

## New records of *Bjuvia* and *Nilssonia* from the Permian of Mexico

Miguel Angel Flores-Barragan and María Patricia Velasco-de Leon

### ABSTRACT

Two new genera have been identified in the Permian of Mexico: cf *Bjuvia* and *Nilssonia*. Along with previously-known *Taeniopteris*, these confirm the presence of Cycadophytes in the upper Paleozoic of Mexico. This substantially increases the geographical and temporal distribution of this group and provides information on the type of environment in which these plants developed. The new reports come from two localities of the Matzitz Formation, in the state of Puebla, Mexico, called Carretera (Ca) and Coatepec (Co). In the first locality, we identified material characterized by the presence of a simple leaf of large size with veins perpendicular to the rachis and always parallel, as well as a stomatal apparatus with papillae. The fragmentary nature of the material from Puebla allows only an affinity to *Bjuvia* of the order Cycadales. Other specimens are assigned to *Taeniopteris* and *Nilssonia*. The *Nilssonia* reported from Carretera, has a segmented lamina attached to the rachis on the upper side. *Taeniopteris* is characterized by an entire lamina, generally narrow, with veins originating perpendicularly to the rachis that dichotomizes one or several times. The species *T. lenticuliformis* and *T. crassinervis* are reported for the first time from Coatepec. Together with these genera, the orders Equisetales, Gigantopteridales, Glossopteridales, Lepidodendrales, Marattiales, Osmundales, Peltaspermales, and Voltziales were also identified. Future studies will aim to confirm the taxonomic affinity of these leaves.

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## INTRODUCTION

Mexico has an extensive plant fossil record that spans from the Paleozoic to the Cenozoic (Silva, 1970, 1984; Velasco-de León and Ortiz-Martínez, 2010). In Mexico, the Paleozoic flora is represented in the Matzitzi (Puebla), Patlanoaya (Puebla), Paso Hondo (Chiapas), and the Tuzancoa Formations (Hidalgo) (Silva, 1970; Rosales-Lagarde et al., 2005; Ramos-Arias et al., 2007). Undoubtedly, the most studied and best known is the Matzitzi Formation, which has been analyzed intermittently since the middle of the century. Silva (1970) conducted the first paleobotanical study in this formation, where she described 25 plant species (mostly *Lepidodendrales* and *Calamitales*). Later, Reinhard Weber (1997) described a new genus, *Lonesomia* Weber of the order *Gigantopteridales*.

Magallón-Puebla (1991) conducted a morphological analysis of the *Marattiales* and described *Fascipteris* Gu et Zhi, which is currently known to correspond to *Diplazites* Goeppert (Cleal, 2015). Galván (2000) accomplished a paleobotanical study in Los Reyes Mezontla and Santiago Coatepec, Puebla, and recorded nine genera and 13 species, including new records of *Annularia* Sternberg, *Sphenophyllum* Brongniart, and *Taeniopteris* Brogniart.

Reports of possible cycadophytes for the Matzitzi Formation are scarce, with only one report of the fossil taxon *Taeniopteris* sp. (Galván, 2000, figure 19). The author mentions 18 specimens collected between the towns of Los Reyes Mezontla and Santiago Coatepec, Puebla. However, the description is poor, as well as the quality of the figures, which does not allow the observation of diagnostic characters and raises doubts about identification of the material as *Taeniopteris*.

We use the concept *Cycadophyta* in the sense of Pott et al. (2012), which refers only to the degree of leaf organization (type of leaf, margin, and venation) and does not imply a phylogenetic relationship. This is because the lack of characters, such as type of stomata or reproductive structures in most cases, complicates the specific assignment of the leaves to any orders of the *Cycadophytes*.

## STUDY AREA

The Matzitzi Formation crops out in the north area of the state of Puebla and has an estimated thickness of 600 m (Figure 1A-B) (Calderón-García, 1956). There are still inconsistencies regarding its age, where assignment has varied

from the upper Carboniferous (Silva, 1970), to the lower Permian (Weber et al., 1987), and to the upper Permian (Flores-Barragan, 2019). We agree with the proposal of the study from 2019 that considers our specimens as late Permian in age.

Sedimentological studies have proposed an anastomosed fluvial facies model with up to six facies associations (Centeno et al., 2009). The material examined in the present work belongs to two localities: Carretera and Coatepec (Figure 1C-D). The first one is located at kilometer #89 of the Tehuacán-Oaxaca federal highway, Mexico, and the second is located on the outskirts of the town of the same name (Santiago Coatepec, Puebla, Mexico).

## MATERIALS AND METHODS

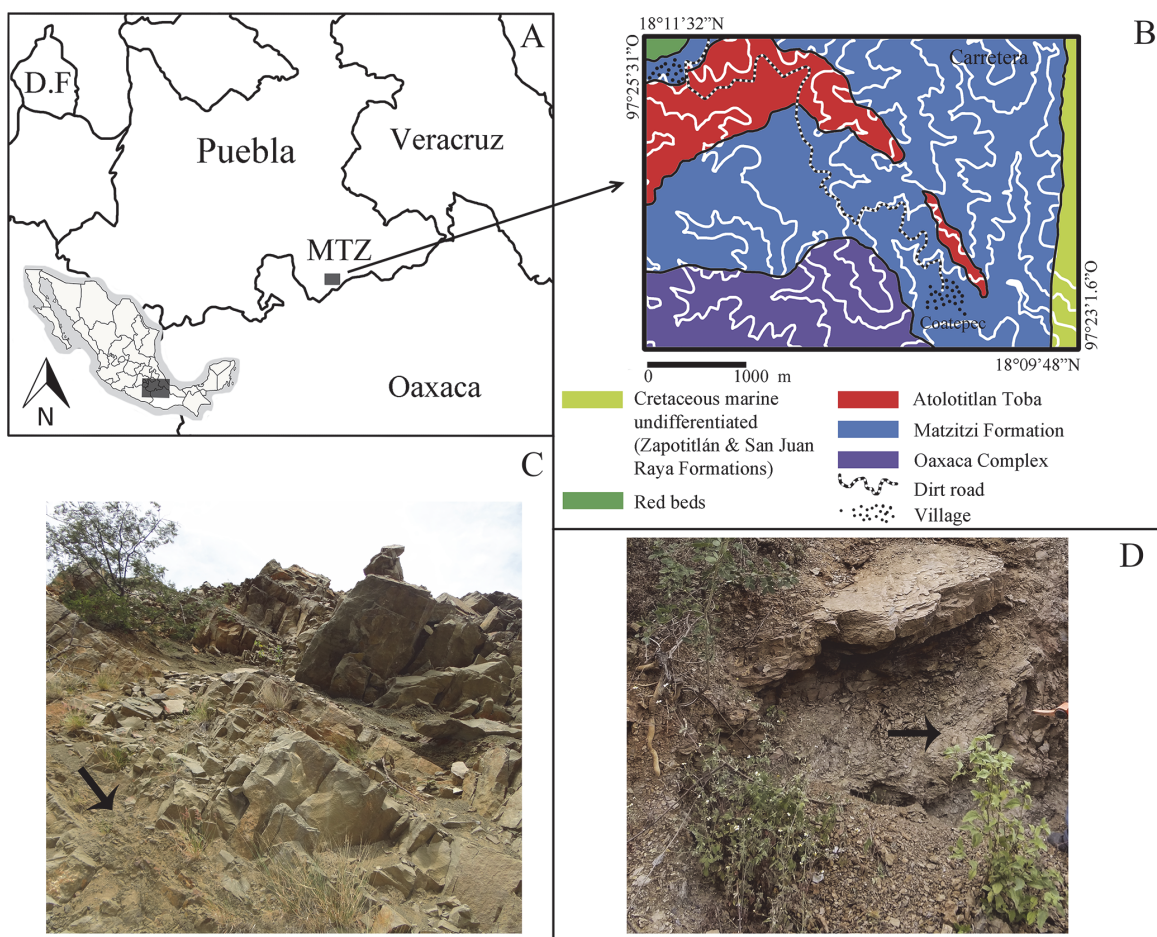
We conducted five visits to the localities of Carretera (Ca) and Coatepec (Co), where we collected a total of 497 specimens. The fossils are impressions in a lutite of fine- to medium-grained sandstone. The stratigraphic horizon was recorded for each specimen. The material is stored in the Paleontological Collection of the Facultad de Estudios Superiores Zaragoza of the National Autonomous University of Mexico under the acronym (CFZ-MTZ).

