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Early Permian conifer remains from Central Mexico and reevaluation of Paleozoic conifer morphotaxa

Genaro R. Hernández-Castillo^{1,*}, Silvia A. Silva-Pineda², Sergio R.S. Cevallos²

¹ Paleoconifer Consulting Ltd., Edmonton, AB, T6X 0X7, Canada.

² Departamento de Paleontología, Instituto de Geología, UNAM, Ciudad Universitaria, Del. Coyoacán, México D.F., 04510, México.

*paleoconifer@gmail.com

Abstract

This paper describes the first Permian walchian conifer from Mexico based on several specimens preserved as compressions/impressions. The material comes from the Tuzancoa Formation in the state of Hidalgo, Central Mexico. It is described as *Calnalia hidalguensis* gen. nov. et sp. nov. a new conifer morphotaxon based on isolated lateral branches with leaves. This new conifer has some of the smallest branches and leaves found among previously described walchians. *Calnalia hidalguensis* has two types of branches (ovoid and deltoid) with simple and helically arranged leaves. Leaves are narrowly triangular to linear in front view, slightly concave and spreading (penultimate shoots) to slightly concave to slightly S-shaped (ultimate shoots), in side view. Leaves range from 3.2 mm long by 0.5 mm wide on penultimate shoots, to 1.3 - 2.9 mm long by 0.4 - 0.9 mm wide on ultimate shoots, with angles of leaf insertion ranging from 16° to 39°. The new species is most similar to *Emporia lockardii* Mapes and Rothwell, *Walchia goeppertiana* Florin, *Walchia mucronata* Florin, and *Otoviclia hypnoides* Kerp, Poort, Swinkels & Verwer. However, none of these have the same ranges of morphological variation found in the leaves of Mexican species. The new taxon expands the diversity of walchian conifers at the end of the Paleozoic in America, and marks the beginning of new research of Permian floras in Mexico. The presence of *C. hidalguensis* and other gymnosperms, to be described, reinforces the presence of an arc along the Oaxaquia block that connected Mexico to the North American craton during the late Paleozoic. These new data also allow us to test hypotheses about the origin and evolution of Paleozoic floras in Euramerica.

Keywords: conifer, Mexico, morphotaxa, Permian, *Walchia*.

Resumen

Este artículo describe la primera conífera pérmica "walchiana" con base en varias compresiones e impresiones fósiles de la Formación Tuzancoa en el Estado de Hidalgo, Centro de México. Se describe como *Calnalia hidalguensis* gen. nov. et sp. nov., un nuevo morfotaxón de coníferas basados en ramas laterales y hojas. Esta nueva conífera tiene unas de las ramas más pequeñas descritas hasta ahora para los miembros "walchianos" en el registro fósil, y cuenta con dos tipos de ramas (ovoide y deltoide), las cuales portan hojas simples con filotaxia helicoidal. Las hojas son ligeramente triangulares a lineares; lateralmente son ligeramente cóncavas a abiertas (penúltimo orden), y ligeramente cóncavas a ligeramente en forma de "S" (último orden). El tamaño de las hojas de penúltimo orden es de 3.2 mm de largo por 0.5 mm de ancho y en las hojas de último orden de 1.3 - 2.9 mm de largo por 0.4 - 0.9 mm de ancho, con ángulos de inserción de las hojas de 16° a 39°. La nueva especie posee mayor similitud con *Emporia lockardii* Mapes and Rothwell, *Walchia goeppertiana* Florin, *Walchia mucronata* Florin y *Otoviclia hypnoides* Kerp, Poort, Swinkels & Verwer. Sin embargo, ninguna de estas especies tiene los mismos rangos de variación morfológica que las hojas de la nueva especie Mexicana presentan. Este nuevo taxón aumenta la diversidad de estas coníferas conocida a finales del Paleozoico en el continente Americano. A su vez, la descripción de esta nueva especie abre la investigación paleobotánica durante el Pérmico en México, y su presencia, así como la de otras especies de plantas aún por describir, refuerzan la teoría de la existencia de un arco a lo largo del bloque Oaxaquilla que conectaba a México

con el Cratón de Norteamérica a finales del Paleozoico. Estos datos nos ayudan a proponer hipótesis sobre el origen y evolución de las floras Paleozoicas de Euramérica.

