin		Ayuquila basin	
	Rosario Fm.	Zorrillo Fm.	Zorrillo/Taberna undiff. Fm.	Ayuquila Fm.	Tecomazúchil Fm.
Bennettitales					
Zamites lucerensis	X	X	X	X	X
Zamites tribulosus	X		X	X	X
Zamites oaxacensis	X	X	X	X	
Williamsonia netzahualcoyotlii	X	X	X	X	
Otozamites hespera	X		X	X	
Ptilophyllum acutifolium	X		X	X	
Williamsonia nathorstii	X		*	X	
Anomozamites sp.1	X	X	X		
Williamsonia huitzilopochtlii	X	X			
Zamites diquiyui	X	X			
Otozamites mandelslohi	X		X		
Williamsonia oaxacensis		X	X	X	X
Zamites feneonis			X	X	X
Ptilophyllum cutchense			X	X	
Anomozamites angustifolium			X	X	
Ptilophyllum sp.			X	X	
Pterophyllum sp.			X		X
Cycadolepis mexicana	X				
Pterophyllum sp. cf. *P. munsteri*	X				
Weltrichia mexicana	X				
Williamsonia cuauhtemocii	X				
Williamsonia diquiyui		X			
Williamsonia sanjuanensis		*			
Zamites truncatus			X		
Otozamites obtusus			X		
Otozamites paratypus			X		
Ptilophyllum pulcherrium			X		
Pterophyllum nathorsti			X		
Anomozamites triangularis			X		
Anomozamites sp. cf. *A. triangularis*			X		
Anomozamites sp. cf. *A. intermedium*			X		
Williamsonia sp. 1			*		
Bennetticarpus sp. 1			*		
Weltrichia sp.			X		
Williamsoniella sp.			X		
Williamsonia oligosperma				X	
Weltrichia ayuquilana				X	
Weltrichia microdigitata				X	
Weltrichia mixtequensis				X	
Weltrichia xochitetlii					X
cf. *Wielandiella* sp.				X	
Williamsonian stems	X				

Original sources by stratigraphic unit: Rosario (Person and Delevoryas, 1982; Silva-Pineda, 1984). Zorrillo (Delevoryas and Gould, 1973; Person and Delevoryas, 1982; Silva-Pineda, 1984). Zorrillo-Taberna (Lozano-Carmona and Velasco de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019). Ayuquila (Silva-Pineda, 1978; Delevoryas, 1991; Silva-Pineda et al., 2011; Velasco-de León et al., 2019). Tecomazúchil (Lozano-Carmona et al., 2021). (*) This study.

increased overflow events of small channels and a decreased contribution of fine and sandy sediments. The combination of intercalated deposit events and the vegetation cover adjacent to the deposit zone allowed the high preservation of plant organs. According to the environmental proposal by Carrasco-Ramírez et al. (2016), the locality of Cañada Alejandro would be corresponded to the fluvial system scenario of the delta complex.

4.2.4. Final comments from the environment of the fossiliferous localities

The sedimentary environments of the localities indicate variations in the deposit conditions, but they all generally correspond to a floodplain environment. Variations between localities are explained by their location, proximal or distal, with respect to the main channel or channels of the basin. However, despite the variations between the three localities, Bennettitales were the main vegetation, which indicates that this group was well adapted to the flooding conditions of the deposit environment. In this sense, the three localities exhibited cyclic flooding during the deposit (intercalation of sandy and fine lithofacies), which could be associated with seasonal precipitation.

4.3. Diversity and biostratigraphy of bennettitales in northwestern Oaxaca

Five lithostratigraphic units of the Lower–Middle Jurassic (Toarcian, Bajocian–Callovian) containing flora outcrops in northwestern Oaxaca. They are the Rosario (Toarcian), Zorrillo (Bajocian), Zorrillo/Taberna undifferentiated (Bajocian), Ayuquila (Bajocian–Bathonian), and Tecomazúchil (Callovian) formations (Fig. 2). The age of each of these units has been dated based on U–Pb analysis and ammonite biostratigraphy (Sandoval and Westermann, 1986; Campos-Madrigal et al., 2013; Zepeda-Martínez et al., 2018; see Fig. 2). Records of Bennettitales in this lithostratigraphic units are composed of 11 fossil-genera and 41 fossil-taxa (Table 4). 30 valid species and 11 species that need taxonomic revision (Delevoryas and Gould, 1973; Silva-Pineda, 1978; Person and Delevoryas, 1982; Silva-Pineda, 1984; Delevoryas, 1991; Silva-Pineda et al., 2011; Lozano-Carmona and Velasco de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019, 2021; Velasco-de León et al., 2019). Almost a quarter of the diversity of the Bennettitales of northwest Oaxaca needs taxonomic revision since some cases have not been resolved the affinity of the species or have remained as undefined species (Table 4).

Fig. 9. Stratigraphic ranges of the Bennettitales species in northwestern Oaxaca. To relate age to northwestern regions, sedimentary basins and lithostratigraphic formations, refer to Fig. 2 and Table 4.

Nevertheless, the formations with highest diversity are Zorrillo/Taberna undifferentiated with 27 species, Ayuquila with 17, and Rosario with 15. The formations with lowest diversity are Zorrillo and Tecomazúchil with 9 and 6 species, respectively (Delevoryas and Gould, 1973; Silva-Pineda, 1978; Silva-Pineda, 1984; Delevoryas, 1991; Silva-Pineda et al., 2011; Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019, 2021; Velasco-de León et al., 2019). The species with the highest number of records are *Zamites lucerensis*, *Z. tribulosus*, *Z. oaxacensis*, *Williamsonia netzahualcoyotlii*, and *W. oaxacensis*. Species that have been recorded in only one lithostratigraphic unit are *Pterophyllum* sp. cf. *P. munsteri* (Presl) Goeppert, *Cycadolepis mexicana* Wieland, *Weltrichia mexicana* Wieland, and *Williamsonia cuauhtemoci* in the Rosario Formation; *Williamsonia diquiyui* and *W. sanjuanensis* in the Zorrillo Formation; *Zamites truncatus* Zeiller, *Otozamites obtusus* (Lindley et Hutton) Brongniart, *O. paratypus* Wieland, *Ptilophyllum pulcherrium* Wieland, *Pterophyllum nathorstii* Schenk, *Anomozamites triangularis* (Nathorst) Pott et McLoughlin, *A.* sp. cf. *A. triangularis*, *A.* sp. cf. *A. intermedium* Antevs, *Williamsonia* sp.1, *Bennetticarpus* sp.1, *Weltrichia* sp., and *Williamsoniella* sp., in the Zorrillo/Taberna undifferentiated Formation; *Williamsonia oligosperma*, *Weltrichia ayuquilana* Delevoryas, *W. microdigitata* Delevoryas, *W. mixtequensis* Silva-Pineda et al., and cf. *Wielandiella* sp., in the Ayuquila Formation; and *Weltrichia xochitetlii* Lozano-Carmona et Velasco-de León in the Tecomazúchil Formation (Table 4). The diversity of organs, according to type, is composed of 22 leaf fossil-taxa, 19 fossil-taxa of reproductive organs, and a single record of stems associated with Williamsoniaceae.

When sorting the records by age, we observed that the species of the Lower–Middle Jurassic have a diverse stratigraphic range. However, it is important to note that the Cualac Formation, Aalenian in age (Zepeda-Martínez et al., 2018), in northwestern Oaxaca, does not have formal records of plant fossils. Because the only records of this unity were reported in theses and congress, therefore they record need mayor revision in taxonomic data. Thus, new findings could change the stratigraphic

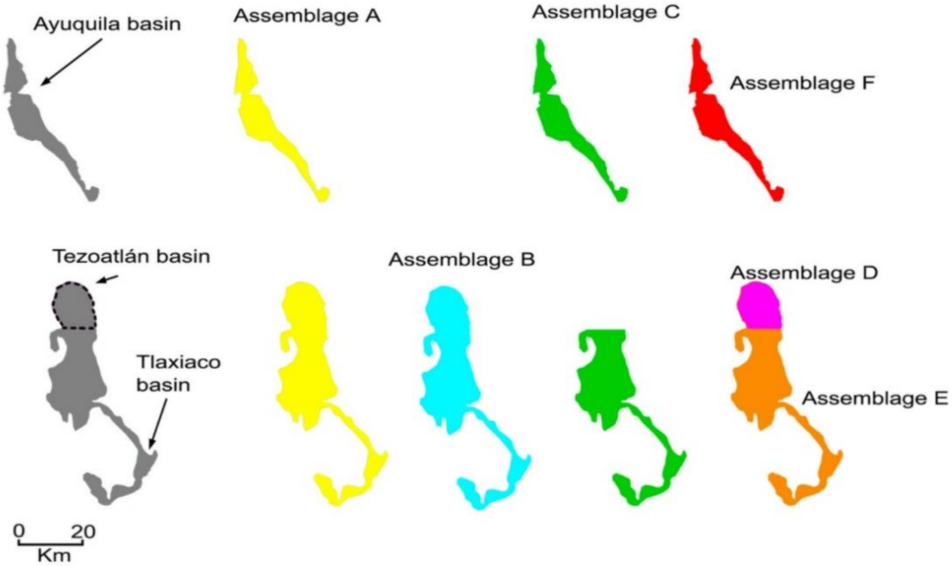


Fig. 10. Jurassic sedimentary basins in northwest Oaxaca (correlated Fig. 1) and the distribution areas of the Bennettitales assemblage. To review which species are in each assemblage, refer to section 4.4 and Table 4. Sedimentary basins area based in Campos-Madrigal et al. (2013), Martini et al. (2017), Zepeda-Martínez et al. (2018) and Oaxaca Geological-Mining Chart E14-9, scale 1: 250,000 from the Mexican Geological Service (SGM, 2000). Colors are to emphasize each assemblage. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

range of Bennettitales in this area. Presently, we can observe the following stratigraphic range (see Fig. 9). The species with mayor temporal range are *Zamites lucerensis* and *Zamites tribulosus*, 19 species have been recorded in only one age: Toarcian, Bajocian or Callovian, while 20 species have different stratigraphic ranges (Table 4, Fig. 9).

Species with a wide and restricted stratigraphic range allow us to define the biostratigraphy of northwest Oaxaca (Barragán et al., 2010). For example, *Zamites lucerensis* is the element that would define the continental Jurassic of northwestern Oaxaca, since it has been recorded in the five lithostratigraphic units of the region from the Toarcian to Callovian in age (Table 4 and Fig. 9). Therefore, we define the *Zamites lucerensis* Biozone, whose limits are the Rosario Formation, Toarcian in age, in El Consuelo area, Oaxaca (lower limit, 17°32′N; 97°52′W) and the Tecomazúchil Formation, Callovian in age, in Santa María Xochixtlapilco area, Oaxaca (upper limit, 17°46′N; 97°48′W). These limits are based on the lower and upper records of the species (Silva--Pineda, 1984; Lozano-Carmona et al., 2021). *Zamites lucerensis* is a foliar species, characterized by long and narrow segmented leaves. The leaflets are small and have a central callus at the base, which is the point of attachment to the spine (Silva-Pineda, 1984). The reference section for the *Zamites lucerensis* Biozone is the San Juan Mixtepec locality (see section 4.2.1)This biozone is based on the data obtained in the present study (Table 4, Fig. 9) and are assigned to the sedimentary cover of the Jurassic of northwestern Oaxaca (Figs. 1 and 2).

4.4. Phytogeography of Bennettitales in northwestern Oaxaca

The phytogeographic distribution of the Bennettitales in southern Mexico (including northwestern Oaxaca; Fig. 1) only has been analyzed by Velasco-de León et al. (2012), using a cluster analysis with six lithostratigraphic units. However, this analysis only considers the spatial variable and not the temporal variable in the Bennettitales record. In addition, they use lists of species that include thesis reports and conferences, but these reports need further review to avoid redundant or subjective distributions. On the other hand, the number of localities and the diversity of Bennettitales in southern Mexico has reviewed and increased considerably (Lozano-Carmona and Velasco-de León, 2016; Flores-Barragan et al., 2017; Lozano-Carmona et al., 2019, 2021; Velasco-de León et al., 2019). Therefore, when revisiting and updating the Bennettitales listings from northwestern Oaxaca in this study, we can observe that the phytogeographic distribution of Bennettitales in northwestern Oaxaca is complex since it is characterized by several spatio-temporal distribution relationships. This phytogeographic analysis was carried out with the intention of identifying the patterns of spatio-temporal consistency (Espinosa-Organista et al., 2001, 2002, ; Morrone and Escalante, 2016) of the Bennettitales in northwestern Oaxaca.

First, it is important to note that, in this analysis, the distribution areas of each fossil-taxon are the sedimentary basins of northwestern Oaxaca where is registered and only are considered valid species (Fig. 1, Table 4). These conditions are based on the proposals to identify areas of endemism of Müller (1973) and Espinosa-Organista et al. (2001). The distribution areas and their range chronostratigraphic correspond to the basins of Tezoatlán (Toarcian), Tlaxiaco (Bajocian), and Ayuquila (Bajocian-Callovian) in a temporal range of 19 Ma (Figs. 1, 2 and 10; Table 4). Thus, the distribution patterns among the Bennettitales are the following (see Fig. 10): assemblage A (*Zamites lucerencis*, *Z. tribulosus*, *Z. oaxacensis*, *Williamsonia netzahualcoyotlii*, *W. oaxacensis*, *W. nathorstii*, *Otozamites hespera*, *Ptilophyllum acutifolium*), distributed in the three basins; assemblage B (*Williamosnia huitzilopochtlii*, *Zamites diquiyui*, *Otozamites mandelslohi*), distributed in the Tezoatlán and Tlaxiaco basins; assemblage C (*Williamsonia oaxacensis*, *Zamites feneonis*, *Ptilophyllum cutchense*, *Anomozamites angustifolium*), distributed in the Tlaxiaco and Ayuquila basins; assemblage D (*Cycadolepis mexicana*, *Weltrichia mexicana*, *Williamsonia cuauhtemoci*), distributed only in the Tezoatlán basin; assemblage E (*Williamsonia diquiyui*, *W. sanjuanensis*, *Zamites truncatus*, *Otozamites obtusus*, *O. paratypus*, *Ptilophyllum pulcherrium*, *Pterophyllum nathorstii*, *Anomozamites triangularis*), distributed only in the Tlaxiaco basin; and assemblage F (*Williamsonia oligosperma*, *Weltrichia ayuquilana*, *W. microdigitata*, *W. mixtequensis*, *W. xochitetlii*), distributed in the Ayuquila basin (Table 4, Fig. 10).

Based on the identification of these consistent distribution patterns among the Bennettitales species we can propose that species from assemblage A, B, and D, are an ancestral element. Assemblage A and B were able to disperse in the region since their records begin in the Toarcian (Tezoatlán basin) and most of them extend to the Bathonian (Ayuquila basin). The elements of ensemble B dispersed only from the Tezoatlán basin to the Tlaxiaco basin and the elements of assemblage C appeared in the Tlaxiaco basin and dispersed as far as the Ayuquila basin. Assemblage D, E, and F include species that were restricted to a single basin (Table 4, Fig. 10). The relationships in the distributions of these assemblage could be associated with the activation of geological faults and sedimentary basins, which are processes derived from the fragmentation of Pangea. The activation of these faults and its influence on the sedimentary basins of Tezoatlán and Ayuquila has been recently documented by Campos-Madrigal et al. (2013) and Zepeda-Martínez et al. (2018).

During the deposit of the Rosario Formation in the Tezoatlán basin, the terrain was elevated but the Río Salado Fault was not active yet (Zepeda-Martínez et al., 2018), which possibly allowed the dispersion of assemblage A and B. During the tectonic activity of the Bajocian, the Tlaxiaco basin was influenced by a continuous subsidence and presented an environment of lowlands and floodplains (Morán-Zenteno et al., 1993; Carrasco-Ramírez et al., 2016), which allowed the establishment of assemblage A, B, C, and E. The Ayuquila basin exhibited the most continental position and the most distant from the marine transgressions, as well as an elevated terrain (Campos-Madrigal et al., 2013), which favored assemblage A, C, and F. Thus, we can identify that, the variations in the distribution of taxa of Bennettitales were influenced by the tectonic activity of the basins and the climatic variations that occurred from the Lower to Middle Jurassic (Ortiz-Martínez et al., 2013).

Finally, the spatio-temporal integration of Bennettitales allows to observe possible areas of endemism (Espinosa-Organista et al., 2001), since there is overlap in the distribution areas of more than two species between the sedimentary basins of northwestern Oaxaca. However, this hypothesis needs to be tested based on biogeographic quantitative methods in order to avoid bias (Espinosa-Organista et al., 2001; Noguera-Urbano, 2016). Presently, we establish the distribution patterns of Bennettitales shown in the present study through the overlap of the distribution areas of the studied taxa and the identification of their spatio-temporal consistency (Müller, 1973).

5. Conclusions

The new data and analyses presented here are fundamental for our understanding of the paleoflora of the Jurassic on western margin of equatorial Pangea since this information was obtained from one of the few sites in the region with paleofloristic records. Bennettitales were the main element of the paleofloristic diversity from northwestern Oaxaca, Mexico and its study are allowing us to discover its diversity and patterns of temporal and spatial distribution. The sedimentological analysis of the fossiliferous localities allows us to recognize the environmental dynamics and the deposit of the different fossiliferous elements in each locality. With this, the plant-environment interaction in this region can be analyzed. The biozone proposed will allow to determine and identify the limits between the lithostratigraphic units of the Jurassic of northwestern Oaxaca. In addition, the distribution patterns of Bennettitales in northwestern Oaxaca show the possibility of performing phytogeographic analyses through methodologies that allow to establish areas of endemism and contribute to a phytogeographic regionalization of the Jurassic.

Authorship statement

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication. Conception and design of study: Diego E. Lozano-Carmona. Acquisition of data: Diego E. Lozano-Carmona and María Patricia Velasco de León. Analysis and/or interpretation of data: Diego E. Lozano-Carmona and María Patricia Velasco de León. Drafting the manuscript: Diego E. Lozano-Carmona.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CUARTO CAPÍTULO

Análisis de trazos de las Bennettitales (familia Williamsoniaceae) del Jurásico

- **Lozano-Carmona, D. E.** Propuesta y diseño del trabajo; revisión de los ejemplares e identificación taxonómica; recopilación de datos de distribución y consulta bibliográfica; depuración de base de datos; análisis e interpretación de datos fitogeográficos; elaboración de figuras; redacción del manuscrito.
- **Velasco-de León, M. P.** Dirección, revisión del trabajo y del manuscrito.

Análisis de trazos de las Bennettitales (familia Williamsoniaceae) en el Jurásico

Track analysis of the Bennettitales (Williamsoniaceae family) from the Jurassic

Diego E. Lozano-Carmona [a,b,*], M. Patricia Velasco-de León [b]

[a] *Posgrado en Ciencias Biológicas, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Ciudad de México, C.P. 09230, México*

[b] *Colección de Paleontología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Ciudad de México C.P. 09230, México.*

RESUMEN

Las Bennettitales son un orden de gimnospermas extinto con un importante significado evolutivo y su distribución espaciotemporal alcanzó ambos hemisferios durante el Mesozoico. En el Jurásico la familia Williamsoniaceae alcanzó una distribución hasta la margen occidente de la Pangea ecuatorial que incluye a México con registros de órganos foliares y reproductivos. Los registros mejor documentados en Norteamérica son los del sur de México. Por lo tanto, se presenta el primer análisis de trazos (método panbiogeográfico) de la familia Williamsoniaceae (Bennettitales) para el Jurásico. Este análisis comprende los registros de ocho géneros a nivel mundial: cinco corresponden a órganos foliares (*Anomozamites*, *Otozamites*, *Pterophyllum*, *Ptilophyllum*, *Zamites*) y tres a órganos reproductivos (*Weltrichia*, *Williamsonia*, *Williamsoniella*). Se identificaron 23 trazos individuales y cinco generalizados (Gt) (Gt1 Laurásico-Gondwánico y Gt2 Chino para el Jurásico Temprano; Gt3 Laurásico y Gt4 Gondwánico en el Jurásico Medio y Gt5 Gondwánico del norte-Euroasiático). Así como dos nodos (N) en el Jurásico Medio: N1 Mesoamericano y N2 Arábico. La relación de estos patrones de distribución con la dinámica tectónica del Jurásico permite evaluar una congruencia entre estos. La fragmentación de Pangea, durante este periodo, y la consecuente evolución ambiental continental de Laurasia y Gondwana son los eventos que nos permiten sugerir como eventos vicariantes que modelaron la distribución y posible provincialismo de los taxones a través del Jurásico.

Palabras clave: Mesozoico, Palaeoflora, Pangea ecuatorial occidental, Gimnospermas, Panbiogeografía.