In order to obtain more precision in the morphological characters, which are of great importance for the identification (Artabe, 1985; Remy and Remy, 1975), we made detailed measurements of the specimens in the program Image J (version 1.8.0.). We also obtained cuticle using cellulose acetate peel as well as dispersed cuticles (Kerp, 1990; Kouwenberg et al., 2007) for fossils that were lustrous or carbonized. The cuticles were photographed with an Olympus E-620 camera and observed under an Olympus bx41 microscope for their description and measurement.

The taxonomic assignment is based on studies that used the morphological characters of the lamina, including Remy and Remy (1975), Artabe, (1985), and Van Konijnenburg-van Cittert et al. (2017).

## RESULTS

In the Carretera locality, we measured a stratigraphic section of 24.5 m. At its base, there are 3.5 m of strata with a grain size of fine- to medium-grained sandstone and parallel lamination. The next 21 m are composed of medium-grained sandstone, with parallel, cross-planar, and ripple stratification. Between the sandstone strata, there are



**FIGURE 1.** Map of the location of the study areas. A) Map of the Mexican Republic showing the location of the localities within the state of Puebla. B) Geological map of the Matzitzi Formation. C) Strata of the “Carretera” locality, the arrow indicates the collecting area. D) Strata of the “Coatepec” locality, the arrow indicates the collection area.

rock packages of up to 1 m in thickness with finer lithology (siltstone and lutite), and in this location is where most specimens were collected (Figure 2A).

In the Ca locality, we identified a total of 164 specimens, belonging to six different orders: Lepidodendrales, Equisetales, Marattiales, Glossopteridales, Peltaspermales, Voltziales, and *Incertae sedis*. Four of these orders had already been reported for this formation (Silva, 1970; Weber, 1987; Galván, 2000), and we add two new reports to these lists: Glossopteridales and Voltziales (Table 1).

In the Coatepec locality, we measured a stratigraphic section of 150 m. In the first 28 m, there is an alternating sequence of sandstone and lutite with plant fossils. Above this sequence, there is 52 m of massive strata of fine- to coarse-grained sandstone. Above this section, there are massive

strata of conglomerates supported by matrix and round, with a thickness of 70 m (Figure 2B).

In this locality, we identified 333 specimens, belonging to nine orders Lepidodendrales, Equisetales, Osmundales, Marattiales, Glossopteridales, Gigantopteridales, Peltaspermales, Cycadales?, Voltziales, and one *insertae sedis*, being the possible Cycadophyte, which is our new record for this formation (Table 1).

Below we describe the new reports of Cycadophytes at the genus and/or species level for the Matzitzi Formation.