Palabras clave: conífera, México, morfotaxa, Pérmico, *Walchia*.

1. Introduction

The earliest fossil conifer remains of Mexico have been described from early Permian sediments of the San Mateo area between the states of Hidalgo and Veracruz (Carrillo-Bravo, 1965; Silva-Pineda, 1987). This fossil material consisted of few isolated and highly fragmentary ultimate shoots of a *Walchia*-like plant. Additional conifer remains have been collected from Paso Hondo, Tuzancoa, and Patlanoaya Formations from Chiapas, Hidalgo, Veracruz and Puebla respectively (Carrillo-Bravo, 1965; Hernández-García, 1973; Moreno-Cano and Patiño-Ruiz, 1981; Silva-Pineda, 1987; Silva-Pineda *et al.*, 2000; Vachard *et al.*, 2000; Silva-Pineda, 2003). These conifers are few in number and preserved as impressions and compressions with poor cuticles. The early Permian age (Wolfcampian-Leonardian) determinations for Mexican localities are based on key brachiopods, pelecypeds and fusulinids species (Carrillo-Bravo, 1965; Hernández-García, 1973; Moreno-Cano and Patiño-Ruiz, 1981; Vachard *et al.*, 2000).

New material has been collected from Tuzancoa Fm. near Calnali river, Hidalgo (Figure 1). These fossils allow us to describe a new conifer species from the early Permian of Mexico. The material is characterized by isolated and fragmentary lateral branches with simple leaves that resemble many other walchian conifers around the world (Florin, 1938-45; Rothwell, 1982; Clement-Westerhof, 1987; Meyen, 1997; Rothwell *et al.*, 1997; Kerp and Clement-Westerhof, 1991). Traditionally, fragmentary conifer remains were described as species belonging to form-genera (Florin, 1938-45; Mapes and Rothwell, 1991; Visscher *et al.*, 1986), now known as morphotaxa (Greuter in McNeill *et al.*, 2006). Paleozoic conifer morphotaxa lack familial affinities due to their incomplete nature and broad ranges of morphological and cuticular variation (Hernandez-Castillo *et al.*, 2001; Hernandez-Castillo, 2005; Rothwell *et al.*, 2005). Thus, prompting the use of different approaches and classifications to understand Paleozoic walchian conifers.

Three classification systems have been proposed for Paleozoic conifers (Mapes and Rothwell, 1991). The first classification was proposed by Florin (1927, 1938-45) and it was later improved and modified by Clement-Westerhof and colleagues (Clement-Westerhof, 1984, 1987; Visscher *et al.*, 1986; Kerp and Clement-Westerhof, 1991). Although both classification systems are and/or have been used widely, they do not recognize nor integrate overlapping ranges of morphological and cuticular variation found among most walchians species (Hernandez-Castillo *et al.*, 2001). A third

classification does employ these broad ranges of variation for species delimitation (Mapes and Rothwell, 1991), therefore providing robust organocorrelations that allow reliable and complete conifer reconstructions (Hernandez-Castillo *et al.*, 2001; Rothwell and Mapes, 2001; Hernandez-Castillo, 2005; Rothwell *et al.*, 2005).

Although, this last method has proven to be most effective in reconstructing conifers as species of extinct plants, no new methods have been recently proposed for dealing with poorly preserved conifer morphotaxa. Therefore, the new Mexican material, from Calnali, offers an opportunity to reevaluate and update current approaches for describing and naming Paleozoic conifer morphotaxa. Furthermore, the discovery of walchian conifers, in central Mexico, may serve to test hypothesis on the origin and accretion of Mexican terranes and blocks at the end of the Paleozoic, as previously discussed by other authors (Ortega-Gutierrez *et al.*, 1995; Sánchez-Zavala *et al.*, 1999; Vachard *et al.*, 2000; Centeno-García, 2005).