Abstract

The Bennettitales are an extinct order of gymnosperms with important evolutionary significance and their spatiotemporal distribution reached both hemispheres during the Mesozoic. In the Jurassic, the Williamsoniaceae family reached a distribution up to the western margin of equatorial Pangea that includes Mexico with records of foliar and reproductive organs. The best documented records in North America are those from southern Mexico. Here we present the first track analysis (panbiogeographic method) of the family Williamsoniaceae (Bennettitales) for the Jurassic. This analysis includes the records of eight genera worldwide: five correspond to foliar organs (*Anomozamites*, *Otozamites*, *Pterophyllum*, *Ptilophyllum*, *Zamites*) and three to reproductive organs (*Weltrichia*, *Williamsonia*, *Williamsoniella*). Twenty-three individual and five generalized (Gt) tracks were identified (Laurasic-Gondwanan Gt1 and Chinese Gt2 for the Early Jurassic; Laurasic Gt3 and Gondwanan Gt4 in the Middle Jurassic and Gondwanan Gt5 from the North-Eurasian). As well as two nodes (N) in the Middle Jurassic: Mesoamerican N1 and Arabic N2. The relationship of these distribution patterns with the tectonic dynamics of the Jurassic allows to evaluate a congruence between them. The fragmentation of Pangea, during this period, and the consequent continental environmental evolution of Laurasia and Gondwana are the events that allow us to suggest vicariant events that shaped the distribution and possible provincialism of the taxa through the Jurassic.

Keywords: Mesozoic, Palaeofloristic, Western equatorial Pangea, Gymnosperms, Panbiogeography.

INTRODUCCIÓN

Las Bennettitales son un orden de gimnospermas extintas. Fueron plantas que se existieron del Triásico al Cretácico, con un aparente último refugio en Australia durante el Oligoceno. Sus registros indican que tuvieron una distribución en ambos hemisferios durante el Mesozoico. Pero, en el Jurásico fueron raras en los reinos paleoflorístico de Angara (en el norte) y Gondwana (en el sur), y abundantes en el Reino de Laurasia (Anderson *et al*., 2007; Taylor *et al*., 2009; McLoughlin *et al*., 2011). Se han clasificado dos familias dentro de las Bennettitales, la primera de ellas es Cycadeoidaceae la cual se ha registrado principalmente en el Cretácico, mientras que la familia Williamsoniaceae dominó desde el Triásico Tardío y todo el Jurásico, pero hay pocos registros en el Cretácico (Stockey y Rothwell, 2003; Anderson *et al*., 2007; Taylor *et al*., 2009; Popa, 2019). La familia Williamsoniaceae incluye plantas con ramificaciones delgadas, de aproximadamente 2 metros de altura, órganos reproductivos tipo-flor unisexuales (*Williamsonia*, *Weltrichia*, *Wielandiella*) o bisexuales (*Williamsoniella*) y órganos foliares segmentados tipo-cycadas (p. e. *Anomozamites*, *Pterophyllum, Ptilophyllum, Zamites, Otozamites*) (Harris, 1969; Watson and Sincock, 1992; Taylor *et al*., 2009; Pott, 2014; Pott & McLoughlin, 2014; Popa, 2019).

Recientemente ha resurgido un interés en las Bennettitales debido al posible rol en la evolución de las angiospermas y otras plantas con semilla. Sin embargo, la posición filogenética de las Bennettitales aún es debatida. Por un lado, se ha considerado como el grupo hermano de las angiospermas (Crane, 1985; Watson & Sincock, 1992; Friis *et al*., 2011), mientras que, por otro lado, las Bennettitales han sido propuestas como un clado independiente (Rothwell *et al*., 2009). Sin embargo, los órganos reproductivos uni- y bisexuales son considerados como una evidencia evolutiva en las estrategias reproductivas de las gimnospermas antes de la aparición de las plantas con flor (Harris, 1969; Popa, 2014; Pott, 2014; McLoughlin *et al.*, 2018).

En este sentido, durante el Mesozoico temprano–medio la diversidad de las Bennettitales, de la familia Williamsoniaceae, permite observar una distribución cosmopolita de los géneros, pero con una provincialización de las especies y con la existencia de varios endemismos (Harris, 1969; Popa, 2014, 2019; Pott, 2014; Pott & McLoughlin, 2014; Pott & Axsmith, 2015; Pott *et al*., 2015; McLoughlin *et al*., 2018; Lozano-Carmona *et al*., 2019, 2021; Xu *et al*., 2019). Sin embargo, los procesos evolutivos y fitogeográficos de estos patrones han sido poco estudiados o aún no son claros. No obstante, algunas propuestas de análisis fitogeográficos del Jurásico, que incluyen a las Bennettitales, entre otros grupos de plantas, han permitido observar varios patrones de distribución de locales a regionales. Sin embargo, la base teórica de estos análisis ha sido principalmente la comparación cualitativa de los listados paleoflorísticos (Meyen, 1987; Wang *et al*., 2008; Pott & McLoughlin, 2009; Pott *et al*., 2016; Na *et al*., 2017) y pocos análisis cuantitativos (Velasco-de León *et al.,* 2012; Barbacka *et al*., 2014). Por otro lado, estudios con enfoque en la distribución ecológica a nivel mundial han propuesto la existencia de cinco biomas durante el Jurásico con base en las composiciones paleoflorísticas de distintas localidades del mundo y diferentes proxis geoquímicos (Rees *et al.*, 1999, 2004; Ziegler *et al.*, 2003; Philippe *et al.*, 2004). Por lo tanto, el objetivo de este estudio fue realizar un análisis de trazos de los ocho géneros con validez taxonómica de la familia Williamsoniaceae (Bennettitales) para identificar patrones de distribución y analizarlos desde la perspectiva biogeográfica histórica (Croizat, 1958; 1964; Craw *et al.*, 1999; Morrone, 2009, 2015).

La biogeografía histórica es un enfoque que analiza los patrones de distribución de los taxones a escalas espaciales y temporales amplias (Morrone, 2009). El análisis de trazos o método panbiogeográfico (Croizat, 1958; 1964; Craw *et al.*, 1999; Morrone, 2009, 2015) permite identificar la congruencia de los patrones de la distribución geográfica de una biota y la representación hipotética de la extensión de su biota ancestral, que subsecuentemente fue fragmentada por cambios geológicos o climáticos (Morrone & Crisci, 1995; Morrone, 2004, 2015). En otras palabras, es un método donde se presupone una evolución conjunta entre las biotas y las barreras geográficas, y que permite llevar a cabo una exploración inicial de los datos hacia la identificación de homología biogeográfica primaría (Morrone, 2004). Por lo tanto, aplicando este método se obtuvieron 23 trazos individuales y cinco generalizados, así como dos nodos en el Jurásico Medio. Relacionando estos patrones con los procesos tectónicos de Pangea durante el Jurásico permite evaluar la congruencia ente ambos. Es decir, la distribución fitogeográfica con la fragmentación de Pangea. Los cambios en ambos patrones, fitogeográfico y tectónico, son los que nos permiten sugerir que eventos vicariantes modelaron la distribución y el posible provincialismo de la familia Williamsoniaceae a través del Jurásico.

MATERIAL Y MÉTODOS

El método panbiogeográfico presupone una evolución conjunta entre las biotas y las barreras geográficas y destaca la relevancia de las distribuciones geográficas como objeto de análisis, así permite que los patrones y procesos evolutivos sean comprendidos adecuadamente (Croizat, 1958, 1964; Craw *et al.*, 1999). El primer paso del método de análisis de trazos es conectar las localidades en donde se tiene registro de distribución de un taxón mediante un árbol de tendido mínimo. Así se obtiene un trazo individual el cual representa las coordenadas primarias de un taxón en el espacio, es decir el sector del espacio en el cual la evolución de ese taxón tuvo lugar. Posteriormente, si es posible se orientan los trazos para formular hipótesis sobre la secuencia de sus disyunciones. Si al comparar dos o más trazos individuales se reconoce una coincidencia o semejanza se determina un trazo generalizado, el cual representa una biota ancestral que fue fragmentada por eventos geológicos y/o climáticos. Por último, sí se superponen dos o más trazos generalizados en un área, esta será considerada como un nodo. Los nodos son áreas complejas que representan convergencia de fragmentos bióticos y geológicos (Croizat, 1958, 1964; Morrone & Crisci, 1995; Morrone, 2009, 2015).

Para obtener los trazos individuales, primero se recopilaron las paleocoordenadas de localidades con registros de ocho géneros (*Anomozamites*, *Otozamites*, *Pterophyllum*, *Ptilophyllum*, *Weltrichia*, *Williamsonia*, *Williamsoniella*, *Zamites*) de la familia Williamsoniaceae (Bennettitales) de las tres épocas del Jurásico. La recopilación de estas paleocoordenadas se realizó en las bases de datos de los sitios web Fossilworks y PaleobiologyDatabase (paleobiodb.org; fossilworks.org). También se incluyeron las paleocoordenadas estimadas obtenidas de los artículos revisados en este trabajo. Las bases de datos se depuraron eliminando recurrencias (datos duplicados) de georreferencias (Anexo 1, Tabla 1-3). Los trazos individuales se construyeron empleando el programa ArcView GIS 3.2 (ESRI, 1999) y la extensión Trazos2004 (Rojas, 2007). Cabe aclarar que ArcView trabaja con mapas geográficos actuales por lo que se emplearon paleomapas del Jurásico (Scotese, 2014) georeferenciados con la herramienta Georreferenciador GDAL del programa QGIS 2.6. Los trazos generalizados fueron determinados con base en la congruencia de los trazos individuales a través del método manual (Morrone & Crisci, 1995; Morrone, 2009, 2015). Los mapas y trazos fueron editados con PhotoShop CC 2019 para una mejor representación gráfica siguiendo las propuestas de Fortino & Morrone (1997).

RESULTADOS

Veintitrés trazos individuales fueron construidos (Figuras 1-6). Los trazos individuales para cada época del Jurásico están constituidos por los mismos géneros (*Anomozamites*, *Otozamites*, *Pterophyllum*, *Ptilophyllum*, *Weltrichia*, *Williamsonia*, *Williamsoniella*, *Zamites*) con excepción de *Williamsoniella* ya que carece de registros en el Jurásico Superior, por lo que no se pudo obtener un trazo individual para este taxón en esta época. La congruencia de los 23 trazos individuales, en diferentes combinaciones, dio como resultado cinco trazos generalizados (Figuras 7-9) dos para el Jurásico Temprano y Jurásico Medio, y un solo trazo generalizado para el Jurásico Tardío. Los trazos generalizados son denominados: Gt1 Laurásico-Gondwánico y Gt2 Chino en el Jurásico Temprano, Gt3 Laurásico y Gt4 Gondanico en el Jurásico Medio, y Gt5 Gondwánico del norte-Euroasiático en el Jurásico Tardío.

Los trazos generalizados de las tres épocas del Jurásico son sustentados por los trazos individuales de los géneros foliares y de órganos reproductivos de la familia Williamsoniaceae. El trazo generalizado Gt1 Laurásico-Gondwánico lo sustenta los trazos individuales de *Ptilophyllum*, *Pterophyllum*, *Zamites*, *Williamsonia* y *Williamsoniella*. Estos géneros en el trazo Gt1 se distribuyeron en Alemania, Argentina, Italia, Irán, México, Romania y Rusia. Todos están registrados en ambientes continentales (paleobiodb.org; fossilworks.org; Popa, 2005; Spalletti *et al*., 2007; Pott & McLoughlin, 2009; Barbacka *et al*., 2014; McLoughlin *et al*., 2018). Los géneros *Anomozamites*, *Otozamites*, *Pterophyllum* y *Ptilophyllum* sustentan el trazo generalizado Chino (Gt2) y su distribución fue en China y Japón (paleobiodb.org; fossilworks.org; Takimoto *et al*., 2008; Wang *et al*., 2008; Xu *et al*., 2019).

En el Jurásico Medio el trazo generalizado Laurásico (Gt3) es sustentado por la congruencia de los trazos individuales de *Zamites*, *Ptilophyllum*, *Pterophyllum*, *Otozamites*, *Anomozamites* y *Williamsonia*. Mientras que los trazos individuales de *Ptilophyllum*, *Pterophyllum* y *Otozamites* sustentan el trazo generalizado Gondwánico (Gt4). Los géneros en el trazo Gt3 se distribuyeron en Azerbaiyán, Bielorrusia, China, Francia, Georgia, Japón, México, Reino Unido, Tayikistán, Turkmenistán, Ucrania y Uzbekistán. En el trazo Gt4 la distribución de los taxones fue en México, Antártida, Argentina, Australia, Chile, Georgia, India y Nueva Zelanda. El registro de estos taxones fue en ambientes continentales (paleobiodb.org; fossilworks.org; Harris, 1969; Sharma, 1974; van Konijnenburg-van Cittert, 2008; Wang *et al*., 2008; McLoughlin *et al*., 2018; Lozano-Carmona & Velasco-de León, 2021).

Finalmente, en el Jurásico Tardío el trazo generalizado Gt5 está sustentado por *Otozamites*, *Ptilophyllum*, *Weltrichia*, *Williamsonia* y *Zamites*. Estos géneros en este trazo se distribuyeron en Alemania, China, Colombia, Francia, Japón, Kazakstán, Portugal y Reino Unido, en ambientes continentales (paleobiodb.org; fossilworks.org; Doludenko &

Orlovskaya, 1976; Barale, 1981; Barale *et al*., 1983; Lemigne, 1984; van Kinijnenburg-van Citter & van der Burgh, 1989; Wang *et al*., 2008; Barbacka *et al*., 2014).

En el Jurásico Medio se detectaron dos nodos. Estos fueron denominados como N1 Mesoamericano y N2 Arábico (Figura 8). Ambos nodos son el resultado de la intersección de los dos trazos generalizados del Jurásico Medio: Gt3 Laurásico y Gt4 Gondwánico. Ambos están localizados cercanos al paleoecuador del supercontinente Pangea.

DISCUSIÓN

Con base en los patrones de distribución obtenidos podemos observar que el origen de la familia Williamsoniaceae ocurrió durante el Triásico en el hemisferio norte de Pangea. Está conjetura es respaldada por los registros de este grupo durante el Triásico (Anderson *et al*., 2007; Pott, 2014; McLoughlin *et al*., 2018). En el Jurásico Temprano el Gt1 muestra que la distribución de Williamsoniaceae fue en el hemisferio norte principalmente, esto permite sustentar la propuesta de origen en este hemisferio, ya que un trazo generalizado es interpretado como una biota (en este caso integrantes de una flora) ancestral (Craw, 1988; Morrone, 2009). Aunque se observa una extensión hacia el hemisferio sur en la margen occidental de Pangea, alcanzando una distribución hasta la Antártida (Figura 7). Esta extensión podría haber sido favorecida por la movilidad de esta flora durante la etapa de máxima extensión de Pangea (Nance *et al*., 2014; Nance, 2019). Durante esta época, la extensión geográfica de Pangea, y ya que su fragmentación apenas comenzaba (Nance *et al*., 2014; Nance, 2019), fue factor decisivo para favorecer la movilidad de la familia de Williamsoniaceae. Esta movilidad y máxima extensión de su distribución se ve reflejada en los trazos Gt3 y Gt4 del Jurásico Medio.

En el Jurásico Medio, la distribución y diversidad de las Bennettitales y en especial los integrantes de la familia Williamsoniaceae alcanzaron su máximo auge (Anderson *et al*., 2007; Crane & Herendeen, 2009; Taylor *et al*., 2009; Barbacka *et al*., 2014; McLoughlin *et al*., 2018). Durante esta época se observa como la distribución en el hemisferio sur se amplió (Figura 8). Esta amplitud es sustentada con la congruencia de tres géneros (*Ptilophyllum*, *Pterophyllum* y *Otozamites*), que permiten proponer un trazo generalizado: Gt4 Gondwánico. Este trazo abarca la costa occidental de la futura Gondwana, la parte central ente la Antártida e India y corre hasta el sur hacia Nueva Zelanda y Australia (Figura 8).

En el Jurásico Medio los trazos Gt3 y Gt4 generan una intersección formando dos nodos: N1 Mesoamericano y N2 Arábigo. Los nodos por lo general se interpretan como zonas en donde ha tenido lugar la evolución tectónica y biótica (Heads, 2004). Por lo tanto, la identificación de nodos, desde la perspectiva de la biogeografía histórica permite explorar sobre la existencia de áreas complejas (Morrone, 2009). Los nodos pueden representar localidades de endemismo, alta diversidad, límites de distribución, disyunciones, entre otras características (Heads, 2004). Por lo tanto, los nodos identificados en el Jurásico Medio, nos permite proponer la existencia de dos áreas complejas. La primera de alta diversidad, tanto a nivel genérico como de especies para las Bennettitales de la familia Williamsoniaceae, en México y este nodo Mesoamericano es congruente con áreas de actividad tectónica extensional durante el Jurásico Medio. (Campos-Madrigal *et al*., 2013; Martini *et al*., 2016, Zepeda-Martínez *et al*., 2018) así como de condiciones climáticas heterogéneas (Ortiz-Martínez *et al*., 2013). Pero, posiblemente también sean el resultado de los procesos compresionales de la conformación de Pangea y que influyeran como barreras geográficas desde el Triásico.

La diversidad que se ha registrado en el área donde el N1 se observa está compuesta por seis géneros utilizados en este análisis, ya se han registrado hasta 30 especies validas (Lozano-Carmona & Velasco-de León, 2021). Por lo tanto, este nodo correspondería a un área de alta diversidad y actividad tectónica. Mientras que en el N2 es sustentado por la congruencia del registro de tres géneros, sin embargo, la definición a nivel de especie de los registros necesita de revisión taxonómica (Delle, 1960; Doludenko & Svanidze, 1969; Svanidze *et al*., 1983). Es posible que aquí la congruencia de los trazos generalizados indique un área de límite de distribución delimitada por el mar de Thetis entre las placas euroasiática y arábiga (Hempton, 1987). En la región del N1 la congruencia con las modificaciones geográficas a causa de la fragmentación de Pangea es considerada como un factor que favoreció la diversificación de las Bennettitales (Campos-Madrigal *et al*., 2013; Martini *et al*., 2016; Zepeda-Martínez *et al*., 2018, Pindell, 2020; Lozano-Carmona & Velasco-de León, 2021).

En el Jurásico Tardío la distribución de las Bennettitales se ve reducida y restringida casi al hemisferio norte como se observa en el trazo Gt5. Esta modificación en la distribución puede haber sido influenciada por la fragmentación activa de Pangea en esta región (Nance, 2019). Sin embargo, los registros de *Ptilophyllum* en el hemisferio sur continuaron hasta el Paleógeno en Nueva Zelanda (McLoughlin *et al*., 2011). Este registro sugiere que las latitudes altas fungieron como un posible refugio para las Bennettitales en este hemisferio. Pero, sus registros son asilados y no permiten el reconocimiento de un trazo generalizado para el Jurásico Tardío.

Durante el Mesozoico el supercontinente Pangea estuvo formado (Triásico Inferior) y culminó su fragmentación (Cretácico). Hasta el Triásico Superior la actividad tectónica inicia la fragmentación con la aparición de los océanos Atlántico e Índico (Nance *et al*., 2014; Nance, 2019). Podemos hipotetizar que la distribución de la familia Williamosniaceae, reflejada en el análisis de trazos, fue modelada principalmente por la actividad tectónica producto de la fragmentación de Pangea en el ciclo de los supercontinentes. El ciclo tiene un profundo efecto sobre el nivel del mar, el clima, la composición atmosférica y la química de los océanos, en los eventos de extinción y radiación evolutiva, entre otros (Nance *et al*., 2014; Nance, 2019). La formación y fragmentación del supercontinente Pangea propicia la estructuración de una fisiografía compleja, orogenias, cuencas, planicies y otros elementos fueron los que pudieron favorecer la movilidad de las Bennettitales durante estas dos etapas del ciclo del supercontinente. A su vez, el ciclo de formación y fragmentación se ha asociado con la extinción y radiaciones evolutivas respectivamente. En este sentido, podemos observar que los patrones de distribución de las Bennettitales se asocian con la fragmentación de Pangea. Por un lado, esta actividad durante el Jurásico Temprano-Medio permitió la mayor amplitud en la distribución generando incluso áreas complejas de diversidad relacionadas a zonas de convergencia tectónica (N1) y de límites de distribución biótica y tectónica (N2). Por lo tanto, este análisis enfatiza el potencial del análisis de trazos para recuperar los patrones de distribución de taxones en el pasado geológico y su relación con las condiciones geológico-geográficas durante su existencia.

