

# 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<sup>1,2</sup>, María Patricia Velasco-de León<sup>2</sup>, Miguel Angel Flores-Barragan<sup>2</sup>

<sup>1</sup>Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Mexico City, Mexico

<sup>2</sup>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

How to cite this paper: Lozano-Carmona, D.E., Velasco-de León, M.P. and Flores-Barragan, M.A. (2019) Jurassic Flora in Southern Mexico: Anomozamites Schimper, 1870 Emend. Pott et McLoughlin, 2009 from Mixteco Terrane, Phytogeographical Implications of Williamsoniaceae Family (Bennettitales). *Open Journal of Geology*, **9**, 142-156.

https://doi.org/10.4236/ojg.2019.93010

**Received:** February 19, 2019 **Accepted:** March 11, 2019 **Published:** March 14, 2019

Copyright © 2019 by author(s) and Scientific Research Publishing Inc. This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

http://creativecommons.org/licenses/by/4.0/

#### 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 *Anomoza-mites* 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 phytogeo-graphic 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 ( $35^\circ - 40^\circ$ ), 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. angustifo*lium* [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.

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 [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.

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* fos-

sil-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 Anomo*zamites*-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.

## Acknowledgements

We are thankful to Josep Antón Moreno Bedmar for the revision of the manuscript and the comments that allowed us to improve this work. The results of this work are part of the doctoral thesis of D.E.L.C., and he give thanks for support to Postgraduate in Biological Sciences (Posgrado en Ciencias Biológicas) of the National Autonomous University of Mexico (UNAM) and the scholarship CONACyT 632315 for the realization of this research.

# **Conflicts of Interest**

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

### References

- Vakhrameev, V.A. (1987) Climates and the Distribution of Some Gymnosperms in Asia during the Jurassic and Cretaceous. *Review of Palaeobotany and Palynology*, 51, 205-212. <u>https://doi.org/10.1016/0034-6667(87)90030-3</u>
- [2] Anderson, J.M., Anderson, H.M. and Cleal, C.J. (2007) Brief History of the Gymnosperms: Classification, Biodiversity, Phytogeography and Ecology. South African National Biodiversity Institute, Pretoria.
- [3] Taylor, T.N., Taylor E.L. and Krings, M. (2009) Paleobotany the Biology and Evolution of Fossil Plants. Elsevier Inc., Amsterdam.
- Zhou, Z.-Y. (2009) An Overview of Fossil Ginkgoales. *Palaeoworld*, 18, 1-22. https://doi.org/10.1016/j.palwor.2009.01.001
- [5] Diéguez, C., Peyrot, D. and Barrón, E. (2010) Floristic and Vegetational Changes in the Iberian Peninsula during Jurassic and Cretaceous. *Review of Palaeobotany and Palynology*, 162, 325-340. https://doi.org/10.1016/j.revpalbo.2010.06.004
- [6] Silva-Pineda, A. (1984) Revisión taxonómica y tipificación de las plantas jurásicas colectadas y estudiadas por Wieland (1914) en la región de El Consuelo, Oaxaca. *Paleontología Mexicana*, 49, 1-103.
- [7] Velasco-de León, M.P., Ortiz-Martínez, E.L., Silva-Pineda, A. and Lozano-Carmona, D.E. (2013) Distribución y ambientes de las gimnospermas fósiles del Terreno Mixteco. *Paleontología Mexicana*, 63, 122-143.
- [8] Velasco-de León, M.P., Lozano-Carmona, D.E., Flores-Barragan, M.A., Martínez, P.O.D. and Silva-Pineda, A. (2014) Two New Species of Ginkgoales from the Middle Jurassic of Mexico: Historical Biology. *An International Journal of Paleobiology*, 27, 1-8. <u>https://doi.org/10.1080/08912963.2013.874423</u>
- [9] Lozano-Carmona, D.E. and Velasco-de León, M.P. (2016) Jurassic Flora in Southeast Mexico: Importance and Prospects of Recent Findings in the Mixteco Terrane. *Paleontología Mexicana*, **5**, 87-101.
- [10] Lozano-Carmona, D.E. (2012) Paleoclima y flora fósil de Río Ñumi, Formación Zorrillo-Taberna Indifernciada, Oaxaca. Bachelor's Thesis, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Mexico City.
- [11] Guerrero-Arévalo, I.D. (2014) Estudio tafonómico de gimnospermas fósiles del Jurásico Medio, en la localidad Barranca de la Mina y Jurásico Inferior en la localidad Peña Colorada. Bachelor's Thesis, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Mexico City.