2. Materials and methods

The fossil material was collected 0.5 km from Calnali, Hidalgo, near Calnali River (Figure 1). This locality was originally described as part of the Guacamaya Formation (Carrillo-Bravo, 1965). However, Ochoa-Camarillo (1996) divides the Guacamaya Formation into the Tuzancoa and Otlamalacatla Formations. Recent work has provided evidence that Calnali Permian strata correspond to the Tuzancoa Formation (Rosales-Lagarde *et al.*, 1997, 2002; Sour-Tovar *et al.*, 2005). The Tuzancoa Formation is exposed in the northeast and central-east portions of Hidalgo state, Mexico (20° 55' - 20° 35' N and 98° 40' - 98° 30' W, Figure 1). This formation is part of the Sierra Madre Oriental and belongs to the Huayacocotla Anticlinorium (Rosales-Lagarde *et al.*, 1997). Tuzancoa Formation is a siliclastic sequence that switches to lava flows and andesitic and basaltic breccia, intercalating with sandstones, shales and lutites of volcanic origin (Figure 2). This formation is found between Precambrian metamorphic rocks (Huiznopala Gneiss) and discordant Mesozoic units (Sour-Tovar *et al.*, 2005; Figure 2). The fossil material comes from a turbiditic section characterized by mid-fine grain vulcanoclastic sandstones alternating with siltstones that correspond to the upper most section described at Tuzancoa's Fm. type section (section 5 of Rosales-Lagarde, 2002).

The Wolfcampian to Leonardian age on this material is constrained by at least two invertebrate localities that