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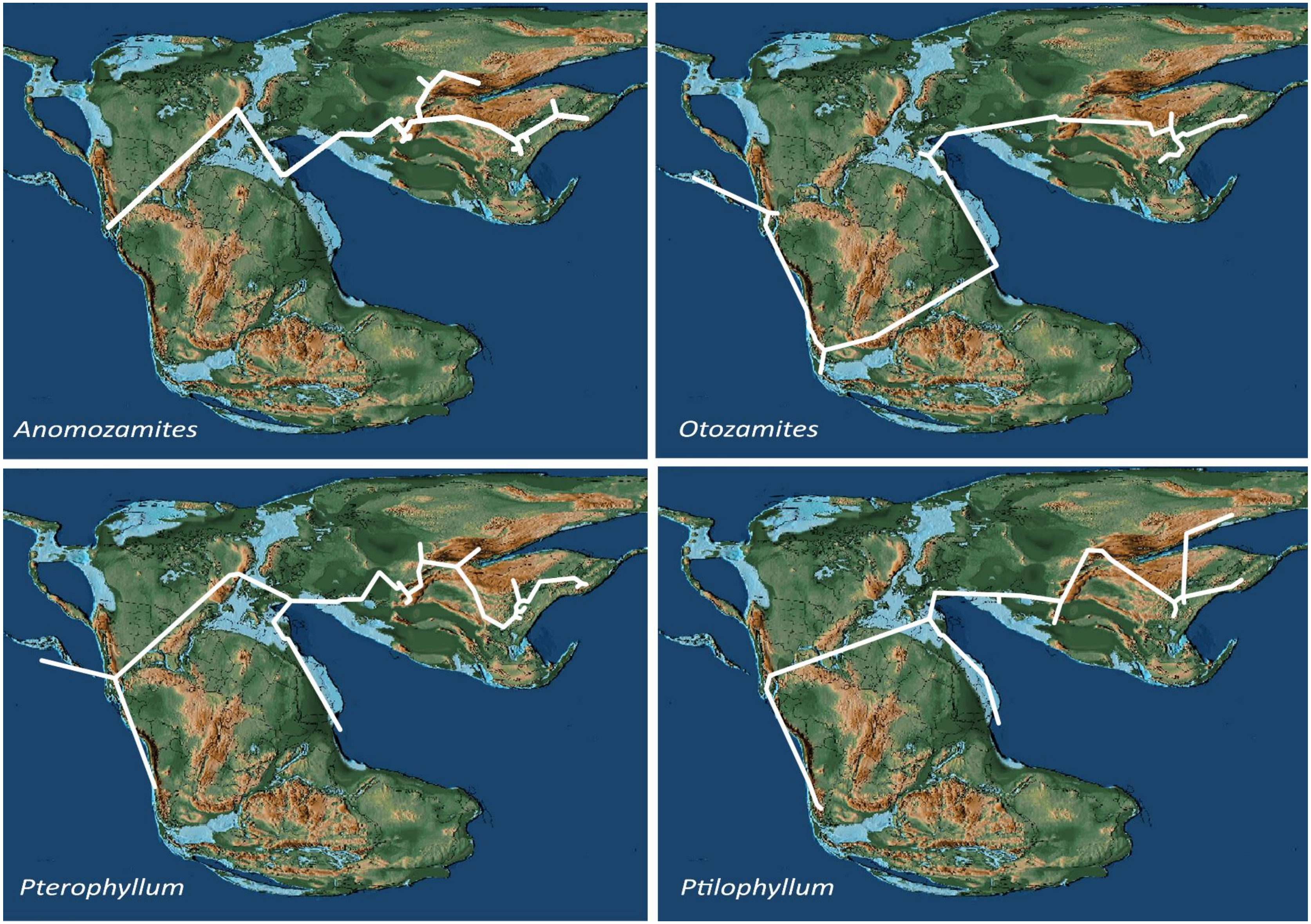


Figura 1. Trazos individuales (en color blanco) de los géneros *Anomozamites*, *Otozamites*, *Pterophyllum* y *Ptilophyllum* correspondientes al Jurásico Temprano.

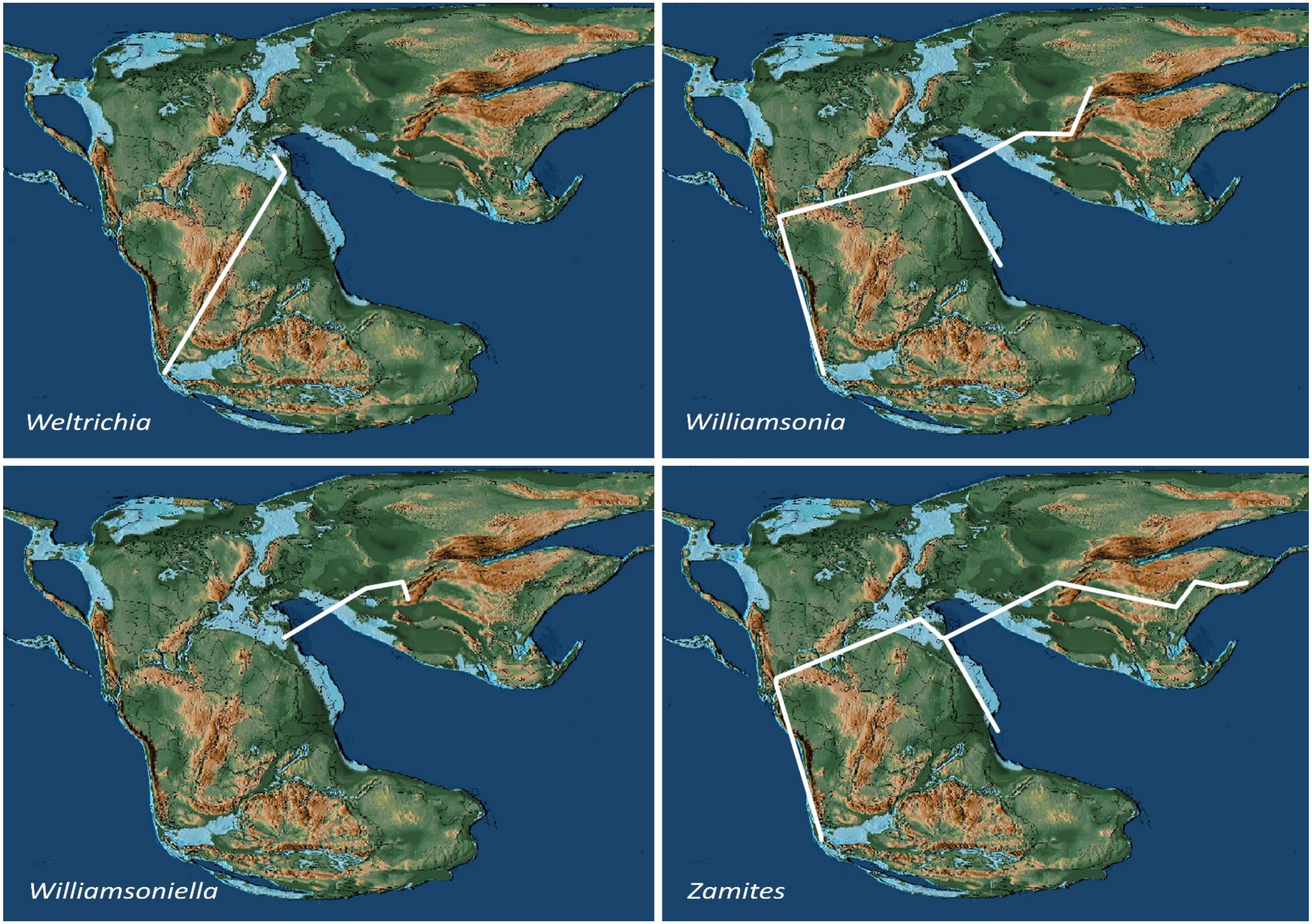


Figura 2. Trazos individuales (en color blanco) de los géneros *Weltrichia*, *Williamsonia*, *Williamsoniella* y *Zamites* correspondientes al Jurásico Temprano.

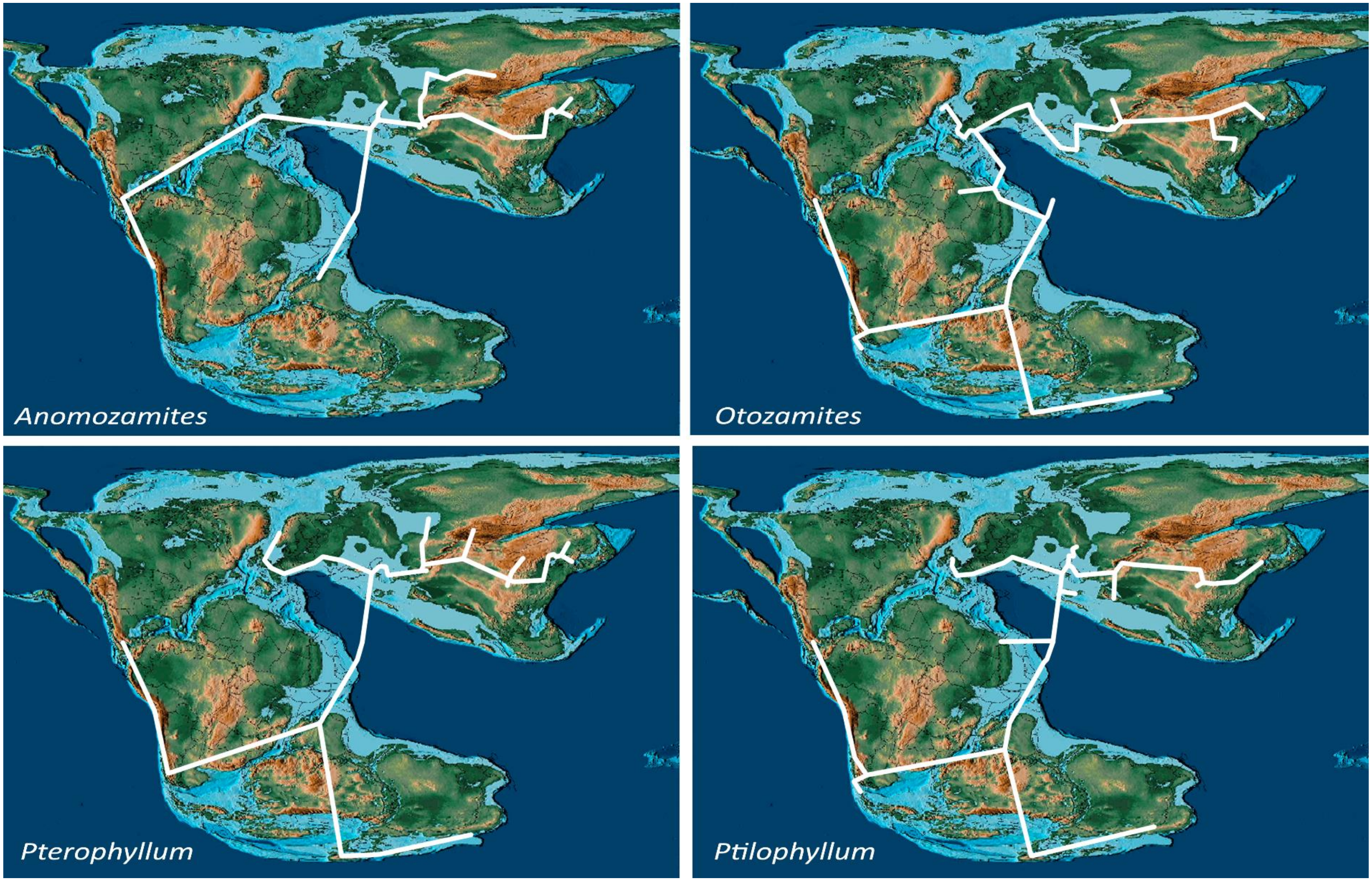


Figura 3. Trazos individuales (en color blanco) de los géneros *Anomozamites*, *Otozamites*, *Pterophyllum* y *Ptilophyllum* correspondientes al Jurásico Medio.

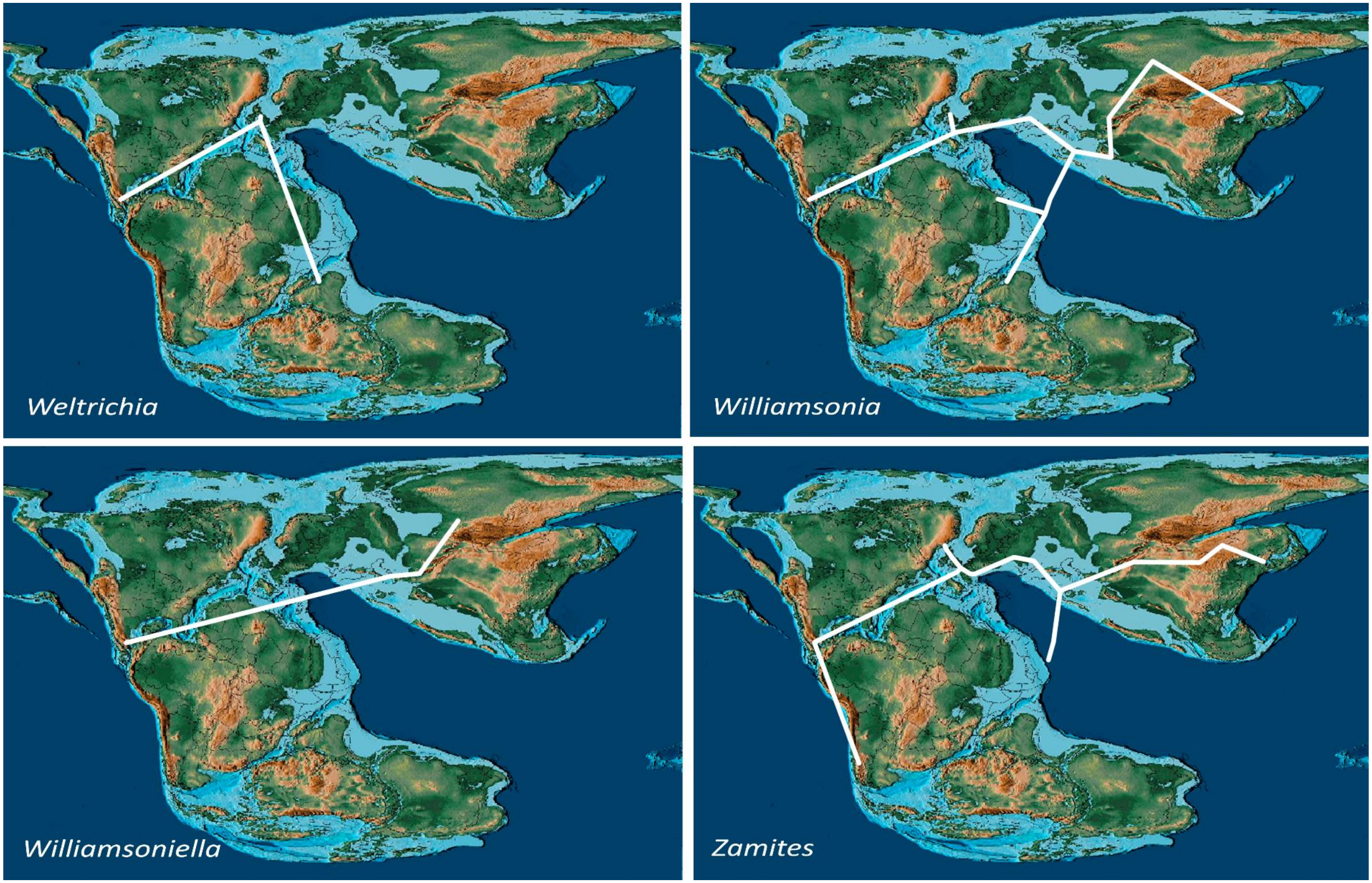


Figura 4. Trazos individuales (en color blanco) de los géneros *Weltrichia*, *Williamsonia*, *Williamsoniella* y *Zamites* correspondientes al Jurásico Medio

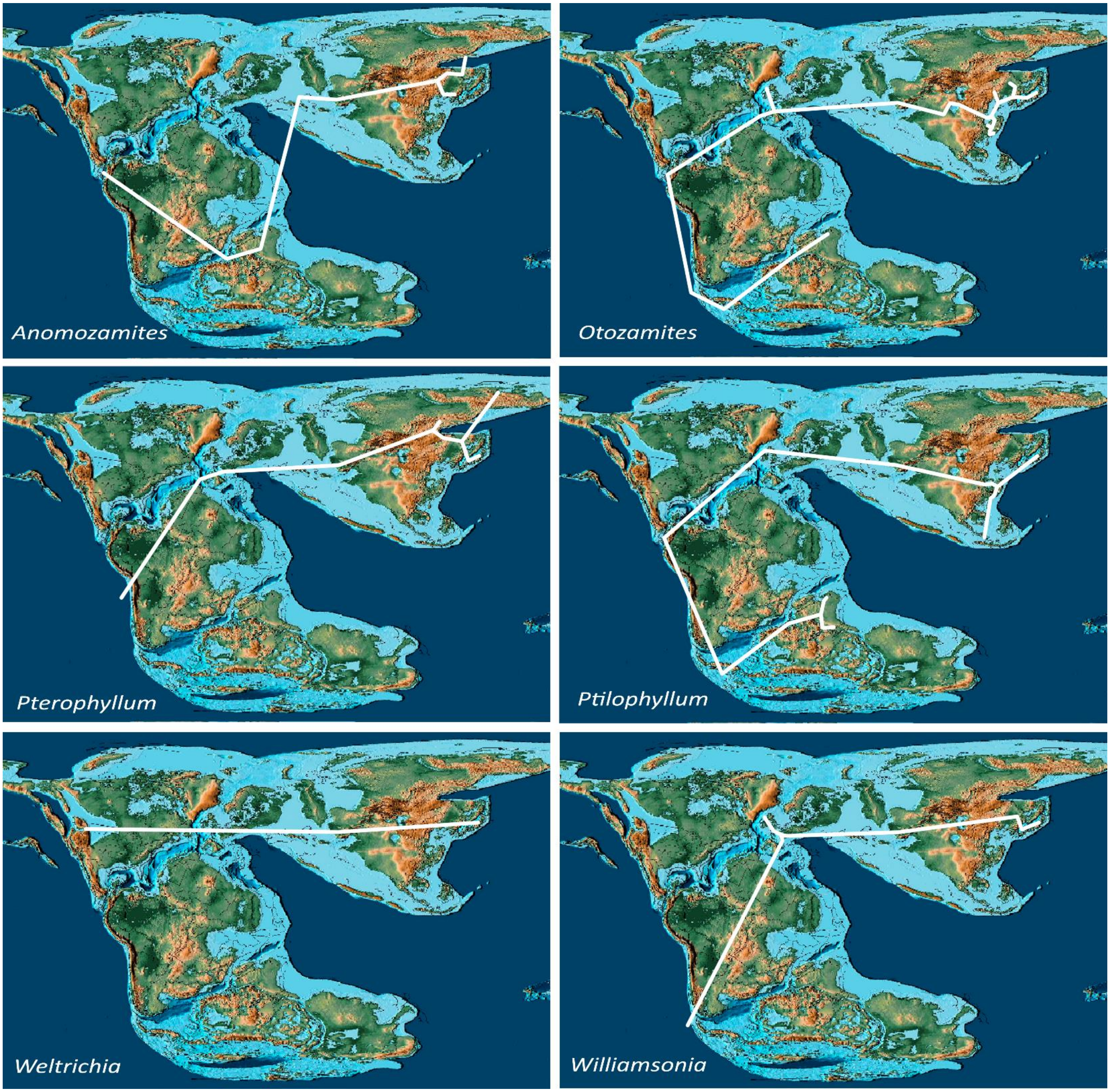


Figura 5. Trazos individuales (en color blanco) de los géneros *Anomozamites*, *Otozamites*, *Pterophyllum*, *Ptilophyllum Weltrichia* y *Williamsonia* correspondientes al Jurásico Tardío.

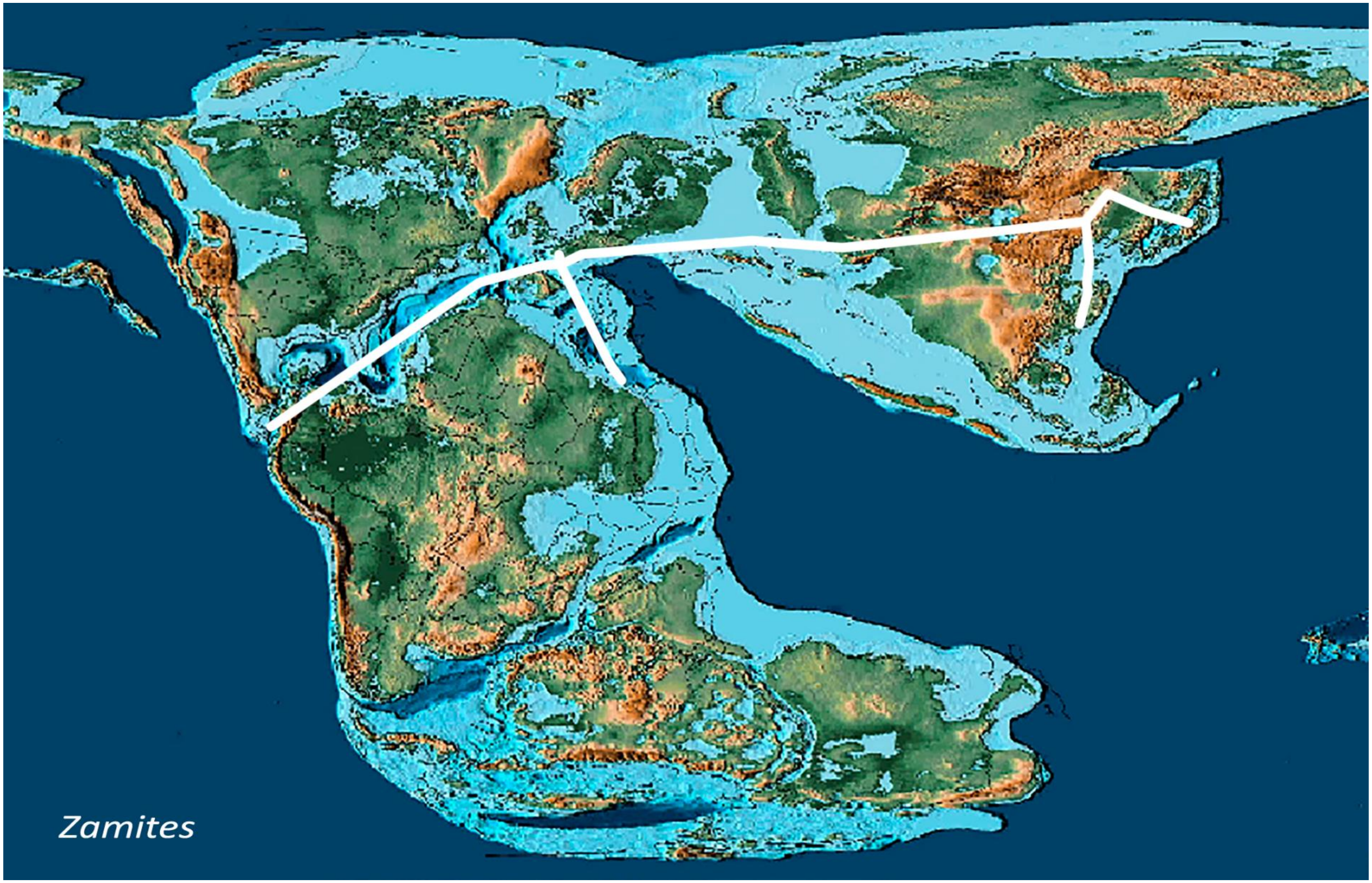


Figura 6. Trazo individual (en color blanco) del género *Zamites* correspondiente al Jurásico Tardío.