### SYSTEMATIC PALEONTOLOGY

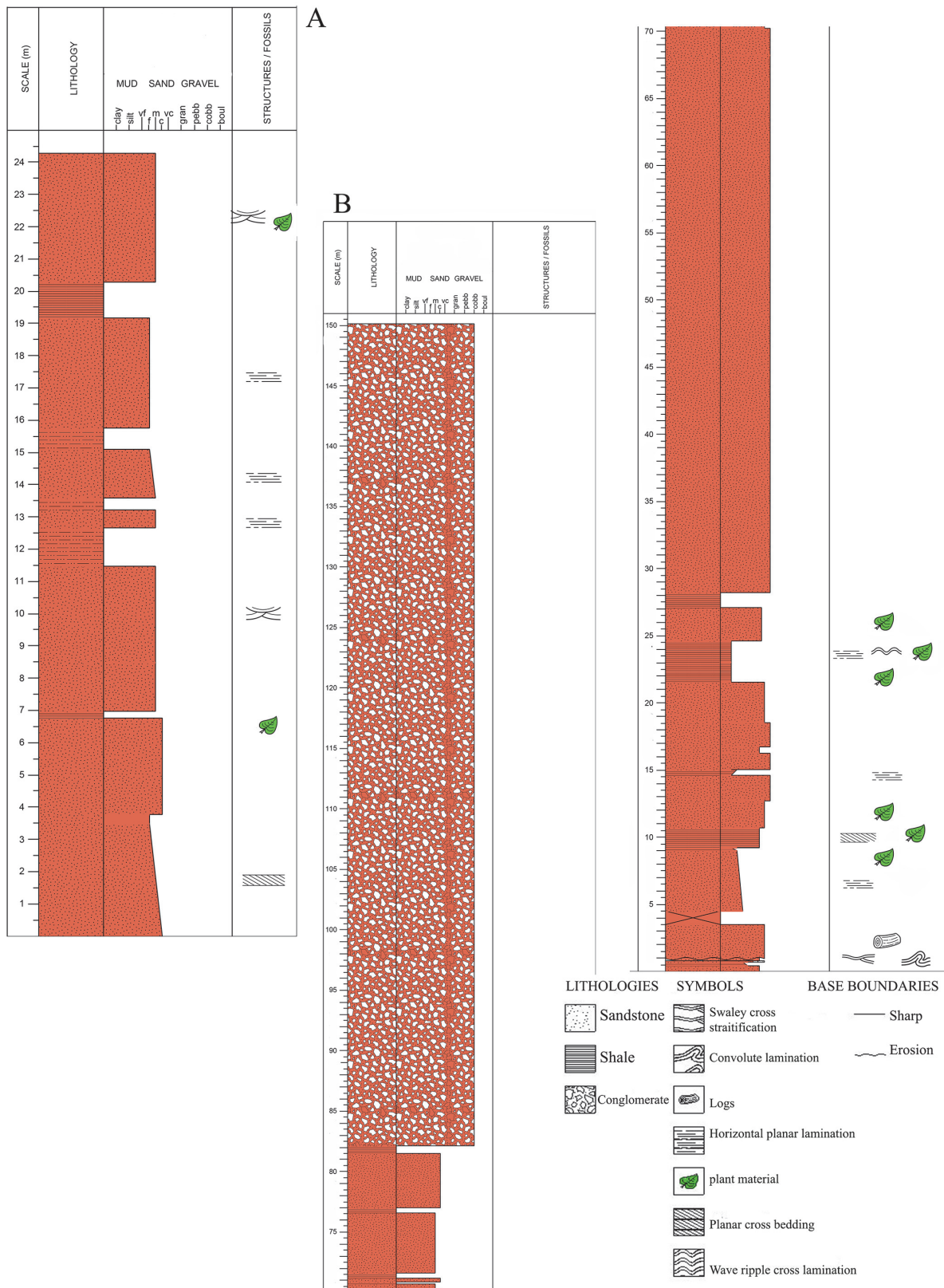
Class CYCADOPSIDA Brongniart, 1843

Order CYCADALES Dumortier, 1829

Genus *BJUVIA* Florin, 1933

cf. *Bjuvia* sp.

Figure 3



**FIGURE 2.** Stratigraphic sections of the collecting outcrops. A) Sequence of rocks that outcrop on kilometer #89 of the Tehuacán-Oaxaca highway, the two collection zones can be observed. B) Sequence of rocks that outcrop from the river “Paso Hondo” to the outskirts of the town of Coatepec, Puebla; the different collecting layers can be observed.



**TABLE 1.** Comparative table of the genera described over time in the Matzitzi Formation.

Order or family	Genus	Silva (1970)	Weber et al. (1987) and Weber (1997)	Galvan (2000)	Valdes Vergara (2017)	Flores-Barragan and Velasco-de León (2021)	
		location unknown	location unknown	location unknown	Carretera	Carretera	Coatepec
Bennettitales	<i>Pterophyllum</i> Brongniart		*				
Cycadales	cf. <i>Bjuvia</i> Florin						*
Cordaithantales	cf. <i>Cordaites</i> Unger						*
Dycranophyllales	<i>Dycranophyllum</i> Grand'Eury					*	*
Equisetales	<i>Annularia</i> Sternberg			*			
Equisetales	<i>Asterophyllites</i> (Schlotheim) Brongniart						*
Equisetales	<i>Calamites</i> Suckow	*		*	*	*	*
Equisetales	<i>Schizoneura</i> Schimper et Mougeot						*
Equisetales	<i>Sphenophyllum</i> Brongniart			*			
Gigantopteridales	Cf. <i>Gigantonoclea</i> Koidzumi						*
Gigantopteridales	<i>Lonesomia</i> Weber		*				
Ginkgoales	<i>Baiera</i> Braun		*				
Ginkgoales	<i>Ginkgoites</i> Seward		*				
Glossopteridales	<i>Gangamopteris</i> McCoy						*
Glossopteridales	<i>Glossopteris</i> Brongniart						*
Glossopteridales	<i>Plumstedtia</i> Rigby						*
Incertae sedis	<i>Cordaicarpus</i> Geinitz						*
Incertae sedis	<i>Cladophebis</i> Brongniart						*
Incertae sedis	<i>Holcospermum</i> Nathorst		*	*		*	*
Incertae sedis	<i>Lesleya</i> Lesquereux					*	
Incertae sedis	<i>Nilssonia</i> Brongniart					*	
Incertae sedis	<i>Taeniopteris</i> Brongniart			*	*	*	*
Incertae sedis	<i>Trigonocarpus</i> Brongniart				*	*	
Incertae sedis	<i>Velascoa</i> Flores Barragan et Ortega Chavez						*
Lepidodendrales	<i>Asolanus</i> Wood	*					
Lepidodendrales	<i>Bothodendron</i> Lindley et Hutton	*					
Lepidodendrales	<i>Cyperites</i> Lindley et Hutton	*			*	*	*
Lepidodendrales	<i>Knorria</i> Sternberg					*	*

TABLE 1 (continued).

Order or family	Genus	Silva (1970)	Weber et al. (1987) and Weber (1997)	Galvan (2000)	Valdes Vergara (2017)	Flores-Barragan and Velasco-de León (2021)	
		location unknown	location unknown	location unknown	Carretera	Carretera	Coatepec
Lepidodendrales	<i>Lepidodendron</i> Sternberg	*		*			
Lepidodendrales	<i>Sigillaria</i> Brongniart	*		*	*	*	*
Lepidodendrales	<i>Stigmaria</i> Brongniart	*				*	*
Lepidodendrales	<i>Stigmariopsis</i> Grand Eury	*					
Lepidodendrales	<i>Syringodendron</i> Sternberg				*	*	*
Marattiales	<i>Astherotheca</i> Presl et Corda	*		*	*	*	*
Marattiales	<i>Diplazites</i> Goeppert					*	*
Marattiales	<i>Lobatopteris</i> Wagner					*	
Osmundales	<i>Dychotomopteris</i> Maithy						*
Peltaspermales	<i>Comia</i> Zalesky				*	*	
Peltaspermales	<i>Neuropteris</i> Brongniart (Sternberg)	*		*		*	*
Peltaspermales	<i>Odontopteris</i> Brongniart (Sternberg)	*				*	*
Peltaspermales	<i>Sphenopteris</i> (Brongniart) Sternberg				*		*
Peltaspermales	<i>Ovopteris</i> Potonie	*				*	
Voltziales	<i>Majonicaeae</i> Clement-Westerhof						*