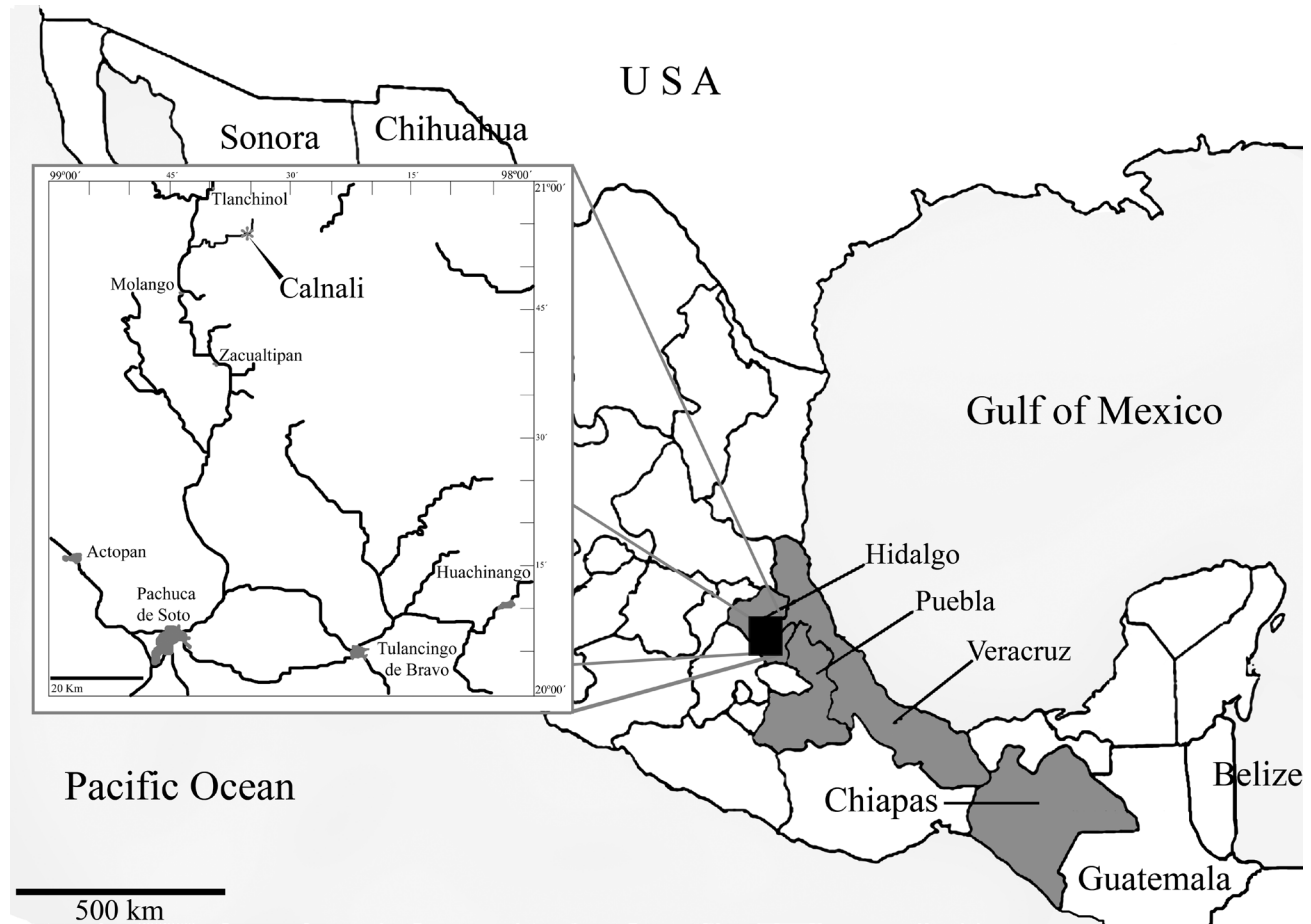


Figure 1. Map of Mexico showing states with Paleozoic conifer remains (dark) and a close up of Hidalgo state showing fossil locality (*).

are located above and below the fossil plant bearing strata (Figure 2; Carrillo-Bravo, 1965; Moreno-Cano and Patiño-Ruiz, 1981; Rosales-Lagarde, 2002; Sour-Tovar *et al.*, 2005). This fossil conifer material is associated to fragmentary remains of *Pecopteris*, *Neuropteris*, *Odontopteris*, cf. *Gangamopteris* and *Taeniopteris* (Silva-Pineda, 1987), and poorly preserved gigapopterid-like? leaf remains.

The specimens are preserved as compressions/impressions in fine to medium grain sandstones and fine-grained shales associated to large grain sandstones, limestones and tobos (Figure 2; Carrillo-Bravo, 1965; Ochoa-Camarillo, 1996; Silva-Pineda *et al.*, 2000). Specimens were prepared using needles to remove sediments on top of branches and leaves. Light microscopy was conducted using Zeiss Stemi DV4 microscope. Images were captured with a Nikon CoolPix 4300 (Nikon Corp., Japan) and an AxioCam MRc Rev. 2/3.3V (Zeiss Inc., Germany) digital cameras. Images were processed using Adobe Photoshop CS3. Measurements of digitized specimens were taken using Image J ver. 1.36 b (Abramoff *et al.*, 2004) according to Hernandez-Castillo (2005). All specimens are stored in the Colección del Laboratorio de

Paleobotanica, Instituto de Geología, Mexico City, Mexico with collection numbers IGM-PB 1254- IGM-PB 1284.

3. Systematics

Class – Coniferopsida

Order – Voltziales

Family – Unknown

Genus – *Calnalia* Hernandez-Castillo, Silva-Pineda et Cevallos Ferriz

Calnalia hidalguensis Hernandez-Castillo, Silva-Pineda et Cevallos Ferriz (Figs. 2-11)

Calnalia hidalguensis diagnosis – Lateral branches plagiotropic, ovoid to deltoid, 4.0 to 15 cm long and 4.5 to 9.4 cm wide; shoots of penultimate order up to 15 cm long, 0.4 cm wide; shoots of ultimate order up to 4.8 cm long, 0.21 cm wide; leaves on penultimate shoots helical, simple, narrowly triangular to linear (front view), slightly concave and spreading (side view), 2.6-3.2 mm long, 0.3-0.5 mm wide; leaves on ultimate shoots helical, simple, narrowly

triangular to linear (front view), slightly concave to slightly S-shaped (side view), 1.3-2.9 mm long, 0.4-0.9 mm wide, angles of insertion 16°-39° (Figures 2-14).

Holotype: Penultimate shoot bearing ultimate shoots with leaves. Specimen IGM-PB 1254, Figures 2, 6.

Paratypes: Branches showing leaf morphology on penultimate and ultimate shoots, IGM-PB 1256, IGM-PB 1258 (Figures 3, 4). Leaves of penultimate shoots IGM-PB 1263, IGM-PB 1264 and IGM-PB 1254 (Figure 5, 6, 7). Leaves on ultimate shoots IGM-PB 1263 (Figures 8, 11), IGM-PB 1274 (Figure 9), IGM-PB 1279 (Figure 10).