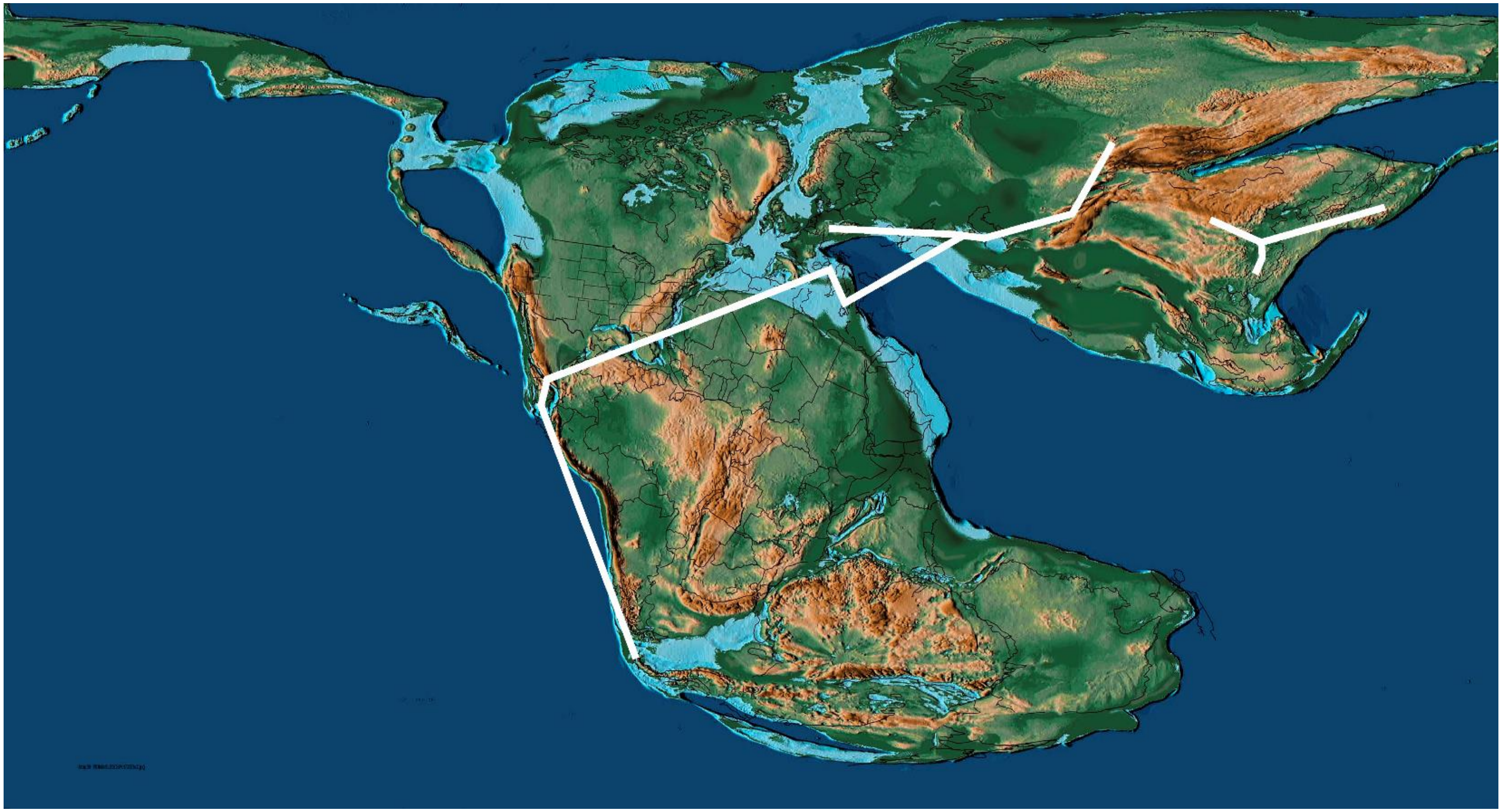


Figura 7. Trazos generalizados (en color blanco) del Jurásico Temprano: Gt1 Laurásico-Gondwánico y Gt2 Chino.

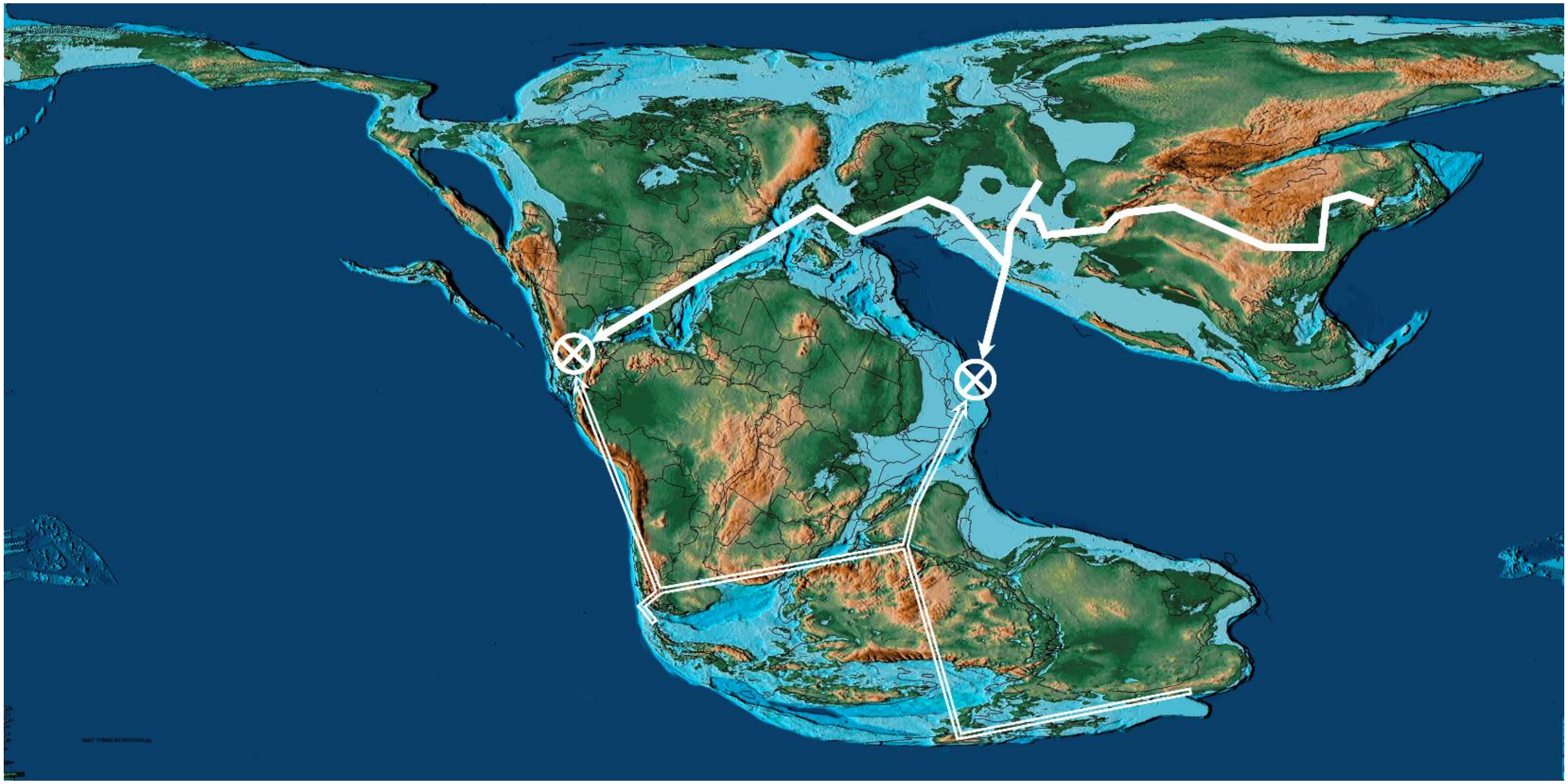


Figura 8. Trazos generalizados del Jurásico Medio: Gt3 Laurásico (color blanco solido) y Gt4 Gondwánico (contorno de color blanco), y los nodos (círculos con x en color blanco) N1 Mesoamericano y N2 Arábico.

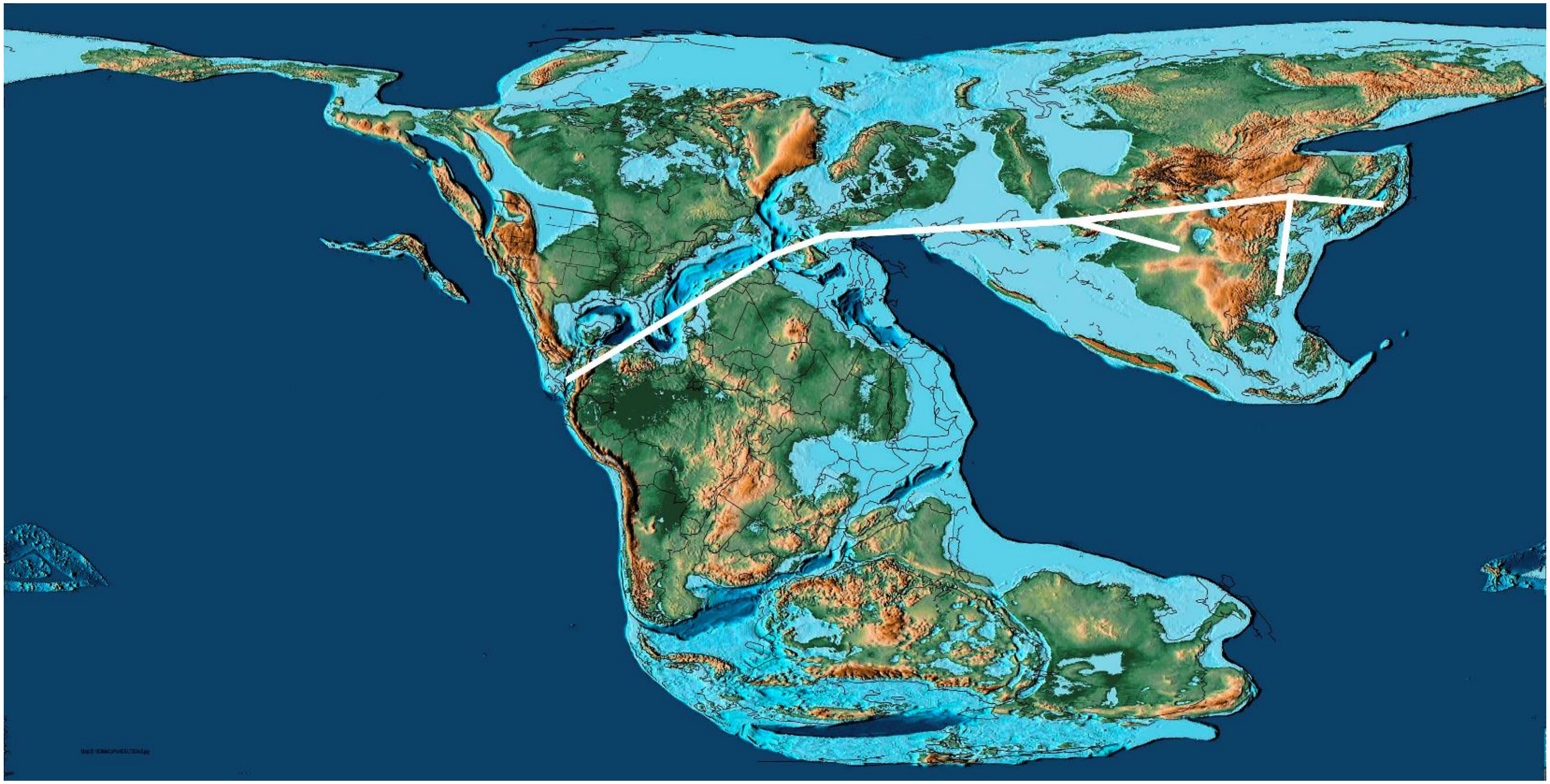


Figura 9. Trazo generalizado (en color blanco) del Jurásico Tardío: Gt5 Gondwánico del norte-Euroasiático.

QUINTO CAPÍTULO

Regionalización fitogeográfica del Jurásico Medio con base en análisis de parsimonia de endemismos de seis ordenes de gimnospermas

- **Lozano-Carmona, D. E.** Propuesta y diseño del trabajo; revisión de los ejemplares e identificación taxonómica; recopilación de datos de distribución y consulta bibliográfica; depuración de base de datos; análisis e interpretación de datos fitogeográficos; elaboración de figuras; redacción del manuscrito.
- **Velasco-de León, M. P.** Revisión del trabajo y manuscrito.
- **Morrone, J.** Revisión del trabajo y manuscrito.

Regionalización fitogeográfica del Jurásico Medio con base en análisis de parsimonia de endemismos de seis ordenes de gimnospermas

Diego E. Lozano-Carmona

Posgrado en Ciencias Biológicas, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Ciudad de México, C.P. 09230, México

Colección de Paleontología, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Ciudad de México C.P. 09230, México.

RESUMEN

Durante el Jurásico las gimnospermas fueron el principal elemento en la vegetación alrededor del Mundo. Los principales grupos fueron las Bennettitales, Cycadales, Pinales, Ginkgoales, Czekanowskiales, Caytoniales. Algunas de estas tuvieron una distribución casi en toda Pangea, mientras que otras estuvieron restringidas a alguno de los hemisferios. Desde 1987 se planteó una regionalización fitogeográfica jerárquica para el Mesozoico que incluye a las categorías de Reino, Área, Provincia, Distrito y Región. Este esquema ha sido utilizado históricamente por varios paleobotánicos y ocasionalmente fue modificado. Sin embargo, tanto la propuesta original como las modificaciones fueron cualitativas, basándose únicamente en la comparación de listados paleoflorísticos. Aquí se presenta una nueva propuesta de regionalización fitogeográfica empleando la metodología del análisis de parsimonia de endemismos de los seis principales órdenes de gimnospermas para el Jurásico. En este nuevo esquema se proponen el reino Pangea, la región Laurásica, el dominio Ecuatorial-Eurosiano y la provincia Paleoecuatorial. Este esquema se fundamenta en un cladograma sucesivamente anidado y sus agrupaciones con base en la concordancia de distribución de dos o más géneros en las áreas de distribución. La revisión de las propuestas históricas y su comparación con este nuevo esquema muestra que no hay concordancia entre estas. Las nuevas aportaciones de registros paleobotánicos y la metodología empleada son la razón de esta incongruencia. Sin embargo, esto debela la posibilidad de aplicar este método para todo el Mesozoico, además de enriquecerlo con datos de otros grupos florísticos y zoológicos y correlacionarlo con el contexto tectónico de esta era geológica.

Palabras clave: Regionalización, PAE, Pangea, Jurásico, Meyen.

ABSTRACT

Gymnosperms were the main element in vegetation around the World in the Jurassic. The main groups were the Bennettitales, Cycadales, Pinales, Ginkgoales, Czekanowskiales, Caytoniales. Some of these had a distribution almost throughout Pangea, while others were restricted to one of the hemispheres. Since 1987, a hierarchical phytogeographic regionalization was proposed for the Mesozoic that includes the categories of Kingdom, Area, Province, District and Region. This scheme has been used historically by various paleobotanists and was occasionally modified. However, both the original proposal and the modifications were qualitative, based solely on the comparison of paleofloristic lists. Here I present a new proposal for phytogeographic regionalization using the methodology of parsimony analysis of endemism of the six main orders of gymnosperms for the Jurassic. In this new scheme the kingdom Pangaea, the Laurasic region, the Equatorial-Eurosian domain and the Paleo-Equatorial province are proposed. This scheme is based on a successively nested cladogram and its groupings based on the agreement of distribution of two or more genera on the distribution areas. The review of the historical proposals and their comparison with this new scheme shows that there is no agreement between them. The new contributions of paleobotanical records and the methodology used are the reason for this inconsistency. However, this reveals the possibility of applying this method to the entire Mesozoic, in addition to enriching it with data from other floristic and zoological groups and correlating it with the tectonic context of this geological era.

Keywords: Regionalization, PAE, Pangea, Jurassic, Meyen.

INTRODUCCIÓN

Los principales elementos florísticos de las gimnospermas en el Jurásico (Bennettitales, Cycadales, Pinales, Ginkgoales, Czekanowskiales, Caytoniales) muestran patrones de distribución que fueron influenciados por acontecimientos geológicos y climáticos. Estos eventos propiciaron movilidad, diversificación y una marcada distribución restringida (denominado "*provincialismo*" por algunos autores) de las especies de cada orden (Harris, 1969; Meyen, 1987; Vakhrameev, 1987; Anderson *et al.*, 1999, 2007; McLoughlin, 2001; Ziegler *et al.*, 2003; Rees *et al.*, 1999, 2004; Chure *et al.*, 2006; Barbacka, 2011; Kostina &

Herman, 2013; Lozano-Carmona & Velasco-de León, 2016, 2021; McLoughlin *et al*., 2018). La existencia del supercontinente Pangea hacia el Permo-Triásico (Nance, 2019) configuró el sustrato geográfico donde éstas gimnospermas alcanzaron su máxima movilidad y distribución. Esta configuración permitió que Meyen (1987) identificara y propusiera tres principales reinos paleoflorísticos desde el Triásico hasta el Cretácico Temprano con base en la asociación taxonómica y la abundancia de los registros. Los reinos son Angara (en latitudes altas del hemisferio norte), Laurasia (en las áreas tropicales a subtropicales del hemisferio norte) y Gondwana (en latitudes medias y altas del hemisferio sur) (Figura 1). Estos reinos han sido referidos tradicionalmente en la paleobotánica del Mesozoico, principalmente para el Triásico (Dobruskina, 1994; Anderson *et al.,* 1999, 2007; McLoughlin, 2001; Artabe *et al.,* 2003; Pott, 2014; Kustatscher *et al*., 2018), y en menor cantidad para el Jurásico (Anderson *et al.,* 1999, 2007; McLoughlin, 2001, McLoughlin *et al.,* 2018). Desde el punto de vista de asociación taxonómica, la distribución de los principales grupos de gimnospermas en el Jurásico muestra un patrón diferencial por categoría. Por ejemplo, el orden Bennettitales y varias familias y géneros de coníferas alcanzaron un área de distribución prácticamente cosmopolita, pero a nivel local se presentó una marcada restricción en la distribución de las especies. Mientras que, Cycadales, Ginkgoales y Czekanowskiales estuvieron más distribuidas al hemisferio norte, donde no fueron exclusivas y también muestran una distribución local restringida de las especies (Vakhrameev, 1987; McLoughlin, 2001; Phillippe *et al.,* 2004; Artabe *et al.,* 2003; Chure *et al.,* 2006; Anderson *et al.,* 2007; Kostina & Herman, 2013; Popa, 2014; McLoughlin *et al.,* 2018; Lozano-Carmona & Velasco-de León, 2021). Por otro lado, también se han realizado propuestas de regionalización con base en criterios paleoecológicos para el Mesozoico empleando principalmente las asociaciones paleoflorísticas y sus inferencias paleoclimáticas (Vakhrameev, 1987, 1991), así como, el tipo de vegetación y las características ecomorfológicas (Rees *et al.,* 1999, 2004; Ziegler *et al.,* 2003).