**Material.** CFZ-MTZ540, 551, 583.

**Locality.** Coatepec.

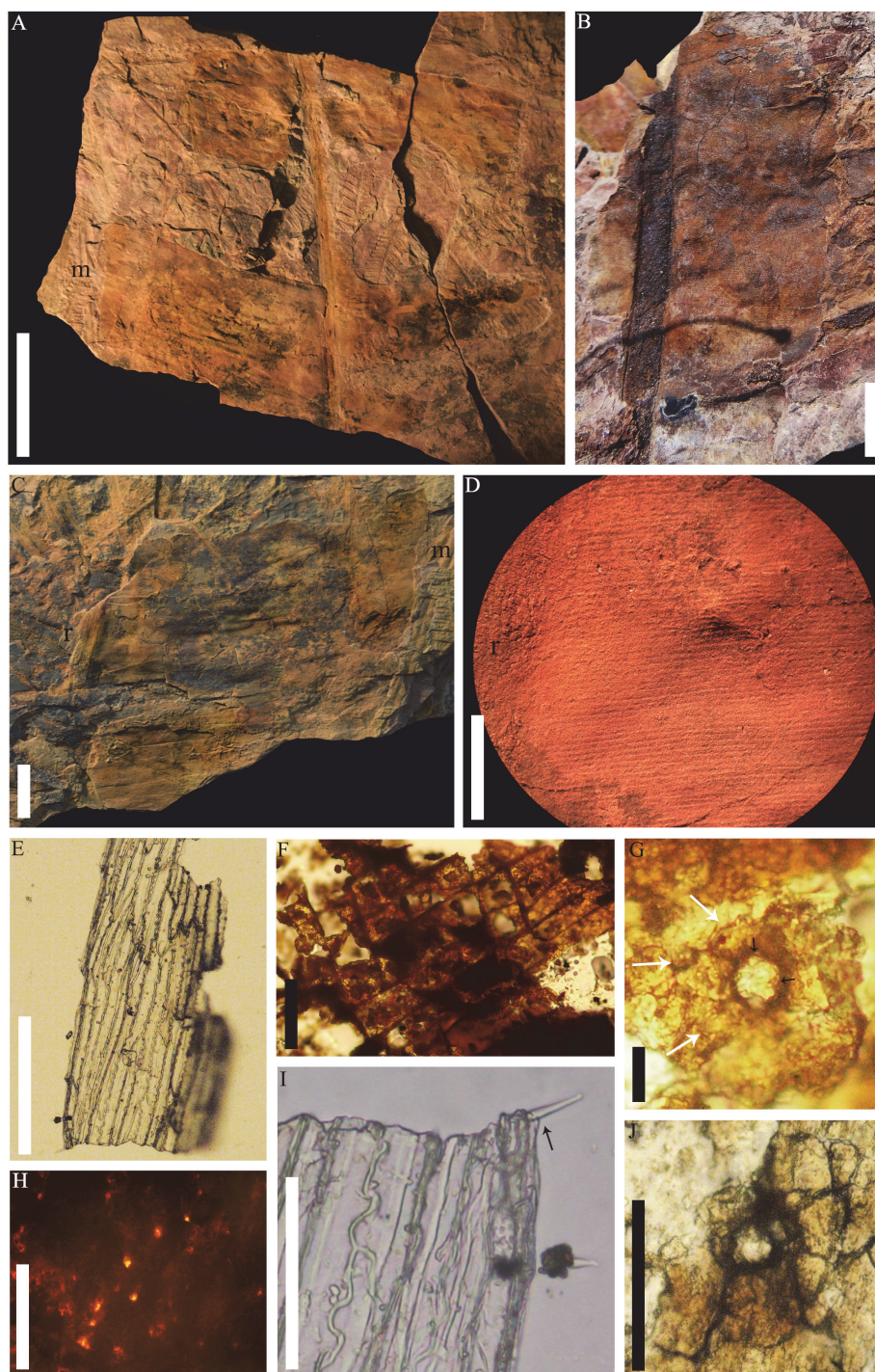
**Description.** Entire lamina, lanceolate, with entire margins, the rachis is prominent and longitudinally striate; veins are fine, numerous, simple, and emanate perpendicularly from the rachis. Irregular to square and/or rectangular epidermal cells have generally straight walls. The stomata are arranged in irregular rows; stomatal apparatus is protected by simple digitate papillae.

Given the large size of the lamina, all specimens are preserved as fragments, with the best-preserved specimen measuring 15.0 cm in length and 18.55 cm in width at the mid-part (Figure 3A). The width of the leaf gradually decreases towards the apex and the base (Figure 3B). The shape of both is unknown. A rachis running along the lamina is longitudinally striated and 0.55 cm wide (Figure 3C). The leaf is laterally inserted into the rachis. The veins are perpendicularly inserted into the rachis. This venation is simple and has a density of

33 to 40 veins per centimeter in the proximal part to the margin (Figure 3D); the number of veins is constant along the entire lamina.

In the adaxial cuticle, the epidermal cells are rectangular to irregular in shape 80 to 90  $\mu$  long and 8 to 10  $\mu$  wide, with straight to slightly undulated anticlinal walls, 1 to 2  $\mu$  thick (Figure 3E). Crest distance is 6 to 8 microns, with a height of 3 microns. The epidermal cells are arranged parallel to the venation and also exhibit simple trichomes of up to 15 microns in length (Figure 3I).

In the abaxial cuticle, there are also irregular to square and/or rectangular epidermal cells, with straight anticlinal walls and a size between 50 and 100  $\mu$  (Figure 3F). The stomatal aperture is 10 to 15  $\mu$  wide with 6-7 subsidiary cells on both sides surrounding the stoma. Four papillae are observed, which protrude from the stomatal aperture (Figure 3G and J). The stomata are arranged in irregular rows (Figure 3H).



**FIGURE 3.** Specimens of cf. *Bjuvia* sp. A) Largest specimen, CFZ-MTZ540. B) Specimen CFZ-MTZ583, in which a reduction in width toward the edges of the lamina can be observed. C) Close-up of specimen CFZ-MTZ540, in which the type of attachment of the lamina can be observed. D) Parallel venation observed in specimen CFZ-MTZ540. E) Adaxial cuticle extracted from specimen CFZ-MTZ583, with undulating epidermal walls. F) Abaxial cuticle extracted from specimen CFZ-MTZ540, in which straight epidermal cells can be observed. G and J) Stomata in the abaxial part of the cuticle of specimen CFZ-MTZ540, black arrows indicate papillae over stomatal opening and white arrows indicate subsidiary cells. H) Stomatal arrangement observed in the abaxial cuticle. I) Close-up of the adaxial cuticle where a simple trichome is observed, arrow indicates simple trichome. Abbreviations: m, leaf margin; r, rachis. Scale: A 5 cm, B and C 1 cm, D 0.5 cm, E, F and H 100µ, G 10 µ, I-J 50µ.

**Remarks.** Entire leaves attached to a central rachis that lack epidermal and reproductive characters are generally located in the fossil taxon *Taeniopteris* (Van Konijnenburg-van Cittert et al., 2017). In this case, we observe seven subsidiary cells. The shape of the epidermal cells, the presence of trichomes, and the absence of dichotomies in the veins also suggest *Bjuvia*. Nevertheless, it is necessary to obtain better preserved material in order to be certain; thus, we consider the specimens CFZ-MTZ540, 551, and 583 as cf. *Bjuvia* sp.