Collecting locality: Calnali River (20° 55' - 20° 35' N and 98° 40' - 98° 30' W), Municipio de Calnali, Hidalgo, Mexico. Figure 1.

Stratigraphic occurrence and age: Huayacocotla Anticlinorium, Tuzcanoa Formation, early Permian (Wolfcampian-Leonardian/Sakmarian-Artinskian), Figure 2.

Etymology: The specific epithet *hidalguensis* refers to Hidalgo State in Central Mexico.

4. Description

The new species is represented by small lateral plagiotropic branches with a penultimate shoot bearing several ultimate shoots (Figures 2-5). Both branching orders are covered by helically arranged simple leaves (Figures 6-11). Branches range in shape from ovoid to slightly deltoid (Figures 2-5). Branches are small (up to 15 cm long), but most of them are often broken. Penultimate shoots are up to 15 cm and up to 4 mm wide. Ultimate order shoots may be straight or slightly recurved depending on branch type and size (Figures 2-5). Some branches display straight ultimate shoots with insertion angles ranging from 45° to 90° (Figures 2-4), while other ones have ultimate shoots that are recurved giving the branch an ovate shape (Figures 3, 5).

Shoots, of penultimate order, are covered by helically arranged, simple leaves (Figures 2, 3), which are often not well preserved. Leaves on penultimate shoots are narrowly triangular to linear in front view and slightly concave and spreading in side view (Figures 6, 7). They are narrowly

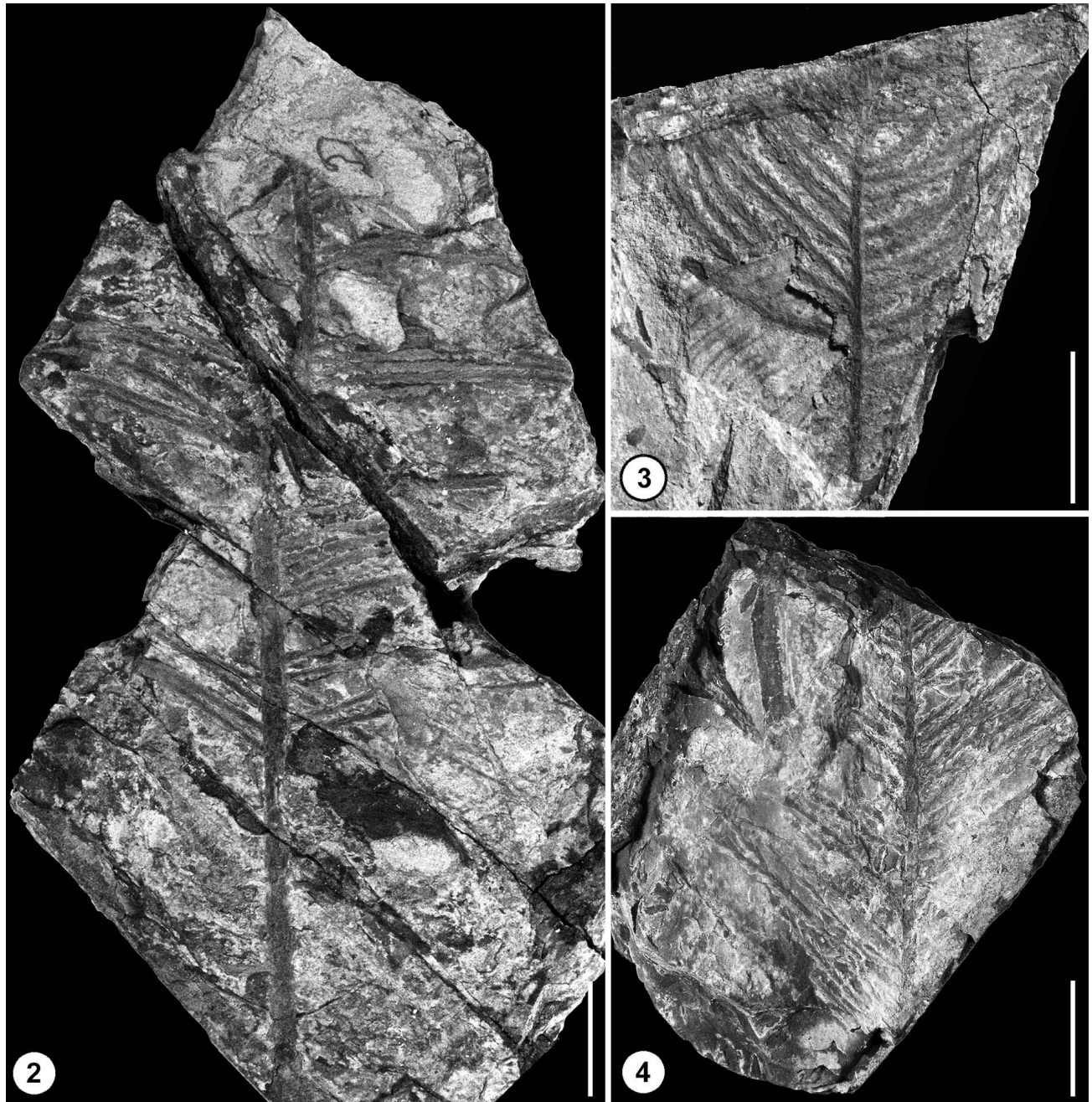
Table 1. Comparison of leaves of penultimate order shoots of *Calnalia hidalguensis* gen. nov. et sp. nov. and other Lebachoid Paleozoic walcchian conifers.