- [12] Person, C.P. and Delevoryas, T. (1982) The Middle Jurassic Flora of Oaxaca Mexico. *Palaentographica, Abt. B.*, **180**, 82-119.
- [13] Wieland, G.R. (1914) La flora liásica de la Mixteca Alta. Boletín del Instituto Geológico de México, 31, 1-165.
- [14] Ortiz-Martínez, E.L., Velasco-de León, M.P., Salgado-Ugarte, I. and Silva-Pineda A. (2013) Clasificación del área foliar de las gimnospermas fósiles de la zona norte de Oaxaca, México. *Revista Mexicana de Ciencias Geológicas*, **30**, 150-158.
- [15] Flores-Barragan, M.A., Velasco-de León, M.P. and Corro-Ortiz, M.G. (2017) El género *Williamsoniella* (Thomas) y flora asociada de la Formación Zorrillo-Taberna Indiferenciadas (Jurásico Medio) Oaxaca, México. *Paleontología Mexicana*, 6, 59-65.
- [16] Lozano-Carmona, D.E. (2017) Distribución y Taxonomía de Ginkgoales (Engler, 1897) y grupos afines del Jurásico del sur de México. Master's Thesis, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, Mexico City.
- [17] Harris, T.M. (1969) The Yorkshire Jurassic flora III Bennettitales. Trustees of the British Museum (Natural History), London, 186 p.
- [18] Kustatscher, E. and Van Konijnenburg-Van Cittert, J.H.A. (2007) Taxonomical and Palaeogeographic Considerations on the Seed Fern Genus *Ptilozamites* with Some Comments on *Amonozamites*, *Dicroidium*, *Pseudoctenis* and *Ctenozamites*. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 243, 71-100. https://doi.org/10.1127/0077-7749/2007/0243-0071
- Pott, C. and McLoughlin, S. (2009) Bennettitalean Foliage in the Rhaetian-Bajocian (Latest Triassic-Middle Jurassic) Floras of Scania, Southern Sweden. *Review of Palaeobotany and Palynology*, 158, 117-166. https://doi.org/10.1016/j.revpalbo.2009.08.004
- [20] Pott, C., McLoughlin, S., Shunqing, W. and Friis, E.M. (2012) Trichomes on the Leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou Beds (Middle Jurassic), Inner Mongolia, China: Mechanical Defense against Herbivorous Arthropods. *Review of Palaeobotany and Palynology*, **169**, 48-60. https://doi.org/10.1016/j.revpalbo.2011.10.005
- [21] Lemoigne, Y. (1984) Données nouvelles sur la paléoflore de Colombie. *Geobios*, 17, 667-690. https://doi.org/10.1016/S0016-6995(84)80115-1
- [22] Kim, J. (2001) New Fossil Plants from the Nampo Group (Lower Mesozoic), Korea. Geosciences Journal, 5, 173-180. <u>https://doi.org/10.1007/BF02910423</u>
- [23] Miao, Z., Chunlin, S., Dilcher, D.L., Zhe, Z. and Yunling, N. (2015) Anomozamites (Bennettitales) from Middle Jurassic Haifanggou Formation, Western Liaoning, China. Global Geology, 18, 75-78.
- [24] Pott, C. (2014) A Revision of Wielandiella angustifolia a Shrub-Sized Bennettite from the Rhaetian-Hettangian of Scania, Sweden, and Jameson Land, Greenland. *International Journal of Plant Sciences*, **175**, 467-499. https://doi.org/10.1086/675577
- [25] Pott, C. and McLoughlin, S. (2014) Divaricate Growth Habit in Williamsoniaceae (Bennettitales): Unravelling the Ecology of a Key Mesozoic Plant Group. *Palaeobiodiversity and Palaeoenvironments*, **94**, 307-325. https://doi.org/10.1007/s12549-014-0157-9
- [26] Pott, C., Xiaoli, W. and Xiaoting, Z. (2015) *Wielandiella villosa* comb. nov. from the Middle Jurassic of Daohugou, China: More Evidence for Divaricate Plan Architecture in Williamsoniaceae. *Botanica Pacifica. A Journal of Plant Science and Conservation*, 4, 137-148.