Thus far, there are only three species of this genus, all located in the Triassic of Europe. *Bjuvia simplex* Florin is characterized by having large leaves of up to 1 m in length and a venation density of 12-14 veins per cm; the venation can dichotomize at the base of the veins. Even though the size of the specimen studied here is incomplete, the venation density completely differs from that observed in *B. simplex*. The same occurs with the species *B. dolomitica* Wachtler et Van Konijnenburg-van Cittert, which only has 14-18 veins per centimeter, as well as a larger leaf width and a thicker rachis with a constant width. Regarding the third species, *B. thalensis* Kustatscher et Van Konijnenburg-van Cittert, though it has a size relatively similar to that of the specimen from Puebla, it also

differs in the venation density, as well as in the width of the rachis (Table 2).

In the case of the epidermal characters of the genus, the three reported species exhibit haplocheilic stomata, amphistomatic leaves, rectangular or square epidermal cells, and stomata generally in irregular rows with subsidiary cells and, in some cases, with papillae. The specimen from Puebla is similar to *Bjuvia simplex* in the shape of the abaxial epidermal cells, the size of the stomatal aperture, number of subsidiary cells and the presence of trichomes (Barbacka, 2001). With *B. dolomitica* it shares the characters of the adaxial cuticle, since both have rectangular to irregular epidermal cells with straight to slightly crenulated walls (Wachtler and Van Konijnenburg-van Cittert, 2000). Finally, with *B. thalensis* it shares the presence of papillae in the stomatal apparatus (Kustatscher and Van Konijnenburg-van Cittert, 2010).

Order *INCERTAE SEDIS*

Genus *NILSSONIA* Brongniart, 1825

*Nilssonia* sp.

Figure 4A-B

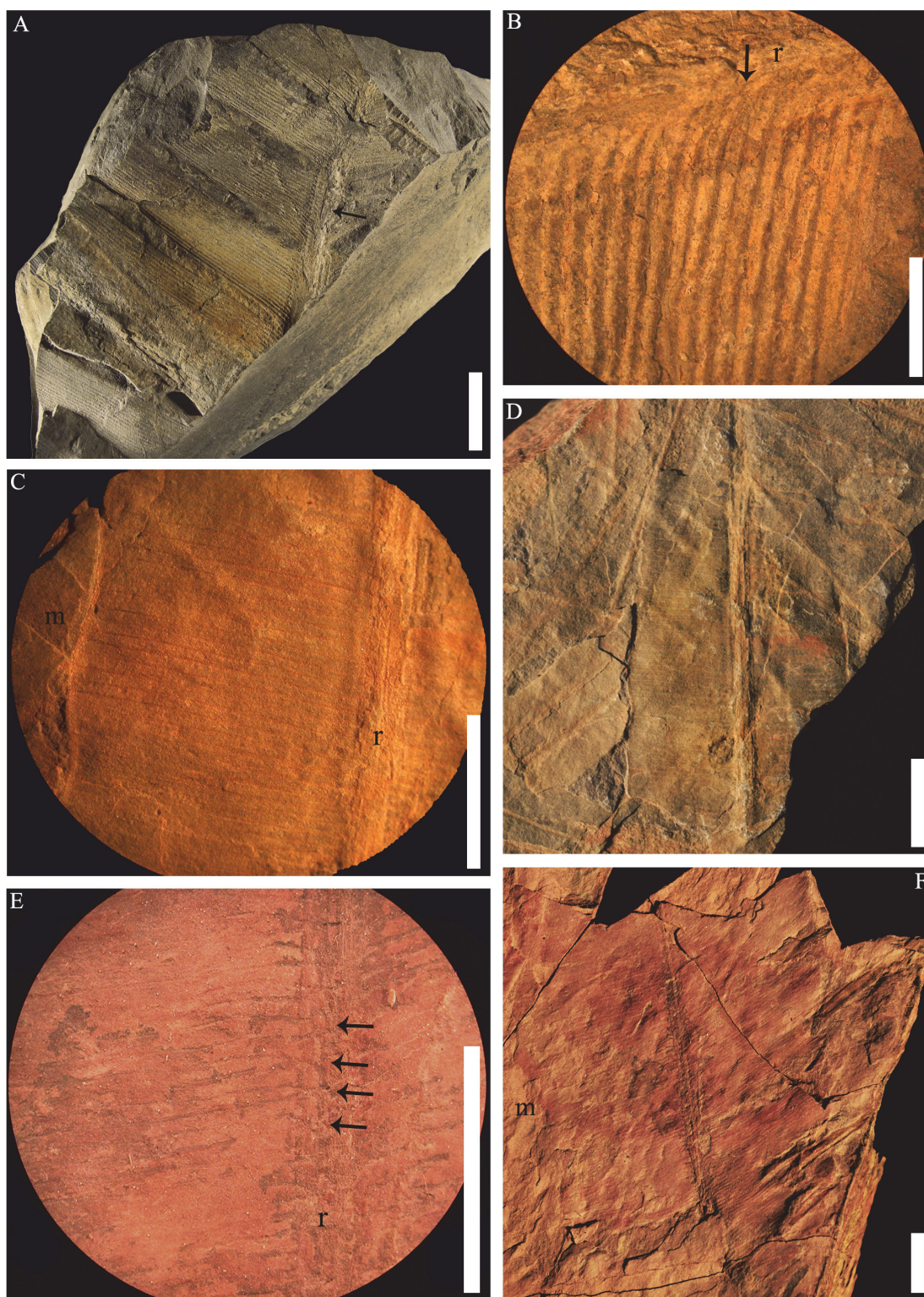
**Material.** CFZ-MTZ266.

**Locality.** Carretera.

**TABLE 2.** Comparative table of the morphological characters of the three reported species of the genus *Bjuvia*, as well as the affinity proposed here.

	cf. <i>Bjuvia</i> sp	<i>B. thalensis</i>	<i>B. simplex</i>	<i>B. dolomitica</i>
Lamina length (cm), with an asterisk indicating an approximation for incomplete leaves	21.5*	20*	/	100
Lamina width (cm)	18.6	15	20	30
Rachis width (cm)	0.6	0.5	1	0.5
Number of veins per cm	40	30	14	18
Rachis type	Fluted	Fluted	Fluted	/
Apex type	/	Round	/	Round
Presence of dichotomies in the veins	No	No	yes	No
Stoma type	/	Haplocheilic	Haplocheilic	Haplocheilic
Number of companion cells	6-7	6-4	7	6-4
Stomatal complex size or stomatal opening*	10-15 $\mu$ *	50-60 $\mu$	10 $\mu$ *	/
Presence of trichomes	Yes	No	Yes	No
Shape of epidermal cells	Irregular - Rectangular	Isodiametric	Irregular-Quadrate	Rectangular
Wall shape in epidermal cells	Right - Undulated	Right	Right	Undulated
Age	Permian	Triassic	Triassic	Triassic
Country	Mexico	Germany	Sweden	Italy





**FIGURE 4.** Specimens of leaves of Cycadophytes. A) *Nilssonsonia* sp. Specimen CFZ-MTZ266, the arrow indicates an area in which it is observed how the leaf covers the rachis. B) Parallel and dichotomous venation of *Nilssonsonia* sp. C) Parallel venation of *Taeniopteris lenticuliformis*, specimen CFZ-MTZ330. D) Specimen of *Taeniopteris lenticuliformis*. E) *Taeniopteris crassinervis*, specimen CFZMTz-713. F) Parallel and dichotomous venation of *Taeniopteris crassinervis*. Symbols: m, leaf margin; r, rachis; the arrows indicate the areas with dichotomous venation. Scale. A, D-F 1 cm, B and C 0.5 cm.