Species/ Characters	Architecture		Leaves of penultimate order			
	Stem	Lateral branches	Length (mm)	Width (mm)	Shape (face view)	Shape (side view)
<i>Calnalia hidalguensis</i>	?	Plagiotropic	3.2	0.5	Nt, Li	Sc, Sp
¹ <i>Emporia lockardii</i> *	Orthotropic?	Plagiotropic	5.0-10.0	1.0-2.1	Nt, Li, Fr	<i>Sc, Sss</i>
² <i>Emporia cryptica</i>	Orthotropic	Plagiotropic	2.4-7.1	0.6-2.0	Nt, Li	Ss, Sp
² <i>Emporia royalii</i> **	Orthotropic?	Plagiotropic	1.6-5.0	0.3-1.5	Nt, Li, Fr	Ss, Sss
³ <i>Lebachia americana</i>	?	Plagiotropic	3.5-7	1-1.5	St, Sl	<i>Sc, Sp, Sss</i>
³ <i>Lebachia angustifolia</i>	?	Plagiotropic	4-15	01-feb	<i>Nt, St, Sl</i>	Sc, Sp
⁴ <i>Lebachia garnettensis</i>	?	Plagiotropic	3.0-16.0	1.5-2.5	Nt, Li	Sc
⁵ <i>Lebachia goeppertiana</i>	?	Plagiotropic	2-4.7	0.3-0.8	<i>Nt, Li, Sl</i>	Sc, Sp
⁵ <i>Lebachia mucronata</i>	?	Plagiotropic	3-8	01-feb	Sl, St	Sc, Sp
⁵ <i>Lebachia parvifolia</i>	?	Plagiotropic	4-15	01-feb	<i>Nt, St, Li</i>	<i>Sc, Li, Slp</i>
⁵ <i>Lebachia piniformis</i> var <i>solmsii</i>	?	Plagiotropic	6.5-10.5	1.4-2.9	Nt, Li	Sc, Sp
⁶ <i>Otovicia hypnoides</i> *	?	Plagiotropic	2.0-8.0	1.0-1.5	St, La, Fr	Sc, Ss
⁷ <i>Thucydia mahoningensis</i>	Orthotropic	Plagiotropic	5-12.5	1.0-1.5	Nt, Li	Sc, Ss
⁸ <i>Utrechtia floriniformis</i> *	Orthotropic?	Plagiotropic	12-25	1.5-3.0	Nt, Li, Fr	Sc

Character combinations that differ from those of *C. hidalguensis* are recorded in bold face type and overlapping characters are recorded in italics.

* Heterophylly present (forked leaves). Modified from Hernández-Castillo *et al.*, 2001. ¹ Hernández-Castillo, 2005; Mapes and Rothwell, 1984, 1991.