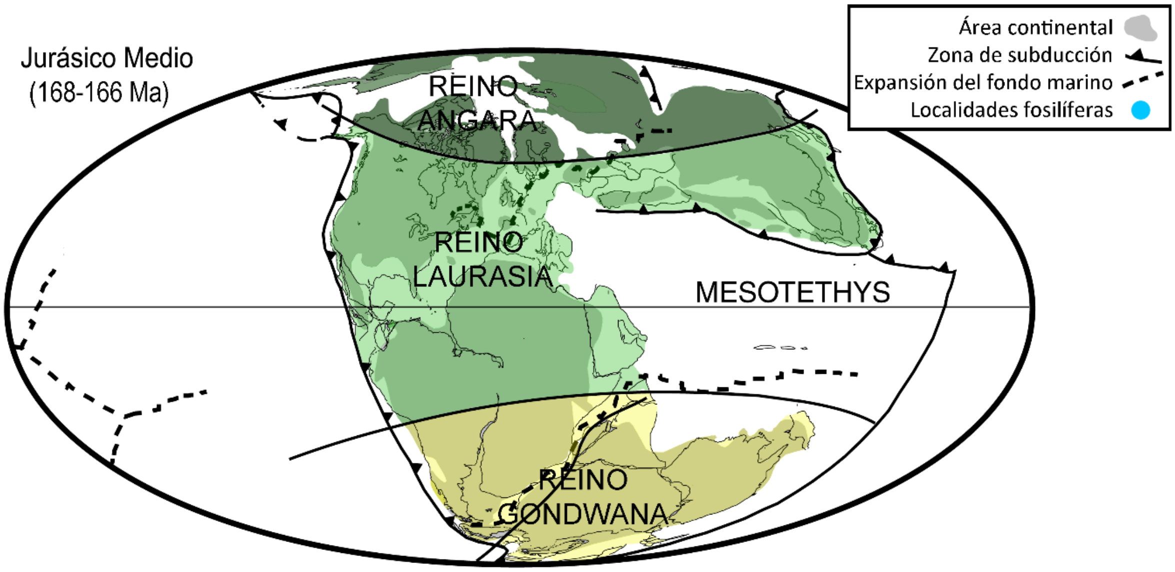


Figura 1. Mapa de la reconstrucción paleogeográfica del Jurásico Medio (Scotese, 2014) con las áreas de distribución de los reinos paleoflorísticos de Angara, Laurasia y Gondwana propuestos por Meyen (1987) para el Jurásico Medio.

Rees *et al.* (1999, 2004) y Ziegler *et al.* (2003) reconocen patrones de distribución con base en el tamaño de las hojas de los diferentes grupos presentes en la flora del Jurásico, así como los registros de paleoindicadores clave como evaporitas, carbón y arrecifes. La distribución de la flora en general presentó una máxima diversidad en las latitudes medias, donde los “bosques” fueron dominados por Bennettitales, Cycadales, coníferas y algunos representantes de plantas sin semilla como los helechos. En latitudes bajas la vegetación se constituyó principalmente por plantas xeromórficas y se formaron parches boscosos representados por coníferas y Bennettitales/Cycadales de hojas pequeñas. Hacía el área polar la vegetación fue dominada por coníferas, Ginkgoales y Czekanowskiales, algunos elementos que probablemente fueron caducifolios y de hojas moderadamente grandes. Por último, en el área tropical la vegetación siempre verde, si es que la hubo, fue restringida (Rees *et al.*, 1999, 2004; Ziegler *et al.*, 2003). Es así como, Rees *et al.* (1999), reconocieron cinco biomas: (1) desierto, (2) estacionalmente seco (verano húmedo o subtropical), (3) de invierno húmedo, (4) cálido húmedo y (5) frio húmedo (Figura 2).

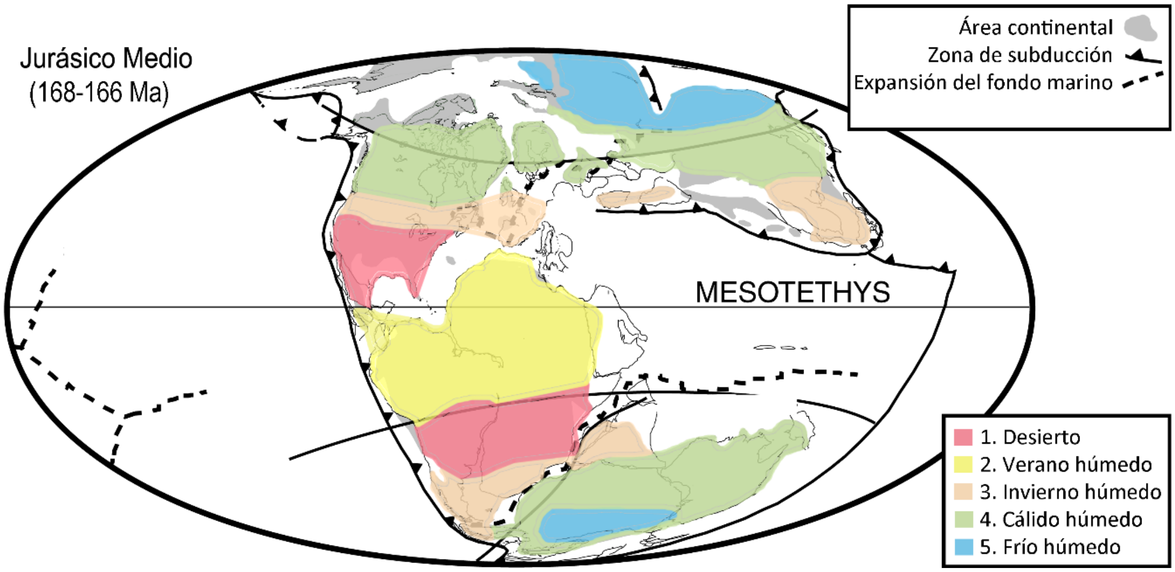
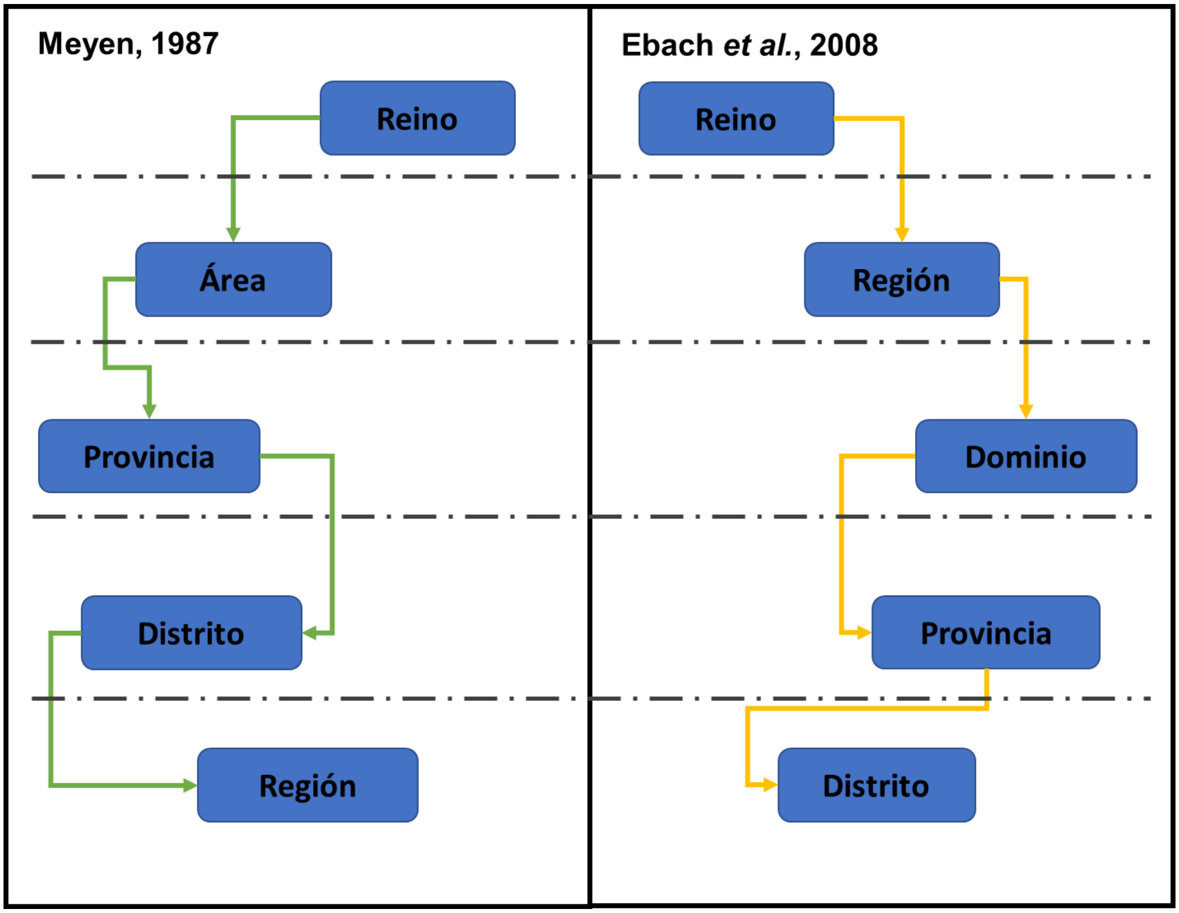


Figura 2. Mapa de la reconstrucción paleogeográfica del Jurásico Medio (Scotese, 2014) con las áreas de distribución de los cinco biomas propuestos por Rees *et al.* (1999) para el Jurásico Medio.

Entonces, el uso de elementos florísticos (principalmente gimnospermas) para una regionalización del Mesozoico y específicamente del Jurásico, ya sea empleando un criterio de asociación taxonómica o ecológico (Meyen, 1987; Rees *et al*., 1999), muestran a las categorías mayores, que son los Reinos o los Biomas (Ebach *et al*., 2008; Escalante, 2009), como las de mayor claridad con respecto a las categorías jerárquicas subsecuentes. Pero, la extensión o ubicación de los reinos (Meyen, 1987) no son compatibles con las de los biomas (Rees *et al*., 1999) (comparar figuras 1 y 2 de este capítulo). Por otro lado, se han realizado, en algunas zonas, el reconocimiento y propuestas de unidades fitogeográficas denominadas "áreas, provincias o regiones". Pero estas propuestas son aisladas, no brindan más de una unidad fitogeográfica en particular, no concuerdan entre ellas y son principalmente del Triásico, por ejemplo, para Eurasia: Meyen (1987); Vakhrameev (1987), Diéguez *et al.* (2010), Kostina & Herman (2013), Barbacka *et al.* (2014), para Euroamerica: Dobruskina (1994) y para Gondwana: Anderson *et al.* (1999), McLoughlin (2001), Artabe *et al.* (2003), Phillippe *et al.* (2004), McLoughlin *et al.* (2018).

El reconocimiento básico de una regionalización fitogeográfica para el Triásico y Jurásico más utilizado (Dobruskina, 1994; Anderson et al., 1999, 2007; McLoughlin, 2001; Kustatscher *et al*., 2018) fue realizado por Meyen (1987) con base en asociaciones taxonómicas y la abundancia de sus registros. La jerarquización propuesta por Meyen (1987) sigue la siguiente nomenclatura y orden de las categorías: reino, área, provincia, distrito y región (Cuadro 1). Meyen (1987) reconoce y propone los tres reinos ya mencionados y las áreas Ecuatorial, Siberiana y Notal, así como las provincias Europea y las de Asia Central y Oriental, pero ya no hace propuesta de distritos o regiones. Esta nomenclatura genera confusión al comparar con el sistema de jerarquización utilizado recientemente con la biota actual y principalmente en el empleo de los términos tales como provincia, distrito y región (Ebach *et al*., 2008; Escalante, 2009; Morrone, 2018). Aquí en este estudio se utiliza la estructura de regionalización fitogeográfica (entiéndase biogeográfica) que incluye en el nivel más alto a los reinos, a los cuales le siguen las regiones, los dominios, provincias y distritos, teniendo como unidad básica a la provincia (Ebach *et al*., 2008; Escalante, 2009; Morrone & Escalante, 2016; Morrone, 2018; Cuadro 1). Este sistema jerárquico permite organizar las unidades geográficas con base en los registros taxonómicos de la flora (Escalante, 2009; Morrone, 2018). Entonces, a la propuesta de regionalización de Meyen (1987) se podría, (1) corroborar sus unidades fitogeográficas y (2) correlacionarse las categorías con el esquema de regionalización actual, o (3) reconocer la congruencia de nuevas unidades fitogeográficas con base en el origen florístico común de los principales grupos de gimnospermas del Jurásico (Espinosa *et al*., 2001; Morrone & Escalante., 2002; Morrone, 2018). Por lo tanto, el objetivo de este capítulo fue estudiar la relación paleoflorística de los reinos de Angara, Gondwana y Laurasia propuestos por Meyen (1987) y las provincias Siberiana, Europea-Siniana, Euroamericana, Paleoecuatorial, Gondwana del Oeste, Gondwana del Este propuestas por McLoughlin (2001), y reconocer la existencia de una regionalización fitogeográfica en el Jurásico Medio. Este estudio se realizó con base en un análisis de parsimonia de endemismos de las localidades paleoflorísticas de los principales grupos de gimnospermas en el Jurásico Medio (Bennettitales, Ginkgoales, Czekanowskiales, Caytoniales, Cycadales, Pinales).

Cuadro 1. Comparación de los esquemas de regionalización y las unidades fitogeográficas de Meyen (1987) y Ebach *et al.*, (2008).



En este sentido, con la intención de reconocer las relaciones históricas entre las áreas donde los taxones se distribuyen, se han propuesto diferentes criterios y métodos de análisis, por ejemplo: análisis de trazos, análisis de endemicidad y análisis de parsimonia de endemismos (Croizat, 1964; Rosen, 1988; Morrone, 1994; Szumik & Goloboff, 2004). Entre estos métodos, el análisis de parsimonia de endemismos (PAE, por sus siglas en inglés) es un método biogeográfico que ha sido empleado para proponer las relaciones entre diferentes unidades biogeográficas (Espinosa *et al*., 2001; Morrone & Escalante, 2002; Escalante *et al*., 2013; Olguín-Monroy *et al*., 2013; Escalante, 2015). Un PAE se puede utilizar para identificar patrones de homología biogeográfica primaria. Esto se refiere a que es posible generar una conjetura sobre una historia biogeográfica común, es decir, que diferentes taxones con medios de movilidad diferentes se encuentran (o encontraron) espaciotemporalmente ligados en una misma biota (Morrone, 2001). Además, con el empleo de un PAE se puede identificar patrones de endemismo que pueden estar sucesivamente anidados y que se utilizan en propuestas de esquemas de regionalización biogeográfica. Es decir, permite obtener un agrupamiento jerárquico que pueden ser interpretados como regiones, dominios, provincias o distritos (Espinosa *et al*., 2001; Escalante, 2009; 2015) e incluso es posible que pueda reflejar eventos vicariantes entre las áreas geográficas por medio de la distribución compartida de los taxones (Morrone & Escalante 2002; Morrone, 2004, 2009). Por lo tanto, en este estudio un PAE es ideal para reconocer una regionalización fitogeográfica en el Jurásico Medio.

En general hay dos explicaciones posibles para los cladogramas resultantes de un PAE: *estática* o *dinámica* (Rosen, 1988; Nihei, 2006). La explicación estática se basa en la reconstrucción a partir de un solo horizonte de tiempo geológico y sin incluir información filogenética. En este estudio en particular, este es el tipo de interpretación que se realizó para el análisis, ya que solo se contempla al Jurásico Medio y no se incluyen las relaciones filogenéticas de los taxones de gimnospermas empleados. A su vez, los patrones que se detectan en un PAE pueden ser interpretados de dos maneras: *ecológica* o *histórica* con base en la condición indicada para el área raíz codificada con ceros (0). En la primera de ellas se interpreta que las condiciones ecológicas fueron tan desfavorables que ningún taxon pudo o puede sobrevivir en ella. Entonces, las relaciones del cladograma estarían indicando afinidades ecológicas. Por otro lado, la segunda de ellas, la interpretación histórica, se considera que el área raíz es una tan antigua geológicamente que ninguno de los taxones habría llegado por dispersión o evolucionado allí. Entonces las relaciones del cladograma indicarán afinidades históricas producto de eventos vicariantes y/o de movilidad de los elementos paleoflorísticos. En este caso, el área raíz es considerada como una muy antigua geológicamente.

MATERIAL Y MÉTODOS

Morrone (1994) propuso un método para identificar áreas de endemismo, el cual está basado en el análisis de simplicidad de endemismos (Rosen, 1988). El algoritmo de parsimonia es el que se emplea en este método para identificar grupos de áreas que estarán sustentados por dos o más especies, estos grupos son considerados como áreas de endemismo (Espinosa *et al*., 2001). El algoritmo del PAE (Morrone, 1994; Olguín-Monroy *et al*., 2013; Morrone & Escalante, 2016) comprende los siguientes pasos que fueron adecuados para este estudio:

- Se emplearon seis unidades geográficas irregulares. En este caso se utilizaron las áreas de las denominadas "provincias" florísticas del Jurásico propuestas por McLoughlin (2001), que están incluidas en los reinos paleoflorísticos de Meyen (1987). Cabe recordar que Meyen (1987) propuso otra nomenclatura y orden en la jerarquización fitogeográfica y que, por lo tanto, las provincias definidas por McLoughlin (2001) no tendrían una correspondencia directa con el esquema propuesto por Ebach *et al.* (2008).
- Se superpusieron las localidades donde se han registrado a los taxones analizados (32 géneros de los órdenes Bennettitales, Cycadales, Ginkgoales, Pinales, Czekanowskiales, Caytoniales) en el paleomapa del Jurásico Medio y las delimitaciones de las unidades geográficas irregulares (Meyen, 1987; McLoughlin, 2001; Scotese, 2014). Los datos de las localidades fueron obtenidos de Lozano-Carmona (2017) y corroborados y complementados con datos de Paleobiology Database (https:\\paleobiodb.org) del 08-15 de octubre de 2021.
- Se construyó una matriz de áreas por taxones (Anexo 2). Donde los renglones (*r*) representan a las unidades geográficas y las columnas (*c*) representan a los taxones. La presencia de un taxon en el área se marca con un '1' y la ausencia con un '0'. Se añadió una unidad geográfica externa hipotética con '0' en todas las casillas con el objetivo de enraizar y orientar el cladograma (Morrone, 1994).
- Se analizó la matriz con el programa Nona 2.0 (Goloboff, 1994) y su interfase Winclada versión 0.9.99 (Nixon, 2000), con los parámetros predeterminados por el programa y no se realizó un consenso estricto ya que solo se obtuvo un cladograma.
- Por último, se identificaron las áreas de endemismo con los clados definidos por al menos dos taxones y se representó en un mapa verificando la congruencia de las distribuciones. Los grupos formados fueron nombrados con base en las áreas geográficas representativas o sus relaciones en cada grupo.
- En este caso, el área raíz es considerada como una muy antigua geológicamente y la interpretación de los patrones resultantes fueron analizados desde la perspectiva histórica.

Datos empleados para el análisis de parsimonia de endemismos

Los datos taxonómicos empleados en este análisis corresponden 32 géneros de los órdenes Bennettitales, Cycadales, Ginkgoales, Pinales, Czekanowskiales, Caytoniales y son enunciados a continuación: (Bennettitales) *Anomozamites, Otozamites, Pterophyllum, Ptillophyllum, Weltrichia, Williamsonia, Williamsoniella, Wielandiella* y *Zamites*; (Cycadales) *Taeniopteris, Pseudoctenis* y *Nilssonia*; (Ginkgoales) *Ginkgo, Eretmophyllum, Ginkgoidium, Ginkgoites, Karkenia, Sphenobaiera, Baiera* y *Nehvizdyella*; (Pinales) *Podozamites, Brachyphyllum, Agathoxylon* y *Pelourdea,* (Czekanowskiales) *Czekanowskia, Leptostrobus,* y *Phoenicopsis*; (Caytoniales) *Sagenopteris, Caytonianthus* y *Caytonia*.

Se empleo el paleomapa del Jurásico Medio (Scotese, 2014) y las unidades geográficas irregulares son Siberiana (Reino Angara), Europea-Siniana (Reino Laurasia), Euroamericana (Reino Laurasia), Paleoecuatorial (Reino Laurasia), Gondwana del Oeste (Reino Gondwana), Dominio Gondwana del Este (Reino Gondwana) (Figura 3).