**Description.** Leaf pinnate (segmented) is subdivided into numerous, regular oppositely positioned segments. The leaf is 6.3 cm long and 4.7 cm wide in the middle part. It has segments with a constant width from 1 to 1.2 cm wide at the base, and the leaf apex is unknown. The distance between the segments is relatively constant at about 0.2-0.3 cm. The lamina is attached to the upper edge of rachis and is completely covered by the rachis, which can measure up to 0.3 cm in width. The venation of the segments is inserted at an angle of 80-90°. The veins can dichotomize near the base then become parallel with a density of 12 to 17 veins per cm in the proximal part to the margin.

**Remarks.** Segmented leaves have been reported for the Permian from different parts of the world, such as *Pterophyllum cotteanaum* Gutbier from the lower Permian of Germany (Barthel et al., 2010), *Pseudoctenis middridgensis* Stonley from the upper Permian of England (Stonley, 1958), and/or

*Pseudoctenis samchokense*, Kawasaki from the upper Permian of China (Pott et al., 2010). However, in these cases, the lamina segments are laterally attached to the rachis and are not similar to the Puebla specimen (Table 3). The leaf described in the present work is assigned to *Nilssonina* based on the leaf lamina clearly being attached to the upper edge of the rachis (Van Konijnenburg-van Cittert, et al., 2017). *Nilssonina* has some records for the upper Paleozoic (Tian and Zhang 1980; He et al., 1996), and the first reliable reports are from the Triassic. The species *Nilssonina sturii* Krasser from the upper Triassic of Austria (Pott et al., 2007) evinces some similarity to the specimen from Mexico but differs from it by having a lower number of veins, as well as the presence of dichotomies in the Mexican specimen.

It is important to mention that the dichotomies in the veins in the genus *Nilssonina* are not common in species from the Northern Hemisphere, but are

**TABLE 3.** Comparative table of morphological characters of some species that have segmented leaves, reported for the Permian, as well as the new report from Mexico. With an asterisk the data of incomplete leaves.

	<i>Nilssonina</i> sp.	<i>Pseudoctenis</i> sp.	<i>Pseudoctenis</i> <i>middridgensis</i> Stoneley	<i>Pseudoctenis</i> <i>samchokense</i> Kawasaki	<i>Pterophyllum</i> sp.	<i>Pterophyllum</i> <i>cotteanaum</i> Gutbier	<i>Pterophyllum</i> <i>pottii</i> Bomfleur et Kerp	<i>Pteronilssonina</i> <i>gopalii</i> Pant et Mehra
Lamina length (cm)	6.3*	7.5*	17*	24*	/	/	5*	15*
Lamina width (cm)	4.7*	7.0*	5.7	22*	/	/	6*	11*
Rachis width (cm)	0.3	0.3	0.2-0.3	/	0.25-0.4	0.7	0.5-0.6	0.2
Union of the leaf with respect to the rachis	Attached to the upper edge of rachis	Laterally attached to the rachis	Laterally attached to the rachis	Laterally attached to the rachis	Laterally attached to the rachis	Laterally attached to the rachis	Laterally attached to the rachis	Laterally attached to the rachis
Base of segments	Decurrent	Decurrent in the basicopic part	Decurrent in the basicopic part	Slightly constricted in the base	Not decurrent	Decurrent	/	Not decurrent
Length of the segments (cm)	3.5*	4.2	3.7	9.2	8.5	1-3.5	/	6*
Width of the segments (cm)	1-1.2	0.7	0.35	0.5-1.1	0.35	0.5-0.7	1.5-2	1
Segment position	Oppositely	Oppositely to sub-oppositely	Sub-opposite	Oppositely to sub-oppositely	Sub-opposite to alternate	Oppositely	/	Sub-opposite
Type of apex in the segments	/	Rounded	Obtuse	Rounded	Rounded	Rounded-Obtuse	/	/
Distance between segments (cm)	0.2-0.3	0.2-0.7	0.5	0.2	0.2-0.6	0.2-0.3	/	0.3-0.5
Number of veins per cm	12-17	13-20	13-20	/	/	20	42-48	10
Venation arrangement	With dichotomies at the base	3	With dichotomies at the base	With dichotomies at different heights	Parallel	Parallel	Parallel	With dichotomies at different heights
Age	upper Permian	upper Permian	upper Permian	Permian	upper Permian	lower Permian	lower Permian	Permian
Country	Mexico	Australia	England	China	Australia	Germany	Jordan	India

common in species from Gondwana (Holmes et al., 2010). Therefore, it is not comparable to other species described for the Triassic of Europe (Barbacka, 2001; Kustatscher and Van Konijnenburg-van Cittert, 2010).

Genus *TAENIOPTERIS* Brongniart, 1828  
*Taeniopteris lenticuliformis* (Etheridge) Walkom,  
 1917

Figure 4C-D

**Material.** CFZMTZ-330.

**Locality.** Coatepec.

**Description.** Entire lamina, with entire margins, probably oblong in shape, leaf width appears to be constant. The apex and base are not preserved. The leaf is 4.1 cm long and 2.5 cm wide. The lamina attaches laterally to the rachis. The rachis is slim, retaining its width throughout the whole leaf with a maximum width of 0.2 cm. The fine veins emanate from the rachis at 90°. The venation is simple, rarely dichotomous, with a density of 23 to 24 veins per cm at the middle-part of the leaf.

**Remarks.** Given the general morphology of the leaf, this specimen resembles an isolated pinna of the genus *Danaeopsis* Heer ex Schimper. However, this taxon is characterized by having strong secondary veins that anastomose near the margin. Even though there are species that can lack anastomoses, such as *D. angustifolia* and *D. fecunda* (Kustatscher et al., 2012a), the differences in leaf size, vein angle, and venation density do not allow assignment to these species. In addition, the lack of compound leaves and/or sporangia that determine the affinity of these specimens makes their comparison with this genus impossible. For this analysis, the specimen from Puebla was compared with 42 species of the fossil taxon *Taeniopteris* described for the Permian-Triassic (Table 4). The observations indicate a higher similarity with the species *Taeniopteris lenticuliformis*, which is characterized by the near absence of bifurcations in the veins. Yet the size of its lamina is comparable to that of *T. vittata* Brongniart, it does differ due to the lower venation density of *T. lenticuliformis* (Artabe, 1985). This species has been reported for the Triassic of Argentina, New Zealand, and Australia (Artabe, 1985; Retallack, 1985).