² Hernández-Castillo, 2005. ³ Florin 1938-45. ⁴ Emended by Winston (1984). ⁵ Florin 1938-45. ⁶ Kerp *et al.*, 1990; Florin (1938-45). ⁷ Hernández-Castillo *et al.*, 2001. ⁸ Florin 1938-45; Mapes and Rothwell, 1991. Leaf shape abbreviations: Li = Linear, Nt = Narrowly triangular, Sc = Slightly concave, Sl = Slightly lanceolate, Sp = Spreading (extending nearly to the horizontal), Slp = Slightly spreading (not necessarily extending nearly to the horizontal plane), Ss = S-shaped, Sss = Slightly S-shaped, St = Sub-triangular.

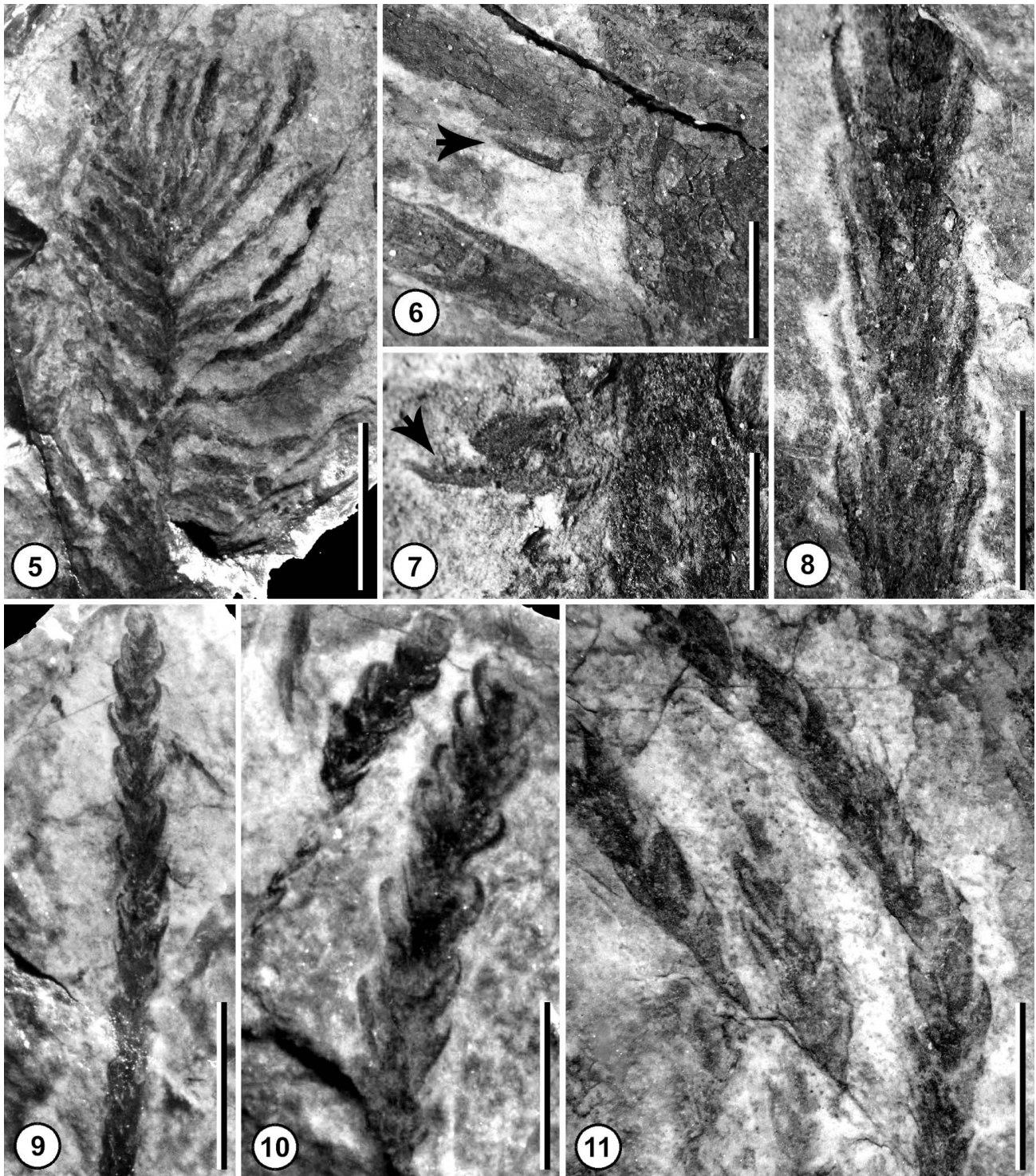


Figures 2-4. *Calnalia hidalguensis* gen. nov. et sp. nov. variation of plagiotropic lateral branches. 2. Lateral branch showing stem of penultimate order and attached shoots of ultimate order. IGM-PB 1254, scale bar = 2 cm. 3. Lateral branch showing several ultimate shoots. Note shoot curvature towards the branch apex. IGM-PB 1256, scale bar = 2 cm. 4. Lateral branch showing penultimate and ultimate shoots. Note the angles of insertion of ultimate order shoots. IGM-PB 1258, scale bar = 2 cm.

triangular to linear in front view and slightly concave to spreading in side view. Leaves range from 2.6 to 3.2 mm in length and 0.3 to 0.5 mm in width. Leaves have angles of insertion close to 90° (Figures 6, 7). However, more leaves are needed to assess the full range of morphological variation of this leaf order.

Shoots of ultimate order are found attached to penultimate shoots in lateral branches, or isolated and often fragmentary (Figures 2-4; Figures 9, 10). Simple and helically arranged

leaves cover these shoots. Leaves range from 1.3 to 2.9 mm in length and 0.4 to 0.9 mm in width. They are narrowly triangular to linear in front view, and slightly S-shaped to slightly concave in side view (Figures 8-11). They can be adpressed with angles of insertion ranging from 16° to 24° (Figures 8, 11) to slightly adpressed with angles ranging from 25° to 39° (Figures 9, 10). Although leaves on ultimate shoots may be slightly to fully adpressed, their angles of insertion at the base and apex of the ultimate shoot are rather