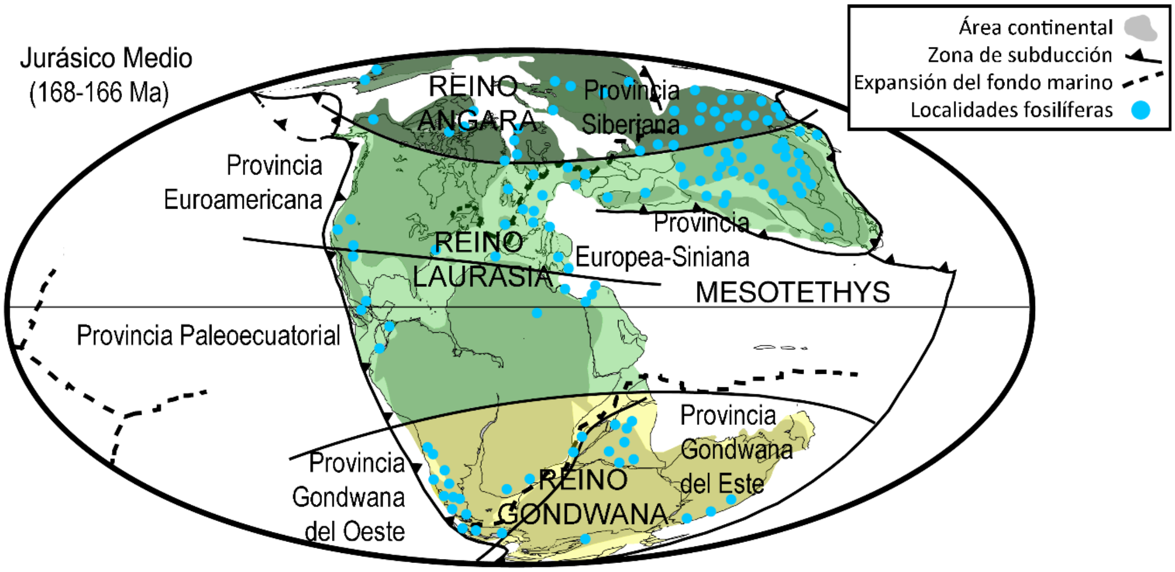


Figura 3. Mapa de la reconstrucción paleogeográfica del Jurásico Medio (Scotese, 2014) con las áreas de distribución de los reinos paleoflorísticos de Angara, Laurasia y Gondwana (Meyen, 1987; Anderson *et al.*, 1999; 2007). A su vez se puede observar la delimitación de las principales provincias florísticas jurásicas (*sensu* McLoughlin, 2001) y las localidades de registro paleoflorístico de los géneros de los principales órdenes de gimnospermas con puntos azules (Lozano-Carmona, 2017; Paleobiology Database [https:\\paleobiodb.org]). También se muestra la fragmentación continental entre Europa y Norteamérica, así como entre Gondwana del Oeste y del Este (Metcalfe, 1996).

RESULTADOS

El Análisis de Parsimonia de Endemismos (PAE) de las unidades geográficas *vs* la presencia/ausencia de los taxones estudiados dio como resultado un único cladograma de áreas (Figura 4), de 46 pasos, con un índice de consistencia (CI) de 0.69 y un índice de retención (RI) de 0.65. El cladograma obtenido permite detectar patrones definidos de agrupación de los grupos florísticos del Jurásico Medio con base en la concordancia de distribución de dos o más especies en las áreas de distribución. El primer clado que se aparta es el de Gondwana del Este. Posteriormente se identifican cuatro áreas de endemismo sucesivamente anidadas (Figura 4): clado A (Paleoecuatorial), clado B (conjunto de Paleoecuatorial-Siberiana-Europea-Siniana), clado C (conjunto de Euroamericana-Paleoecuatorial-Siberiana-Europea-Siniana) y clado D (conjunto de Gondwana del Este-Euroamericana-Paleoecuatorial-Siberiana-Europea-Siniana). Hay otro clado compuesto por las unidades Siberiana y Europea-Siniana, pero este solo tiene una sinapomorfía, por lo tanto, no se considera como un área de endemismo (Morrone, 1994; Espinosa *et al*., 2001, Morrone, 2009). Cada uno de estos clados (áreas de endemismo) fueron nombrados con base en su área geográfica-geológica, en su composición de las unidades fitogeográficas preestablecidas y/o las relaciones de estas, quedando con la siguiente nomenclatura: provincia Paleoecuatorial (clado A); dominio Ecuatorial-Eurosiniano (clado B); región Laurásica (clado C) y reino Pangea (clado D) (Figuras 5-8).

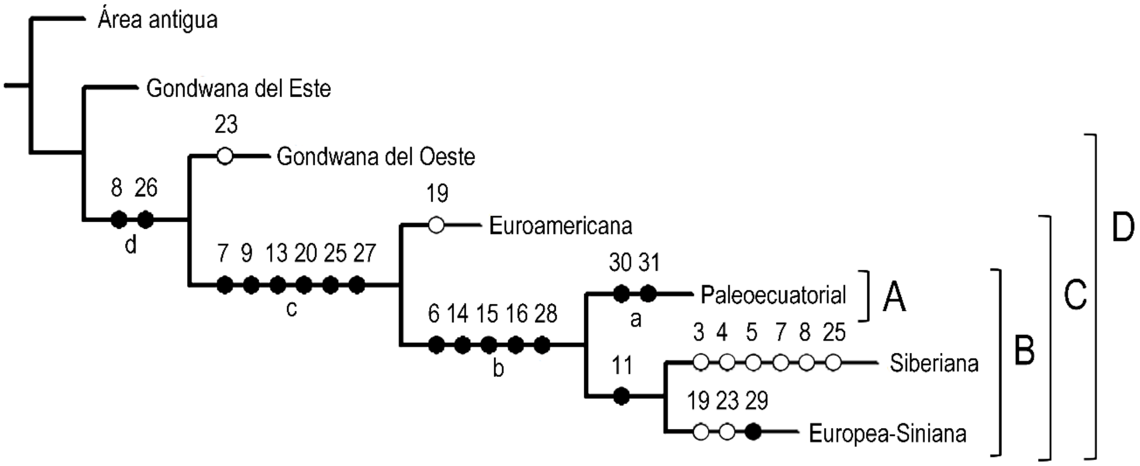


Figura 4. Cladograma de áreas de las unidades fitogeográficas del Jurásico Medio. A–D son las cuatro áreas de endemismo definidas por dos o más especies en común (sinapormorfías a-d, ver Tabla 1). A, provincia Paleoecuatorial; B, dominio Ecuatorial-Eurosiniano; C, región Laurásica; D, reino Pangea.

Los nodos (Tabla 1) que sustentan estas áreas de endemismo están apoyados por al menos dos géneros (clado A y D), cinco y seis (clado B y C respectivamente). El área de endemismo del reino Pangea (clado D) se sustenta por los géneros *Zamites* y *Brachyphyllum*, una bennettital y pinal respectivamente. A continuación, la región Laurásica (clado C) es un clado sustentado por seis géneros (*Wiellandiella*, *Czekanowskia*, *Eretmophyllum*, *Sphenobaiera*, *Pseudoctenis* y *Nilssonia*) de las Bennettitales, Czekanowskiales, Ginkgoales y Cycadales. El clado B del dominio Ecuatorial-Eurosiniano se sustenta por cinco géneros (*Williamsoniella, Ginkgoidium, Ginkgoites, Karkenia* y *Podozamites*), en este caso únicamente tres órdenes, Bennettitales, Ginkgoales y Pinales. Por último, la provincia Paleoecuatorial (clado A) es soportado por los géneros *Mexiglossa* y *Perezlaria* ambos de posición incierta (*Incertae sedis*), pero con afinidades a gimnospermas (Delevoryas & Gould, 1971; Delevoryas & Person, 1975).

Tabla 1. Clados y nodos del cladograma de áreas, denotando las sinapomorfias encontradas (géneros), su orden taxonómico y el esquema de regionalización.

Área	Nodo	Géneros	Orden/categoría taxonómica	Regionalización
A	a	*Mexiglossa;* *Perezlaria*	Incertae sedis	Provincia Paleoecuatorial
B	b	*Williamsoniella;* *Ginkgoidium;* *Ginkgoites,* *Karkenia;* *Podozamites*	Bennettitales; Ginkgoales; Pinales	Dominio Ecuatorial-Eurosiniano
C	c	*Wielandiella;* *Czekanowskia;* *Eretmophyllum;* *Sphenobaiera;* *Pseudoctenis;* *Nilssonia*	Bennettitales; Czekanowskiales; Ginkgoales; Cycadales	Región Laurásica
D	d	*Zamites;* *Brachyphyllum*	Bennettitales; Pinales	Reino Pangea

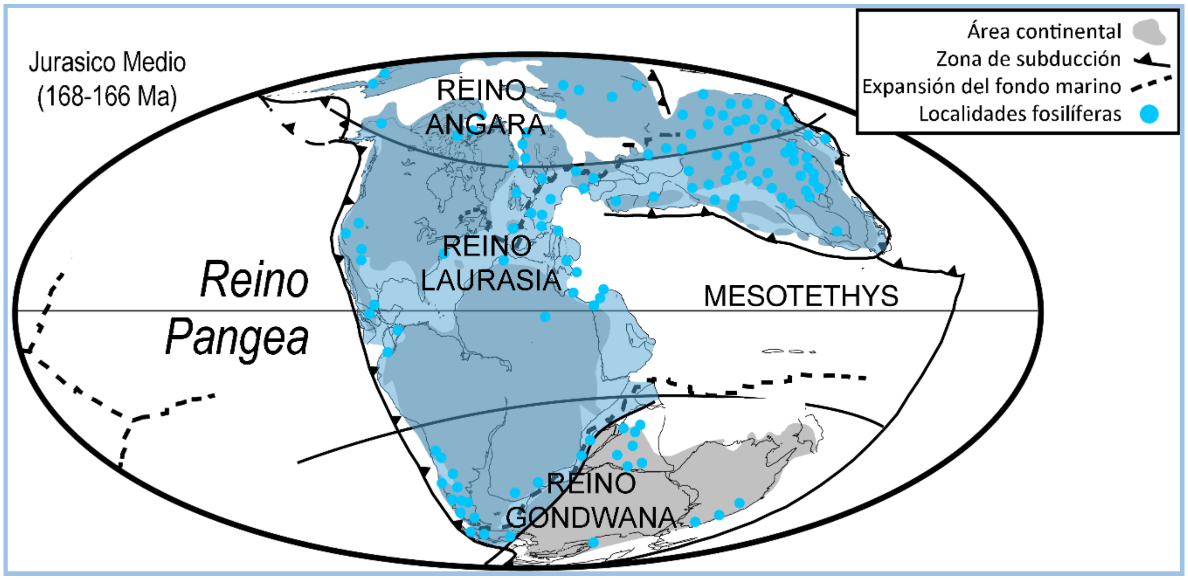


Figura 5. Mapa paleogeográfico del Jurásico Medio con el polígono del reino Pangea en azul celeste superpuesto a las áreas de los reinos de Angara, Laurasia y Gondwana *sensu* Meyen (1987).

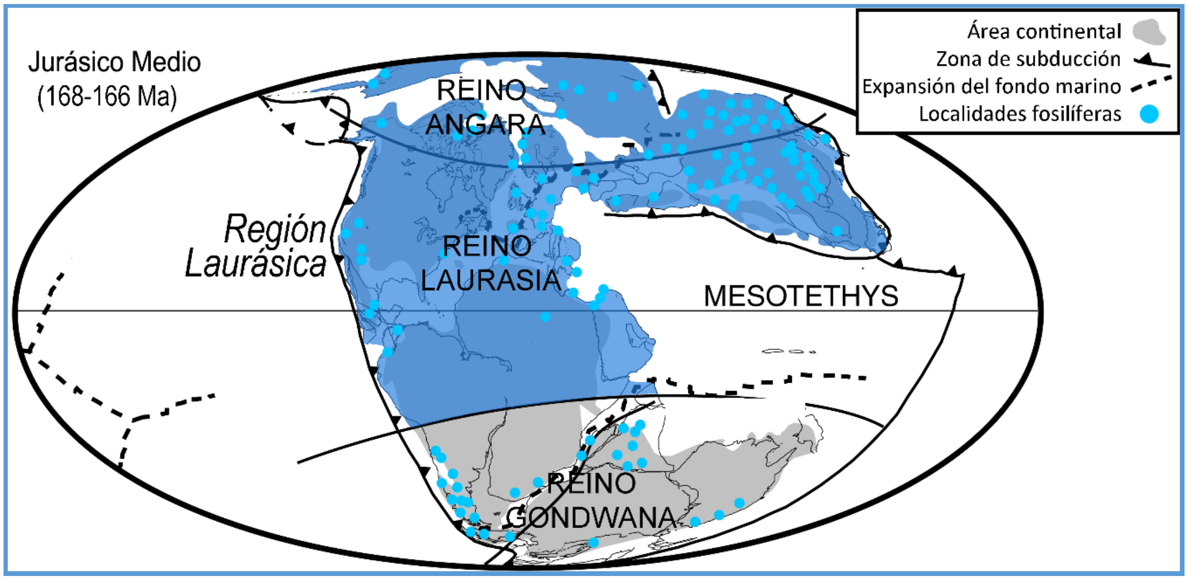


Figura 6. Mapa paleogeográfico del Jurásico Medio con el polígono de la región Laurásica en azul marino superpuesto a las áreas de los reinos de Angara, Laurasia y Gondwana *sensu* Meyen (1987).

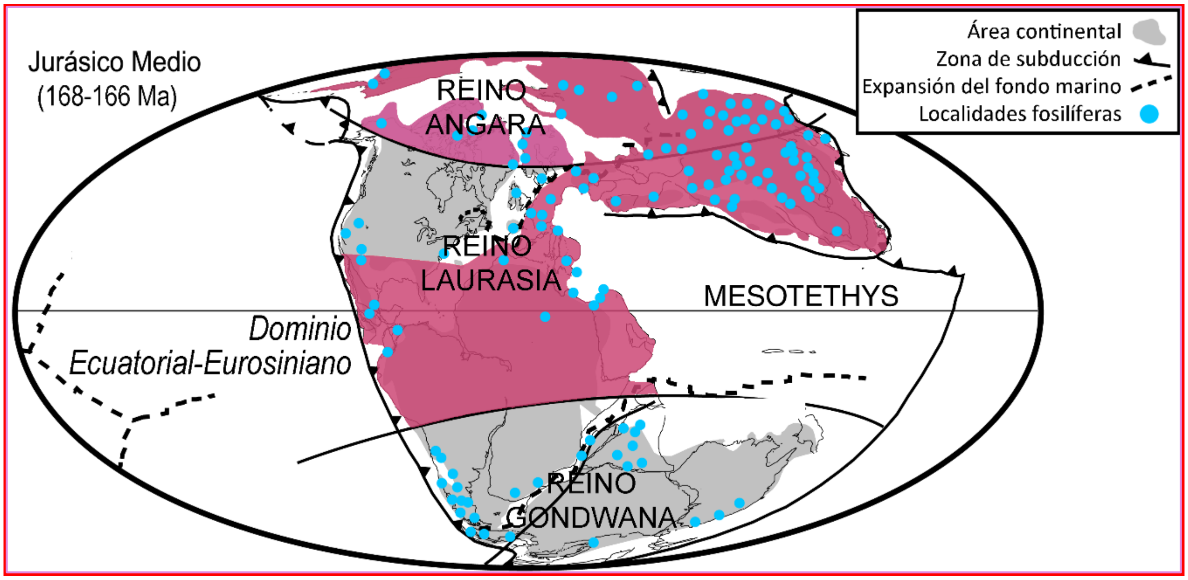


Figura 7. Mapa paleogeográfico del Jurásico Medio con el polígono de la Dominio Ecuatorial-Eurosiniano en rosa superpuesto a las áreas de los reinos de Angara, Laurasia y Gondwana *sensu* Meyen (1987).

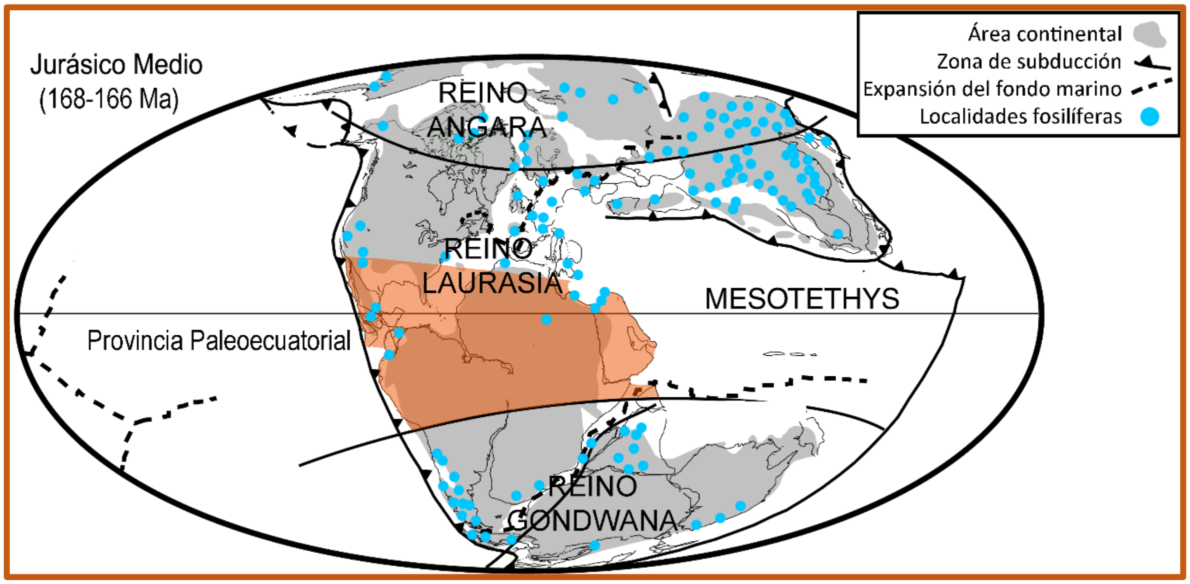


Figura 8. Mapa paleogeográfico del Jurásico Medio con el polígono de la provincia Paleoecuatorial en anaranjado superpuesto a las áreas de los reinos de Angara, Laurasia y Gondwana *sensu* Meyen (1987).

ANÁLISIS DE RESULTADOS

El análisis de parsimonia de endemismos (PAE) elaborado en este estudio permite discutir dos resultados principales: en el primero de estos se demuestra que no es posible reconocer un patrón de equivalencia o correlación entre las unidades fitogeográficas de Meyen (1987) y McLoughlin (2001) con las obtenidas en este estudio (Figuras 3-8). La única posible equivalencia entre las propuestas previas y los resultados de este estudio es la unidad fitogeográfica paleoecuatorial (Figura 3 y 8). Aunque el área de estas unidades fitogeográficas y el nombre serían los mismos, la equivalencia en el nivel dentro del esquema jerárquico no lo son. La unidad fitogeográfica denominada paleoecuatorial corresponde a un área para Meyen (1987), recordemos que esta es la segunda categoría en su esquema, y para McLoughlin (2001) corresponde a una provincia, la tercera categoría dentro del mismo esquema. Mientras que, aquí resultó como una provincia, que es la cuarta categoría y es la unidad básica en el esquema de regionalización empleado (Ebach *et al.*, 2008; Escalante, 2009). En este caso la provincia es la unidad más pequeña identificable dentro de este esquema y prácticamente no habría otras unidades anidadas o incluidas dentro de esta. Aunque hay algunos autores que llegan a sugerir distritos como la unidad más pequeña (Escalante, 2009), este no es el caso. Esto indica una obvia incompatibilidad (Cuadro 1) de la provincia Paleoecuatorial de este estudio con la posición del área (Paleo)Ecuatorial de Meyen (1987) y con la provincia Paleoecuatorial de McLoughlin (2001), ya que estas dos últimas unidades tendrían incluidas entre dos y tres unidades del siguiente orden de magnitud (Eldredge, 1997). El segundo resultado principal es el reconocimiento de un nuevo esquema de regionalización fitogeográfica para el Jurásico Medio, el cual será discutido más adelante.

La propuesta de Meyen (1987) constituye el primer esfuerzo por regionalizar fitogeográficamente la historia de las floras desde el Devónico hasta la actualidad con base en las afinidades taxonómicas y la abundancia de sus registros en las localidades fosilíferas. Tradicionalmente, Dobruskina (1994), Anderson *et al*., (1999, 2007), McLoughlin (2001), Artabe *et al*., (2003), Kustatscher *et al.*, (2018) y McLoughlin *et al.*, (2018), entre otros, siguieron la regionalización del Mesozoico propuesta por Meyen (1987). En específico para el Jurásico, además de los reinos ya mencionados, Meyen (1987) propone tres áreas: (Paleo)Ecuatorial, Siberiana y Notal; así como tres provincias: Europea y las de Asia Central y Oriental, pero no completa su esquema con las unidades más pequeñas: distritos o regiones. Sin embargo, este esquema de regionalización, a pesar de ser la base de varios estudios no fue reevaluado utilizando una metodología diferente. Únicamente, se llegó a sugerir cambios o nuevas propuestas en las provincias, pero empleando la misma metodología (McLoughlin, 2001). McLoughlin (2001), menciona que entre Gondwana y Laurasia hay varios elementos generalizados a nivel de orden y familia, pero con un evidente “provincialismo” de especies y sugiere las denominadas mayores provincias: Siberiana, Europea-Siniana, Paleoecuatorial, y las de Gondwana del Este y Oeste. Pero, a pesar de ello solo se enfoca en la descripción de las provincias de Gondwana. Además, no hay equivalencia entre las provincias de Meyen (1987) y las de McLoughlin (2001), ya que, por ejemplo, las provincias Europea y las de Asia Central y Oriental estarían incorporadas en la provincia Europea-Siniana. Por lo tanto, esto deja al descubierto una problemática en la regionalización fitogeográfica tanto del Jurásico como de todo el Mesozoico. Por un lado, debido a la falta de actualización de nuevos registros paleoflorísticos en el esquema de Meyen (1987) y de una reevaluación con base en diferentes metodologías que evalúen la naturalidad de las unidades fitogeográficas (Morrone, 2001; Escalante, 2009), y por otro lado, la falta de claridad en los criterios empleados para seguir tradicionalmente y/o modificar ocasionalmente este esquema de regionalización y sus unidades fitogeográficas (Meyen, 1987; Dobruskina, 1994; Anderson *et al*., 1999, 2007; McLoughlin, 2001; Artabe *et al*., 2003; Kustatscher *et al*., 2018; McLoughlin *et al.,* 2018).