*Taeniopteris crassinervis* (Feismantel) Arber, 1917  
 Figure 4E-F

**Material.** CFZMTZ-713.

**Locality.** Coatepec.

**Description.** Entire lamina, with entire margins, 6.8 cm long and 5.3 cm wide at the mid-part. The leaf width appears to be constant. The shape of the

base and apex are unknown. Undulations are observed in the lamina, which could be the result of desiccation and/or the fossilization process. The lamina attaches laterally to the rachis. The rachis is slim, retaining its width throughout the whole leaf with a maximum width of 0.3 cm. The veins emanate from the rachis at 90°. This venation divides at the proximal part of the rachis and then becomes parallel along it. It can have a density of up to 14 to 16 veins per centimeter at the mid-part of the leaf.

**Remarks.** After comparing it with 42 different species of the genus (Table 4), the specimen from Puebla was assigned to the species *Taeniopteris crassinervis*, since it exhibits strong veins with a similar venation density and perpendicular angle at which they are inserted regarding to the rachis. Another diagnostic characteristic of this species is the dichotomy of the veins in the contact area with the rachis (Figure 4E). This species has been reported for the Triassic of Argentina (Artabe, 1985), United States, India, Australia, New Zealand, and Africa (Behrensmeier and Turner, 2019). This new report would correspond to the most southern record of North America.

## DISCUSSION

The importance of epidermal characters has been emphasised for the taxonomic assignment of different plant groups, e.g., Cycadales (Pott et al., 2010). However, the cuticle is not always preserved since it depends on the fossilization process and the texture of the leaves. In most localities of Mexico, the preservation of cuticle in fossils is rare. There are reports of cuticles from the Permian of Hidalgo for the genera *Taeniopteris* and *Comia* Zalessky (Velasco et al., 2020). There are also informal records from the Jurassic, in the states of Puebla and Oaxaca, for some Bennettitalean genera: *Zamites* Brongniart and *Otozamites* Braun (Silva, 1969; Ortiz-Martínez, 2014). We add to these reports the cuticle obtained from the specimen of cf. *Bjuvia* sp., from which we were able to observe stomata and epidermal cells.

The genus *Bjuvia* has simple leaves, entire margins, rachis that runs through the entire lamina and veins almost perpendicular concerning to the rachis. The veins, most always, are not dichotomous. Based on the epidermal characteristics (haplocheilic stomata), its assignment to the order Cycadales has been proposed (Wachtler and Van Konijnenburg-van Cittert, 2000). This genus has a stratigraphic range from the Triassic to the Jurassic. There are three described species thus far (Wachtler and Van Konijnenburg-van Cittert, 2000;

**TABLE 4.** Table of morphological characters of the 42 species of the genus *Taeniopteris* and of the two specimens from Puebla. These species correspond to the Paleozoic-Mesozoic transition reported for the province of Euramerica and Gondwana. Abbreviations: L.L. lamina length (cm). W.L. lamina width (cm). T.A. apex type. T.B. base type. W.R. rachis width (mm). D.V. vein density per cm. A.I.V. insertion angle of veins. A.V. arrangement of veins, 1) Dichotomies at the base of the veins, 2) Dichotomies at the mid-part of the veins, 3) Dichotomies at the base and mid-part of the veins, 4) veins without dichotomies, 5) Dichotomies at the base and then irregularly in the veins, 6) Dichotomy in the terminal part of the veins, and 7) irregular dichotomies in the veins.

Species	L.L.	W.L.	T.A.	T.B.	W.R.	D.V.	A.I.V.	A.V.
Specimen CFZMTZ-330	4.1	2.5	/	/	0.2	23-24	90°	4
Specimen CFZMTZ-713	6.8	5.3	/	/	0.3	14-16	90°	1
<i>Taeniopteris</i> sp1 Galtier et Broutin	15	6	/	/	0.4-0.6	12-15	70°-80°	1
<i>Taeniopteris</i> sp2 Galtier et Broutin	17	7	acute	/	/	14-17	70°-80°	/
<i>Taeniopteris</i> sp A Kustatscher, Bauer, Butzmann, Fischer, Meller, Van Konijnenburg-van Cittert et Kerpi	12	2.1	/	/	0.3-0.5	15-18	80-90°	4
<i>Taeniopteris</i> sp B Kustatscher, Bauer, Butzmann, Fischer, Meller, Van Konijnenburg-van Cittert et Kerpi	6	9-7			0.6	12-18	70°	1
<i>T. abnorvis</i> Gutbier	15	9.5	/	/	/	28-32	45°	7
<i>T. anavolans</i> Anderson et Anderson	17	3.5	/	cuneiform	0.7	14-16	80°-09°	7
<i>T. anglica</i> White	50	4.5	/	/	0.4-0.1	28	60°-70°	/
<i>T. angustifolia</i> Stockm et Math	13	2	/	/	0.1	28	70°-80°	3
<i>T. ardesica</i> Grand eury	4.2	1.7	/	/	0.05	20-22	80°	1
<i>T. bertrandiana</i> Teixeira	6.5	3	/	/	/	12	75°	1
<i>T. bosniackii</i> Stefani	6	2.4	/	/	0.25	20	85-90°	1
<i>T. carnoti</i> Zeiller	/	2.5-3	/	/	0.1-0.2	25-30	70-80°	3
<i>T. crassinervis</i> (Feistmantel) Walkom	7	4.5-5.5	/	/	0.2	12-14	90°	1
<i>T. cricumensis</i> Dolianiti	10	1.8	/	/	0.2-0.5	32-40	45°	7
<i>T. densinervis</i> Menéndez	/	1.8	/	/	0.1	28-32	85-90°	4
<i>T. doubingeri</i> Remy	11	3.4	/	/	0.1-0.6	23-34	70°-75°	1
<i>T. eckardti</i> German	20	2.3	/	/	0.2-0.4	08-09	60°	4
<i>T. feddeni</i> Feistmantel	25	12.5	/	/	0.2	20	90°	7
<i>T. gemmina</i> Plumstead	4.5	1.3	/	/	0.07	15-20	60°-70°	7
<i>T. homerifolius</i> Anderson et Anderson	/	6.5	/	/	0.4	10-12	75°	7
<i>T. jejuna</i> grand eury	8-15	1.4-2	/	/	0.1	12-20	70°	/
<i>T. kelberi</i> Kustatscher et Van Konijnenburg-Van Cittert	21	2.0-2.8	/	/	0.55	20-25	80°	4
<i>T. lata</i> Oldham et Morris	36	11	/	/	0.5	10	/	5
<i>T. lentriculiformis</i> (Feistmantel) Walkom	9	2.5-3			0.1	22	80°-90°	4
<i>T. lescuriana</i> Fontaine et white	7	8	/	/	0.2	/	85°	3
<i>T. lutzae</i> Gnaedinger et Herbst	20	5	retuse	round	/	14-20	80°-90	4
<i>T. magnifolia</i> Rogers	10	7-22	/	/	0.4-1	16-20	85-90°	4
<i>T. multinervia</i> Weiss	7.5-20	12-2	/	/	0.6-0.5	36	80°-90°	1
<i>T. novomundensis</i> Pott et Launis	15	2.1	acute	contracted	0.2-0.4	/	75-80°	1
<i>T. parva</i> Jongmans	3	0.8	/	/	/	50	80°-85°	3



TABLE 4 (continued).