- [27] Pott, C. and Jiang, B. (2017) Plant Remains from the Middle-Late Jurassic Daohugou Site of the Yanliao Biota in Inner Mongolia, China. Acta Palaeobotanica, 57, 185-222. <u>https://doi.org/10.1515/acpa-2017-0012</u>
- [28] Kerp, H. and Bomfleur, B. (2001) Photography of Plant Fossils—New Tecniques, Old Tricks. *Review of Palaeobotany and Palynology*, **166**, 117-151. https://doi.org/10.1016/j.revpalbo.2011.05.001
- [29] Behrensmeyer, A.K. and Turner, A. (2018) Taxonomic Occurrences of Bennettitales Recorded in the Paleobiology Database, Fossilworks. <u>http://fossilworks.org</u>
- [30] Corro-Ortiz, M.G. and Ruiz-González, F.J. (2011) Análisis estratigráfico de las secuencias Jurásicas del área de Tlaxiaco, Oaxaca. Bachelor's Thesis, Facultad de Ingeniería, Universidad Nacional Autónoma de México, Mexico City.
- [31] Carrasco-Ramírez, R.S., Ferrusquía-Villafranca, I., Buitrón-Sánchez, B.E. and Ruiz-González, J.E. (2016) Litoestratigrafía del Grupo Tecocoyunca (Jurásico Medio) en el área del río Ñumí (cercanías de Tlaxiaco), Oaxaca y Consideraciones sobre la distribución regional de su biota. *Revista Geológica de América Central*, 55, 115-136.
- [32] Sandoval, J. and Westermann, G.E.G. (1986) The Bajocian (Jurassic) Ammonite Fauna of Oaxaca, Mexico. *Journal of Paleontology*, **60**, 1220-1271. https://doi.org/10.1017/S0022336000002985
- [33] Servicio Geológico Mexicano (SGM) (2000) Carta geológico-minera Tlaxiaco E14-D34, escala 1:50,000. Pachuca, Hidalgo, México, Oaxaca, Servicio Geológico Mexicano, 1 map.
- [34] Churre, D.J., Litwin, R. Hasiotis, S.T., Evanoff, E. and Carpenter, K. (2006) The Fauna and Flora of the Morrison Formation. In: Foster, J.R. and Lucas, S.G., Eds., *Paleontology and Geology of the Upper Jurassic Morrison Formation*, New Mexico Museum of Natural History and Science Bullet, Albuquerque, Vol. 36, 233-249.
- [35] Delevoryas, T. and Gould, R.E. (1971) An Unusual Fossil Fructification from the Jurassic of Oaxaca, Mexico. *American Journal of Botany*, 58, 616-620. https://doi.org/10.1002/j.1537-2197.1971.tb10011.x
- [36] Delevoryas, T. (1991) Investigations of North American Cycadeoids: Weltrichia and Williamsonia from the Jurassic of Oaxaca, Mexico. *American Journal of Botany*, 78, 177-182. <u>https://doi.org/10.1002/j.1537-2197.1991.tb15744.x</u>
- [37] Silva-Pineda, A., Velasco de León., M.P., Arellano-Gil, J. and Grimaldo, J.R. (2011) A New Species of *Weltrichia* (Bennettitales) from the Middle Jurassic of the Tecomazuchil Formation (Oaxaca, Mexico). *Geobios*, 44, 519-525.