Entonces, el reconocimiento de un nuevo esquema de regionalización fitogeográfica para el Jurásico Medio (Figura 9) está fundamentado en las áreas de endemismo identificadas mediante el uso del Análisis de Parsimonia de Endemismos (Figuras 4-9). Estas están sustentadas por el patrón de distribución de 32 géneros y esto permite visualizar un arreglo sucesivamente anidado entre estas áreas (Figura 4). Este arreglo puede aún ser enriquecido y puesto a prueba con la adición de otros elementos florísticos, por ejemplo, de pteridofitas y/o inclusive de vertebrados e invertebrados continentales. Por lo pronto, el uso de los principales géneros de los órdenes de gimnospermas muestra este arreglo jerárquico, donde las relaciones del cladograma indican afinidades históricas producto de eventos de dispersión y/o vicariantes (Morrone, 2004). Considerando el escenario geográfico ancestral, es decir la existencia y extensión de Pangea, como el sustrato en donde estas gimnospermas pudieron dispersarse y ampliar su rango de distribución, se puede visualizar que el área del reino Pangea corresponde a la máxima movilidad de las Bennettitales y Pinales principalmente desde el Triásico y hasta el Jurásico Temprano (Anderson et al., 2007; Nance *et al*., 2014). Posteriormente las barreras geográficas y condiciones climáticas latitudinales asociadas a la fragmentación de Pangea (Rees *et al.,* 1999, 2004; Nance *et al.,* 2014; Martini *et al*., 2016) pudieron ser los factores extrínsecos que comenzaron a fragmentar las distribuciones de estas gimnospermas propiciando la evolución aislada en la región Laurásica, en el dominio Ecuatorial-Siberiano y la provincia Paleoecuatorial hacia el Jurásico Medio (Figuras 5-8). Este proceso vicariante puede ser el posible responsable de la marcada diferenciación a nivel de especie en las diferentes unidades geográficas y la distribución local restringida de estas.

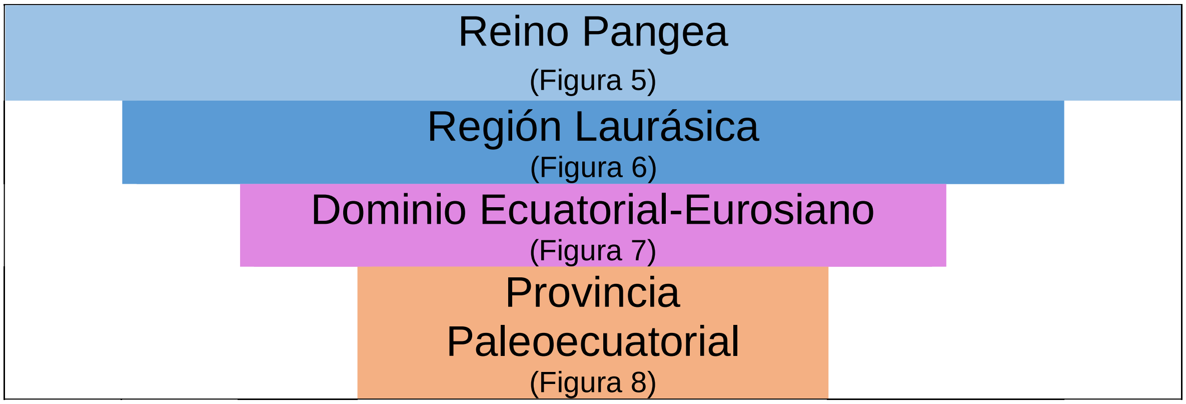


Figura 9. Propuesta del esquema de regionalización fitogeográfica del Jurásico Medio con base en análisis de parsimonia de endemismos de seis órdenes de gimnospermas.

Por otro lado, una problemática evidente es que los límites de las unidades fitogeográficas del Jurásico no son claros y distinguibles a la escala continental de Pangea (Meyen, 1987; McLoughlin, 2001). Esta ambigüedad podría influir en la inclusión de algunas localidades fosilíferas en una u otra área de distribución. Por ejemplo, las localidades que están en el límite entre los reinos de Angara y Laurasia, o entre las provincias de flora Euroamericana y Europea-Sineana (Meyen, 1987; McLoughlin, 2001). Esta dificil ubicación para cada localidad debe revisarse a detalle en estos límites. Meyen (1987) plantea los límites entre sus unidades fitogeográficas como límites ecológicos, transición entre las zonas templadas del norte y sur, y la región tropical (Figura 1). Sin embargo, también hizo énfasis en que su propuesta no debía ser tratada como un mapa paleoclimático, ya que los límites entre las unidades fitogeográficas pudieron no estar asociados con las divisiones climáticas, sino con barreras geográficas. En este sentido, se observa que las unidades fitogeográficas de Meyen (1987) no son congruentes con las propuestas de los biomas (Rees *et al*., 1999) y/o mapas paleoclimáticos (Scotese *et al*., 2014) para el Jurásico. El caso particular de la provincia Paleoecuatorial tendría una aparente congruencia con el bioma de verano húmedo propuesto por Rees et al. (1999) (ver figuras 2 y 8 de este capítulo), sin embargo, los límites no son totalmente congruentes. Por otro lado, McLoughlin (2001) emplea las evidencias de expansión del fondo oceánico producto de la fragmentación de Pangea entre Norteamérica y Europa (océano Atlántico central), y entre África-Sudamérica y Antártica-India (océano Índico del oeste) (Metcalfe, 1996; Ziegler *et al*., 2003) para sustentar su propuesta de límites entre las provincias respectivas para ambos lados de estos rifts. Entonces, de manera general los límites de las demás unidades fitogeográficas de esta nueva propuesta (figuras 5-8) podrían ser revisados y reevaluados con base en criterios geológicos y paleoclimáticos, además de la clara distinción entre las localidades fosilíferas y su pertenencia a cada unidad geográfica irregular. No obstante, este análisis corresponde a una identificación de homología biogeográfica primaria (Morrone, 2001, 2004), la cual se considera como un primer paso en el reconocimiento de la historia geobiótica en común de los elementos florísticos del Jurásico Medio. Por lo tanto, se están identificando nuevos componentes bióticos que a la luz de datos filogenéticos deberán ser analizados y contrastados. Esto debido a que las relaciones entre las áreas están mejor fundamentadas a partir de patrones filogenéticos (Nelson & Platnick, 1981).

CONCLUSIONES

El análisis de parsimonia de endemismos elaborado en este estudio permitió evaluar la congruencia de la regionalización fitogeográfica tradicional del Mesozoico. Esta regionalización no mostró una congruencia con las unidades fitogeográficas obtenidas en este estudio. Las principales razones, la metodología empleada y el consecuente reconocimiento de los patrones de distribución, así como el incremento en nuevos datos de distribución de los taxones recientemente aportados a la paleobotánica del Jurásico. Esto permite proponer un nuevo esquema de regionalización fitogeográfica para el Jurásico Medio, y debela la posibilidad de aplicarlo para todo el Mesozoico, además de enriquecerlo con datos de otros grupos florísticos y zoológicos. Para formular futuras hipótesis evolutivas de los taxones de gimnospermas es necesaria la correlación con el contexto tectónico que fue evolucionando desde el Triásico con los últimos momentos de la extensa geografía de Pangea y su consecuente fragmentación y total separación hacia el Jurásico-Cretácico.

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EPÍLOGO (CONCLUSIONES)

Aunque el estudio de la flora del Jurásico en los afloramientos del sur de México inició desde hace más de 100 años, aún se continúa aportando nuevos registros y nuevas especies a la paleobotánica de este periodo. En este sentido, durante prácticamente todo este tiempo siempre se abordó el estudio básico del registro fósil, es decir, la descripción de especies. Lo que dejó en un segundo plano la exploración de nuevos afloramientos, la consolidación taxonómica de aquellos taxones que necesitan de revisión y la realización de análisis fitogeográficos locales y/o a nivel mundial. Es decir, solo se habría trabajado sobre la taxonomía alfa y poco se habría explorado la posibilidad de ir completando el esquema de estudio sistemático hacia la taxonomía beta y gamma. En particular el orden de las Bennettitales, a pesar de ser el grupo de gimnospermas con mayor abundancia y riqueza en las localidades fosilíferas de esta región, no había sido revisado bajo este enfoque sistemático. Por lo tanto, aquí se realizó el primer estudio paleobotánico de este orden en el área noroccidental de Oaxaca. Esto permitió abordar estas tres etapas, taxonomía alfa, beta y gamma e ir completando dicho esquema sistemático.

Con respecto al trabajo con este esquema, se puede concluir que la exploración y el reconocimiento de afloramientos fosilíferos debe ir integrando la información estratigráfica y sedimentológica de cada localidad con los datos taxonómicos. Esto permite completar la información paleoambiental que nos ayuda, a su vez, a visualizar la distribución florística dentro de cada cuenca sedimentaria. Así mismo, esta integración, aporta datos de distribución espaciotemporal que se correlacionan entre cuencas y permite identificar los patrones de distribución fitogeográfica en la región. De este modo, se contribuyó a la taxonomía alfa y gamma. Además, la revisión de los taxones de Bennettitales reportados en el área de estudio permitió ubicar y confirmar aquellas especies validas, y también a los taxones que necesitan de revisión, en particular para definir su estatus a nivel de especie. Esto podrá, muy seguramente, incrementar la riqueza florística y aproximarse a la consolidación taxonómica en cada unidad litoestratigráfica. Es decir, complementar a la etapa beta del esquema.

Entonces, con los resultados alcanzados en esta tesis doctoral se contribuyó con nuevas especies y nuevos reportes de Bennettitales, los cuales están ubicados espaciotemporalmente y asociados el ambiente sedimentario correspondiente en cada unidad litoestratigráfica. Además, se propusieron patrones de distribución en las cuencas sedimentarias del Jurásico Temprano-Medio en el área de estudio que muestran hasta seis ensambles de Bennettitales. Esta distribución de los ensambles va del Toarciano al Calloviano en un rango de 19 Ma y el traslape en dicha distribución indica que corresponden a áreas de endemismo incorporadas en tres cuencas sedimentarias.

Importantes aportes taxonómicos del área de estudio han sido incorporados en los últimos 10 años, aproximadamente, incluyendo los realizados en este estudio, permitió revisar los patrones de distribución de ocho géneros de las Bennettitales a nivel mundial durante el Jurásico mediante un análisis de trazos. Los datos obtenidos permiten concluir que este grupo de plantas tuvo una amplia distribución durante todo el Jurásico, pero que fue reduciéndose hacia el Jurásico Tardío conforme las masas continentales se fueron separando más unas de otras por actividad tectónica. Esto permite observar que los eventos de dispersión durante el Triásico-Jurásico Temprano permitieron la máxima expansión de las Bennettitales en Pangea y que la posterior fragmentación fue causando la distribución restringida. Este patrón es identificado también en otros cinco órdenes de gimnospermas. El cual fue puesto al descubierto mediante un análisis de parsimonia de endemismos. Los resultados de este análisis son los más controversiales de este estudio. Esto sucede por la clara incongruencia entre la regionalización tradicional del Mesozoico seguida por varios autores y el nuevo esquema propuesto aquí. La regionalización que se reconoce con este análisis está constituida por el reino Pangea, la región Laurásica, el dominio Ecuatorial-Eurosiniano y la provincia Paleoecuatorial. Aunque aún existe la posibilidad de poder complementar este análisis y generar algunos cambios, por ahora es una primera hipótesis que nos genera la inquietud de revisar y reevaluar los patrones de distribución de las Bennettitales y otras gimnospermas durante el Jurásico. Para futuros aportes a este análisis será necesaria la integración de datos de distribución de grupos como las pteridospermas y los de fauna. En este sentido se podrá identificar los componentes bióticos integrados espaciotemporalmente durante el Jurásico y quizás explorar la paleobiogeografía del Mesozoico de forma integrativa.

Por lo tanto, el esquema sistemático empleado en este estudio muestra que es posible aplicarlo a los demás grupos de plantas con registro en el Jurásico del sur de México y otras regiones donde hay reportes. Esto fundamentará indudablemente un cambio en el paradigma paleobotánico de esta región y edad geológica. Que además podrá aportar datos suficientes para reconsiderar la importancia de los registros paleoflorísticos de México y su posición geográfica en el margen occidental de la Pangea ecuatorial, lo que podrá ser integrado al estudio y entendimiento de los procesos evolutivos de la flora que se desarrollaron durante la fragmentación de Pangea.

ANEXOS

Anexo 1. Relación de las localidades fosilíferas de los géneros de Bennettitales durante las tres épocas del Jurásico. Latitud y longitud en grados decimales.

Tabla 1. Jurásico Temprano.

Género	País	Latitud	Longitud
Anomozamites	México	3.3	-47.9
Anomozamites	Groenlandia	52.1	5.2
Anomozamites	Rumania	25.2	25.6
Anomozamites	Rumania	24.8	23.6
Anomozamites	China	33.5	122.2
Anomozamites	China	38.7	120.1
Anomozamites	China	40.5	121.9
Anomozamites	China	35.8	121.8
Anomozamites	China	38.7	124.9
Anomozamites	China	48.5	96.4
Anomozamites	China	45.2	109.2
Anomozamites	China	35.3	119.2
Anomozamites	China	49.3	136.9
Anomozamites	China	41.3	123.8
Anomozamites	China	55.4	135.2
Anomozamites	Japón	47.9	149.6
Anomozamites	Kazakstán	47.6	72.7
Anomozamites	Rusia	41.5	56.7
Anomozamites	Rusia	46.7	76.5
Anomozamites	Rusia	60.9	84.5
Anomozamites	Rusia	64.5	80.3
Anomozamites	Rusia	62.5	105
Anomozamites	Rusia	41	60
Anomozamites	Rusia	41.9	47.8
Anomozamites	Rusia	53	79.5
Anomozamites	Rusia	47.1	81.2
Anomozamites	Rusia	67.2	90.2
Anomozamites	Tayikistán	41.1	76.4
Anomozamites	Tayikistán	48.1	71.6
Anomozamites	Tayikistán	47.6	68.9
Anomozamites	Tayikistán	45.8	70.7
Anomozamites	Tayikistán	43.7	75.3
Anomozamites	Tayikistán	39.9	76.6
Anomozamites	Tayikistán	42.9	73.1
Anomozamites	Tayikistán	40	74.7
Anomozamites	Tayikistán	38.5	73
Anomozamites	Tayikistán	40.5	74.4
Otozamites	Italia	32.1	19.3
Otozamites	Italia	33.2	15.6
Otozamites	Serbia	26.5	23.2
Otozamites	Rumania	24.8	23.6
Otozamites	Polonia	40.8	26.7
Otozamites	México	3.3	-47.9
Otozamites	México	8.8	-46.4
Otozamites	Alaska	22.7	-76.9
Otozamites	Antártica	-57.4	-25
Otozamites	Argentina	-41.5	-28
Otozamites	Argentina	-36.6	-29.7
Otozamites	Argentina	-45.9	-25.2
Otozamites	Argentina	-44.5	-26.9
Otozamites	Argentina	-38.1	-30.1

Tabla 1. Jurásico Temprano, continuación

Género	País	Latitud	Longitud
Otozamites	Argentina	-32	-30.6
Otozamites	Argentina	-34	-30.6
Otozamites	Argentina	-47.9	-23.7
Otozamites	China	31.8	121.8
Otozamites	China	33.5	122.2
Otozamites	China	38.7	120.1
Otozamites	China	40.4	125.3
Otozamites	China	49.3	119.1
Otozamites	China	32.7	117.5
Otozamites	China	36	122.9
Otozamites	China	34.5	123.7
Otozamites	China	45.2	110.1
Otozamites	China	40.4	111.4
Otozamites	China	43.2	118.8
Otozamites	China	41.2	123.8
Otozamites	China	29.7	114.3
Otozamites	Irán	-13.1	47.5
Otozamites	Japón	47.9	149.6
Otozamites	Japón	46.4	145.4
Otozamites	Japón	48.2	147.8
Otozamites	Japón	46.1	139.8
Otozamites	Sudáfrica	-42.8	-3.2
Otozamites	Tayikistán	46.8	72.7
Otozamites	Tayikistán	48.1	71.6
Otozamites	Tayikistán	47.6	68.9
Otozamites	Venezuela	8.2	-42.4
Otozamites	Rumania	25.2	25.6

Género	País	Latitud	Longitud
Pterophyllum	Groenlandia	51.5	1.2
Pterophyllum	Groenlandia	52.1	5.2
Pterophyllum	Italia	32.1	19.3
Pterophyllum	Rumania	24.8	23.6
Pterophyllum	Polonia	40.8	26.7
Pterophyllum	Polonia	42.3	25.2
Pterophyllum	México	8.8	-46.4
Pterophyllum	Alaska	16.1	-76.6
Pterophyllum	Argentina	-36.6	-29.7
Pterophyllum	China	34.1	119.8
Pterophyllum	China	33.5	122.2
Pterophyllum	China	38.7	120.1
Pterophyllum	China	40.5	121.9
Pterophyllum	China	40.4	125.3
Pterophyllum	China	49.3	119.1
Pterophyllum	China	34.4	106.9
Pterophyllum	China	36	122.9
Pterophyllum	China	41.2	123.8
Pterophyllum	China	38.1	124.2
Pterophyllum	China	47.4	120
Pterophyllum	China	29.7	115
Pterophyllum	China	36.6	120.5
Pterophyllum	China	45.3	102.9
Pterophyllum	China	49.1	130.4
Pterophyllum	Georgia	41.2	47.4
Pterophyllum	Irán	-13.1	47.5

Tabla 1. Jurásico Temprano, continuación

Género	País	Latitud	Longitud
Pterophyllum	Japón	47.9	149.6
Pterophyllum	Japón	46.4	145.4
Pterophyllum	Japón	48.2	147.8
Pterophyllum	Kazakstán	53.1	63.4
Pterophyllum	Kazakstán	47.8	72.4
Pterophyllum	Kazakstán	57.2	81
Pterophyllum	Mongolia	55.1	95.5
Pterophyllum	Rusia	41.5	56.7
Pterophyllum	Rusia	64.5	80.3
Pterophyllum	Rusia	62.5	105
Pterophyllum	Rusia	50.3	144.8
Pterophyllum	Rusia	40.5	45.9
Pterophyllum	Rusia	53.2	79.8
Pterophyllum	Rusia	47.1	81.2
Pterophyllum	Tayikistán	41.1	76.4
Pterophyllum	Tayikistán	46.8	72.7
Pterophyllum	Tayikistán	48.1	71.6
Pterophyllum	Tayikistán	47.6	68.9
Pterophyllum	Tayikistán	45.8	70.7
Pterophyllum	Tayikistán	43.7	75.3
Pterophyllum	Tayikistán	40	74.7
Pterophyllum	Rumania	25.2	23.8
Pterophyllum	Rumania	25.2	25.6
Ptilophyllum	Italia	32.1	19.3
Ptilophyllum	Serbia	26.5	23.2
Ptilophyllum	Polonia	42.9	21.6
Ptilophyllum	México	3.3	-47.9
Ptilophyllum	México	8.8	-46.4
Ptilophyllum	Afganistán	30	70.6
Ptilophyllum	Argentina	-36.6	-29.7
Ptilophyllum	Argentina	-45.9	-25.2
Ptilophyllum	Argentina	-44.5	-26.9
Ptilophyllum	Argentina	-40.5	-28.4
Ptilophyllum	China	33.1	119.8
Ptilophyllum	China	38.7	120.1
Ptilophyllum	China	40.5	121.9
Ptilophyllum	China	36	120.8
Ptilophyllum	China	41.2	123.8
Ptilophyllum	China	38.1	124.2
Ptilophyllum	Irán	-11	47.9
Ptilophyllum	Japón	46.4	145.4
Ptilophyllum	Japón	48.2	147.8
Ptilophyllum	Japón	45.2	144.1
Ptilophyllum	Mongolia	60	90.6
Ptilophyllum	Mongolia	56.1	94.2
Ptilophyllum	Rusia	41.5	56.7
Ptilophyllum	Rusia	40.3	74.5
Ptilophyllum	Rusia	67.2	125
Ptilophyllum	Rusia	41.9	47.8
Ptilophyllum	Rusia	38.9	48
Ptilophyllum	Rusia	74.7	143.7
Ptilophyllum	Rusia	60.5	84.4
Ptilophyllum	Tayikistán	39.2	73.6
Ptilophyllum	Venezuela	8.2	42.4

Tabla 1. Jurásico Temprano, continuación

Género	País	Latitud	Longitud
Ptilophyllum	Rumania	25.2	23.8
Ptilophyllum	Rumania	25.2	25.6
Weltrichia	Antártica	-57.1	-25.4
Weltrichia	Italia	32.1	19.3
Weltrichia	Rumania	25.2	23.8
Williamsonia	Antártica	-57.1	-25.4
Williamsonia	Irán	-13.1	47.5
Williamsonia	Rusia	41.5	56.7
Williamsonia	Rusia	60.5	84.3
Williamsonia	Tayikistán	41.1	76.4
Williamsonia	Rumania	25.2	23.8
Williamsonia	Rumania	25.2	25.6
Williamsonia	México	3.3	-47.9
Williamsoniella	Kazakstán	47.8	72.4
Williamsoniella	Rumania	24.8	23.6
Williamsoniella	Rusia	40.3	74.5
Williamsoniella	Rusia	44.9	56.8
Zamites	Antártica	-57.4	-25
Zamites	China	37.7	120.9
Zamites	China	48.5	128.7
Zamites	Irán	-13.1	47.5
Zamites	Italia	33.2	15.6
Zamites	Japón	47.9	149.6
Zamites	Japón	46.1	139.8
Zamites	México	3.3	-47.9
Zamites	México	8.8	-46.4
Zamites	Rumania	25.2	23.8
Zamites	Romania	25.2	25.6
Zamites	Serbia	26.5	23.2
Zamites	Tayikistán	48.1	71.6

Tabla 2. Jurásico Medio.