Species	L.L.	W.L.	T.A.	T.B.	W.R.	D.V.	A.I.V.	A.V.
<i>T. plauensis</i> Sterzel	9	1-3.2	/	/	0.1-.07	13-24	70°-80°	2
<i>T. plicatella</i> (Solms-Laubach) Menéndez	6	1.5	/	/	0.5	9	40°	7
<i>T. schlotheimi</i> Remy	5	0.7	/	/	.05-.03	12-14	78-82°	7
<i>T. smithii</i> Lesquereux	15	5	/	/	0.1	40	/	/
<i>T. submultinervia</i> Sterzel		0.32	/	/	0.1	10	75°	3
<i>T. taiuanensis</i> Halle	13	12	/	/	.8-.5	35-50	65°-80°	1
<i>T. tenuis</i> Doubinger et Vetter	6.5-7	1.5	/	/	.07-.05	28-36	80°-90°	3
<i>T. thomsoniana</i> (Arber) Blaschke et Grant-Mackie	/	2	/	/	0.2	28-36	85°-90°	7
<i>T. troncosoi</i> Gnaedinger et Herbst	20	5-1	retuse	cuneiform	/	22-24	40°-50°	7
<i>T. vittata</i> Brongniart	/	2.8-4	acute	/	/	24-30	50°-60°	1
<i>T. wianamattae</i> (Feistmantel) Walkom	/	3.5-6	/	/	0.2-0.6	24-28	75°	1
<i>T. zeilleri</i> Bertrand	30	40	/	/	.3-.2	28	70°-90°	4 and 7

Barbacka, 2001; Kustatscher and Van Konijnenburg-van Cittert, 2010), which completely differ from the specimen from Puebla. However, this assignment can only be corroborated by obtaining more cuticle fragments, which would be of great importance since they would confirm the geographic and temporal extension of this genus to the Permian of North America.

With regard to *Nilssonina*, there are other genera of Cycadophytes that have a segmented lamina, e.g., *Pseudoctenis* Seward, which differs from *Nilssonina* in having leaves laterally inserted into the rachis, never dorsally (Pott et al., 2010), and *Ctenis* Lindley et Hutton, which has an anastomosing venation (Pott et al., 2007). Given the insertion of the lamina into the rachis and the type of venation, it is possible to assign the specimen from Mexico to the genus *Nilssonina*. Nevertheless, poor preservation precludes proposing a new species or assigning it to an existing one.

From the Matzitzi Formation, we also studied leaves with an entire margin, a rachis, and less than 5 cm in width. We assigned these to *Taeniopteris*. However, it must be clarified that, thus far, *Taeniopteris* is considered an artificial genus with different taxonomic affinities and that should only be used for leaves that lack cuticular characters, which could ensure the taxonomic identity of the leaves (Pott and Launis, 2015). Thus, in the present work, they were not assigned to any order and remain in the category of *Incertae sedis*. Yet, the presence of two new reports for the Permian of Mexico is of great importance since, in addition to

the record of *Taeniopteris* cf. *T. magnifolia* from the lower Permian of the state of Hidalgo, Mexico (Velasco et al., 2020), they confirm the presence of this morphotype of leaves in Mexico. These new reports demonstrate that only a few formal taxonomic studies have been conducted in the Matzitzi Formation. Therefore, the knowledge of the taxonomy is alpha level sensu Anderson and Anderson (2003).

The record of *Taeniopteris* cf. *T. magnifolia* occurs in a humid environment with periods of hydric stress in the Tuzancoa Formation (Velasco et al., 2020), which have characteristics very similar to those proposed for the Matzitzi Formation, where there is a mixture of both hygrophilic elements and those better adapted to water scarcity (Flores-Barragan, 2019). We propose that, in Mexico, this genus appears to be present at the end of the Paleozoic in environments with variable climate and intermittent periods of hydric stress.

Looy et al. (2014) mention that derived genera (recent appearance), such as these types of Cycadophyte leaves, evolved under conditions of environmental drought. This could be the case of the localities from the Permian of Mexico, with the prevalence of a sub-humid environment with seasonal rainfall, which indicates hydric stress in some strata (Flores-Barragan, 2019; Velasco et al., 2020). This condition limited the fossilization of the leaves, resulting in a sparse fossil record for these genera compared to those that inhabited more humid places. This would explain the isolated (geographically) and intermittent (chronologically)

reports of these types of leaves during the Paleozoic.

Localities with reports similar to those recorded here are located in the Triassic of Europe, specifically in the middle Triassic of Italy and Germany (Wachtler and Van Konijnenburg-van Cittert, 2000; Kustatscher and Van Konijnenburg-van Cittert, 2010). In Italy, there is a prevalence of conifers over other plant groups, which, together with taxonomic and geological data, is interpreted as an environment with a sub-humid climate (Kustatscher and Van Konijnenburg-Van Cittert, 2005). On the other hand, Germany is considered to have had a generally more humid climate due to the abundance of hygrophilic elements such as Marattiales (Kustatscher et al., 2012b). The material from these environments is not floristically comparable with the Matzitzi Formation for it exhibits an abundance of genera typical of the upper Paleozoic, such as *Asterotheca* Presl and Corda, *Calamites* Brongniart, *Cyperites* Lindley and Hutton, and *Sigillaria* Brongniart. It appears that taxa with morphology similar to Cycadophyta have been established in partially sub-humid environments since the Permian-Triassic transition.

In the present work, we propose a sub-humid environment based on the floristic elements. However, studies on the edaphic and taphonomic conditions are still necessary in order to better understand the depositional environments of the Matzitzi Formation that allowed the establishment and coexistence of different floristic elements. New records, such as those reported in the present work, are important to answer questions on envi-

ronmental, taxonomic, and distributional aspects. For example, does *Bjuvia* or *Nilssonina* have an earlier origin than that estimated based on the records in the literature? And did they have a larger geographic distribution? Much remains to be discovered in the localities of the end of the Paleozoic in what is now known as Mexico.

## CONCLUSIONS

The presence of cf. *Bjuvia* sp., *Nilssonina* sp., *Taeniopteris crassinervis*, and *T. lenticuliformis* makes the existence of Cycadophytes in the Permian of Mexico conclusive. These records increase the described diversity for the Matzitzi Formation and have an impact on the spatial and temporal distribution of these genera. This will help to determine their origin and diversification.

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