Género	País	Latitud	Longitud
Anomozamites	Reino Unido	42.9	9.6
Anomozamites	México	9.4	-48.1
Anomozamites	México	8.9	-47.5
Anomozamites	Chile	-18.7	-35
Anomozamites	China	34	115.9
Anomozamites	China	43.3	91.3
Anomozamites	China	33.8	111.8
Anomozamites	China	45.5	128.6
Anomozamites	China	44.5	126
Anomozamites	China	44.7	131.1
Anomozamites	China	34.8	110
Anomozamites	China	49.6	135.6
Anomozamites	China	45	131.2
Anomozamites	China	44	129.3
Anomozamites	China	34	124.9
Anomozamites	Georgia	3	48.1
Anomozamites	Georgia	2.7	47.9
Anomozamites	India	-23.8	32.5
Anomozamites	Japón	42.3	135.9
Anomozamites	Kazakstán	42.7	74
Anomozamites	Kazakstán	49.4	74.2
Anomozamites	Kazakstán	51.6	75.9

Tabla 2. Jurásico Medio, continuación

Género	País	Latitud	Longitud
Anomozamites	Rusia	42.7	78.4
Anomozamites	Rusia	57.5	85
Anomozamites	Rusia	37.9	73.9
Anomozamites	Rusia	45.2	57.2
Anomozamites	Rusia	37.5	53.9
Anomozamites	Rusia	39.1	74.2
Anomozamites	Rusia	40.9	56.4
Anomozamites	Rusia	42	78.7
Anomozamites	Rusia	48.4	60.1
Anomozamites	Rusia	40.2	59.9
Anomozamites	Rusia	45.8	58.1
Anomozamites	Rusia	58.9	104.9
Anomozamites	Rusia	58.7	86.3
Anomozamites	Rusia	3.7	48.5
Anomozamites	Rusia	60.1	77
Anomozamites	Rusia	61	92.8
Anomozamites	Tayikistán	39.9	75.6
Anomozamites	Tayikistán	38.7	76.3
Anomozamites	Tayikistán	39.3	74.1
Anomozamites	Tayikistán	38.8	73.9
Otozamites	Reino Unido	43.6	9.1
Otozamites	Reino Unido	43.4	9.6
Otozamites	Reino Unido	45.9	4.6
Otozamites	Reino Unido	47.7	6.2
Otozamites	Francia	36.5	10.9
Otozamites	Bulgaria	22.5	29.8
Otozamites	Suiza	37.2	17.8
Otozamites	México	9.4	-48.1
Otozamites	México	8.9	-47.5
Otozamites	Antártica	-51.5	-28.3
Otozamites	Argentina	-41.6	-28.6
Otozamites	Argentina	-47.4	-31.5
Otozamites	Argentina	-40	-29.4
Otozamites	Argentina	-44.9	-25.6
Otozamites	Argentina	-36.6	-31
Otozamites	Australia	-69.4	94.8
Otozamites	Azerbaiyán	30.3	52.9
Otozamites	Bielorrusia	45.5	33
Otozamites	China	34	115.9
Otozamites	China	43.2	114.6
Otozamites	China	29.1	123.5
Otozamites	China	48.5	128.7
Otozamites	China	42.1	106
Otozamites	China	43.9	117.3
Otozamites	China	34	124.9
Otozamites	Georgia	3.7	48.4
Otozamites	Georgia	2	47.9
Otozamites	Georgia	1.5	46.9
Otozamites	India	-23.8	32.5
Otozamites	India	-34.4	30.8
Otozamites	Irán	29.1	60
Otozamites	Israel	9.7	28
Otozamites	Japón	42.3	135.9
Otozamites	Kazakstán	49.9	74.2

Tabla 2. Jurásico Medio, continuación

Género	País	Latitud	Longitud
Otozamites	Libia	12.2	11.5
Otozamites	Mozambique	-40	0.5
Otozamites	Nueva Zelanda	-78.3	41.4
Otozamites	Rusia	37.9	73.9
Otozamites	Rusia	38.4	74.4
Otozamites	Rusia	9.4	50
Otozamites	Rusia	48.4	40.3
Otozamites	Rusia	40.1	59.2
Otozamites	Rusia	3.7	48.5
Otozamites	Tayikistán	37.7	75.8
Otozamites	Tayikistán	38.1	73.8
Otozamites	Tayikistán	39.3	74.1
Otozamites	Ucrania	42.6	42.1
Otozamites	Uzbekistán	40.9	78
Otozamites	Uzbekistán	37.7	72.9
Otozamites	Egipto	14.1	25.9
Otozamites	Francia	34.1	13.7
Otozamites	Francia	38.1	10.8
Otozamites	Francia	37.4	15.8
Otozamites	Francia	39.7	12.3
Pterophyllum	Reino Unido	42.9	9.6
Pterophyllum	Suiza	37.2	17.8
Pterophyllum	Noruega	54	16.2
Pterophyllum	México	9.4	-48.1
Pterophyllum	Bielorrusia	44.3	33.8
Pterophyllum	China	34	115.9
Pterophyllum	China	43.3	91.3
Pterophyllum	China	34.5	124.2
Pterophyllum	China	33.8	111.8
Pterophyllum	China	43.7	115.8
Pterophyllum	China	45.5	128.6
Pterophyllum	China	32.4	109.2
Pterophyllum	China	44.5	126
Pterophyllum	China	44.7	131.1
Pterophyllum	China	38	111.2
Pterophyllum	China	34.8	110
Pterophyllum	China	50.1	134.3
Pterophyllum	China	44	129.3
Pterophyllum	Georgia	3.7	48.4
Pterophyllum	Georgia	2	47.9
Pterophyllum	Japón	42.3	135.9
Pterophyllum	Kazakstán	51.8	75.9
Pterophyllum	Kazakstán	49.4	74.2
Pterophyllum	Mongolia	55.1	95.5
Pterophyllum	Nueva Zelandia	-78.3	41.4
Pterophyllum	Nueva Zelandia	-77.5	56.6
Pterophyllum	Rusia	38.4	74.4
Pterophyllum	Rusia	37.5	53.9
Pterophyllum	Rusia	42	78.7
Pterophyllum	Rusia	9.4	50
Pterophyllum	Rusia	40.5	57.3
Pterophyllum	Rusia	40.2	59.9
Pterophyllum	Rusia	60.1	77
Pterophyllum	Rusia	4.1	48.5

Tabla 2. Jurásico Medio, continuación

Género	País	Latitud	Longitud
Pterophyllum	Tayikistán	38.7	76.3
Pterophyllum	Tayikistán	39.3	74.1
Pterophyllum	Turkmenistán	36.5	60.3
Pterophyllum	Ucrania	42.6	42.1
Pterophyllum	Ucrania	41.9	30.7
Pterophyllum	Uzbekistán	40.8	74.9
Pterophyllum	Uzbekistán	38.3	73.2
Pterophyllum	Francia	39.7	12.3
Pterophyllum	Argentina	-44.6	-29.5
Pterophyllum	Australia	-69.4	94.8
Pterophyllum	Chile	-18.7	-35
Pterophyllum	India	-23.8	32.5
Ptilophyllum	Reino Unido	43.6	9.1
Ptilophyllum	Reino Unido	41.4	9
Ptilophyllum	Reino Unido	42.9	9.6
Ptilophyllum	Francia	36.5	10.9
Ptilophyllum	Suiza	37.2	17.8
Ptilophyllum	México	9.4	-47.9
Ptilophyllum	Afganistán	26.6	75.3
Ptilophyllum	Antártica	-51.5	-28.3
Ptilophyllum	Argentina	-47.4	-31.5
Ptilophyllum	Argentina	-44.9	-25.6
Ptilophyllum	Argentina	-37.6	-30.8
Ptilophyllum	Australia	-66	91.8
Ptilophyllum	Azerbaiyán	30.3	52.9
Ptilophyllum	Bielorrusia	44.2	33.8
Ptilophyllum	Chile	-18.7	-35
Ptilophyllum	China	33.8	111.8
Ptilophyllum	China	32.4	109.2
Ptilophyllum	China	33.2	116.2
Ptilophyllum	China	39	110.5
Ptilophyllum	China	41.1	83.7
Ptilophyllum	China	34	124.9
Ptilophyllum	Georgia	3.8	48.7
Ptilophyllum	Georgia	2	47.9
Ptilophyllum	Georgia	4.2	48.5
Ptilophyllum	Georgia	1.5	46.9
Ptilophyllum	India	-23.8	32.5
Ptilophyllum	India	-34.4	30.8
Ptilophyllum	Irán	29.1	60
Ptilophyllum	Israel	9.7	29
Ptilophyllum	Japón	42.3	135.9
Ptilophyllum	Kazakstán	47.5	58.1
Ptilophyllum	Nueva Zelanda	-78.3	41.4
Ptilophyllum	Rusia	37.9	73.9
Ptilophyllum	Rusia	37.5	53.9
Ptilophyllum	Rusia	40.9	56.4
Ptilophyllum	Rusia	42	78.7
Ptilophyllum	Rusia	44.8	56.8
Ptilophyllum	Rusia	48.4	60.1
Ptilophyllum	Rusia	40.1	58.5
Ptilophyllum	Rusia	45.1	58.9
Ptilophyllum	Rusia	44.3	58.8
Ptilophyllum	Rusia	3.4	48.4

Tabla 2. Jurásico Medio, continuación

Género	País	Latitud	Longitud
Ptilophyllum	Rusia	9.8	50.6
Ptilophyllum	Tayikistán	37.4	72.6
Ptilophyllum	Tayikistán	37.7	75.8
Ptilophyllum	Tayikistán	38.1	73.8
Ptilophyllum	Turkmenistán	36.5	60.3
Ptilophyllum	Ucrania	41.9	30.7
Ptilophyllum	Ucrania	41.8	40.2
Ptilophyllum	Uzbekistán	40.9	78
Ptilophyllum	Uzbekistán	37.7	72.9
Ptilophyllum	Venezuela	10	42.6
Weltrichia	India	-23.8	32.8
Weltrichia	Reino Unido	43.6	9.1
Weltrichia	Reino Unido	41.4	9
Weltrichia	México	9.4	-47.9
Williamsonia	Reino Unido	44	9.2
Williamsonia	Reino Unido	42.9	9.6
Williamsonia	Francia	36.5	10.9
Williamsonia	México	9.4	-47.9
Williamsonia	Afganistán	26.4	75.4
Williamsonia	Australia	66	91.8
Williamsonia	China	44.6	128.3
Williamsonia	Georgia	3.7	48.4
Williamsonia	India	-23.8	32.5
Williamsonia	Irán	29.1	60
Williamsonia	Israel	9.7	29
Williamsonia	Kazakstán	42.7	74
Williamsonia	Rusia	38.4	74.4
Williamsonia	Rusia	9.4	50
Williamsonia	Rusia	3.7	48.5
Williamsonia	Tayikistán	38.6	74
Williamsonia	Tayikistán	38.7	76.3
Williamsonia	Ucrania	42.6	42.1
Williamsonia	Uzbekistán	38.3	73.2
Williamsoniella	Rusia	59.6	88.7
Williamsoniella	Turkmenistán	36.5	60.3
Williamsoniella	Uzbekistán	37.7	72.9
Williamsoniella	México	9.4	-47.1
Zamites	Argentina	-40	-29.4
Zamites	Argentina	-36.6	-31
Zamites	Azerbaiyán	30.3	52.9
Zamites	Bielorrusia	44.3	33.8
Zamites	China	42.1	82.8
Zamites	China	41.9	110
Zamites	Francia	38.1	10.8
Zamites	Francia	37.4	15.8
Zamites	Francia	39.7	12.3
Zamites	Georgia	2	47.9
Zamites	Georgia	3.7	48.4
Zamites	Japón	42.3	135.9
Zamites	México	9.4	-47.9
Zamites	México	9.4	-47.1
Zamites	México	8.9	-47.5
Zamites	Mongolia	49.2	119
Zamites	Rusia	9.4	50

Tabla 2. Jurásico Medio, continuación

Género	País	Latitud	Longitud
Zamites	Suiza	37.2	17.8
Zamites	Ucrania	42.6	42.1
Zamites	Reino Unido	42.9	9.6
Zamites	Reino Unido	48.6	6
Zamites	Reino Unido	47.7	6.2

Tabla 3. Jurásico Tardío.

Género	País	Latitud	Longitud
Anomozamites	EUA	42.6	53.8
Anomozamites	China	43.6	127
Anomozamites	China	43.8	132.2
Anomozamites	China	50.9	124
Anomozamites	Colombia	4.4	-45
Anomozamites	India	-34.3	34.7
Anomozamites	Kazakstán	41.1	73.3
Anomozamites	Rusia	54.5	128.9
Anomozamites	Rusia	62.7	137.8
Anomozamites	Rusia	53.6	136.6
Anomozamites	Sri Lanka	-39.2	17.6
Otozamites	Reino Unido	48.6	6
Otozamites	Portugal	34.2	2.2
Otozamites	Portugal	33.7	1.9
Otozamites	Francia	36.5	10.3
Otozamites	Antártica	-56.3	-32.6
Otozamites	Antártica	-64.9	-15.6
Otozamites	China	51.3	130.8
Otozamites	China	41	100.1
Otozamites	China	24.5	120.7
Otozamites	China	43.8	132.2
Otozamites	China	38.3	123.6
Otozamites	China	46.6	122.8
Otozamites	China	33	119.7
Otozamites	China	26.7	120.4
Otozamites	China	28	122
Otozamites	China	29.7	119.8
Otozamites	China	40.3	104.5
Otozamites	China	34.9	97.2
Otozamites	China	34.1	121.3
Otozamites	China	31	123
Otozamites	China	49.3	133.9
Otozamites	China	40.9	125
Otozamites	China	32.3	123.5
Otozamites	China	25.7	122.6
Otozamites	Colombia	4.4	-45
Otozamites	India	-26.1	37.4
Otozamites	Japón	46.4	144.7
Otozamites	Japón	43.3	139.2
Otozamites	Kazakstán	41.1	73.3
Otozamites	Sri Lanka	-39.2	17.6
Pterophyllum	Francia	38	14.7
Pterophyllum	India	-26.1	-37.4
Pterophyllum	Japón	45.9	144.6
Pterophyllum	Japón	43.3	139.2

Tabla 3. Jurásico Tardío, continuación

Género	País	Latitud	Longitud
Pterophyllum	Kazakstán	41.1	73.3
Pterophyllum	Portugal	34.2	2.2
Pterophyllum	Rusia	54.5	128.9
Pterophyllum	Rusia	55.3	125.7
Pterophyllum	Rusia	58.9	121
Pterophyllum	Rusia	53.3	135.9
Pterophyllum	Rusia	78.4	154.6
Pterophyllum	Rusia	63.6	124.8
Ptilophyllum	Reino Unido	48.6	6
Ptilophyllum	Antártica	-64.9	-15.6
Ptilophyllum	China	27.5	121.5
Ptilophyllum	China	24.5	120.7
Ptilophyllum	China	31.3	118.3
Ptilophyllum	China	32	121.7
Ptilophyllum	China	27.2	123
Ptilophyllum	China	30.3	124.1
Ptilophyllum	China	25.7	122.6
Ptilophyllum	Colombia	4.4	-45
Ptilophyllum	India	-41.4	35.3
Ptilophyllum	India	-27.5	36
Ptilophyllum	India	-34.3	34.7
Ptilophyllum	India	-26.1	37.4
Ptilophyllum	India	-41	41.2
Ptilophyllum	Japón	45.9	144.6
Ptilophyllum	Kazakstán	41.1	73.3
Ptilophyllum	Malasia	4.2	117.5
Ptilophyllum	Sri Lanka	-39.2	17.6
Weltrichia	Japón	45.9	144.6
Weltrichia	Kazakstán	41.1	73.3
Weltrichia	EUA	42.6	-53.8
Williamsonia	Reino Unido	48.6	6
Williamsonia	Francia	40.1	14.5
Williamsonia	Francia	37	15.2
Williamsonia	Francia	41.5	11
Williamsonia	China	49.3	133.9
Williamsonia	Japón	45.9	144.6
Williamsonia	Japón	42.3	135.9
Williamsonia	Kazakstán	41.1	73.3
Williamsonia	Antártica	-56.3	-32.6
Williamsonia	Alemania	39.2	17.5
Williamsoniella	Kazakstán	41.1	73.3
Zamites	China	32.7	122.8
Zamites	China	38.3	123.6
Zamites	China	46.6	122.8
Zamites	China	52.3	127.1
Zamites	China	25.1	121.4
Zamites	China	31	123
Zamites	China	49.3	133.9
Zamites	China	32.3	123.5
Zamites	Colombia	4.4	-45
Zamites	Francia	37.5	11.5
Zamites	Francia	40.1	14.5
Zamites	Francia	37.5	15.2
Zamites	Francia	36.7	14.9

Tabla 3. Jurásico Tardío, continuación

Género	País	Latitud	Longitud
Zamites	Francia	38	14.7
Zamites	Alemania	40.1	19.1
Zamites	Alemania	39.2	17.6
Zamites	Japón	45.9	144.6
Zamites	Kazakstán	41.1	73.3
Zamites	Portugal	34.2	-2
Zamites	Turquía	14.7	26.1
Zamites	EUA	42.6	53.8

Anexo 2. Matriz de datos de las unidades geográficas irregulares *vs* la presencia/ausencia de los géneros de los principales órdenes de gimnospermas del Jurásico Medio.

32	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
7	A1	O	P1	P2	W1	W2	W3	W4	Z	C1	L	P3	G1	E	G2	G3	K	S1	C2	C3	S2	B	P4	A2	T	P5	B2	N1	P6	N2	M	P7
Región raíz ancestral	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siberiana	1	1	1	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	0	1	1	0	0	1	0	1	1	1	0	0	0
Europeana-Siniana	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	0
Euroamericana	1	1	1	1	1	1	0	1	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0
Paleoequatorial	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	1	0	1	1
Gondwana del Oeste	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0
Gondwana del Este	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Abreviaciones en orden alfabético: A1: *Anomozamites*; A2: *Agathoxylon*; B1: *Baiera*; B2: *Brachyphyllum*; C1: *Czekanowskia*; C2: *Caytonianthus*; C3: *Caytonia*; E: *Eretmophyllum*; G1: *Ginkgo*; G2: *Ginkgoidium*; G3: *Ginkgoites*; K: *Karkenia*; L: *Leptostrobus*; M: *Mexiglossa*; N1: *Nilssonia*; N2: *Nehvyzdiella*; O: *Otozamites*; P1: *Pterophyllum*; P2: *Ptilophyllum*; P3: *Phoenicopsis*; P4: *Pelourdea*; P5: *Pseudoctenis*; P6: *Podozamites*; P7: *Perezlaria*; S1: *Sagenopteris*; S2: *Sphenobaiera*; T: *Taeniopteris*; W1: *Weltrichia*; W2: *Williamsonia*; W3: *Williamsoniella*; W4: *Wielandiella*; Z: *Zamites*.

“NO SOY BRILLANTE, SOY EL MÁS LENTO DE MI FAMILIA, LUCHO POR LA EDUCACIÓN Y NUNCA FUI BUEN ESTUDIANTE”

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