Figures 5-11. *Calnalia hidalguensis* gen. nov. et sp. nov. lateral branch and leaf variation on shoots of ultimate order. Note the angles of insertion of leaves, see text for explanation. 5. Ovate plagiotropic lateral branch showing branch apex. IGM-PB 1263, scale bar = 3 mm. 6. Penultimate shoot showing attached leaf. Note that the leaf is located below a shoot of ultimate order (arrow). IGM-PB 1264, scale bar = 2 mm. 7. Penultimate shoot showing attached slightly spreading leaf. IGM-PB 1254, scale bar = 2 mm. 8. Shoot showing adpressed, slightly concave leaves. IGM-PB 1263, scale bar = 2 mm. 9. Shoot showing non-adpressed and slightly concave leaves. IGM-PB 1274, scale bar = 2 mm. 10. Shoot showing non-adpressed, slightly concave to slightly S-shaped leaves. IGM-PB 1279, scale bar = 2 mm. 11. Shoot showing adpressed, slightly concave leaves. Note the leaf thickness. IGM-PB 1263, scale bar = 2 mm.

similar. Leaf shape (in side view) and angles of insertion depend on the branch type, position within the branch, and overall preservation (Figures 8-11). No heterophylly has been observed between the leaves on penultimate and ultimate shoots so far.

5. Discussion

5.1. *Calnalia hidalguensis* and its relationship to Paleozoic walchian conifers

Calnalia hidalguensis is described as a new morphotaxon for vegetative lateral plagiotropic branches of Paleozoic conifers, with simple, helically arranged leaves and no cuticles preserved. Lateral branches of *C. hidalguensis* conform to the traditional walchian conifer morphology (Florin, 1938-45). Walchian conifers are common gymnosperms from Upper Paleozoic sediments

of Euramerica (Florin, 1938-45; Rothwell, 1982; Clement-Westerhof, 1984). These conifers typically display lateral plagiotropic branches composed of a penultimate shoot that bears several ultimate shoots similar to those of *C. hidalguensis*. This new taxon is similar to commonly known Euramerican Paleozoic conifers previously described by Florin (1938-45), Winston (1984), Kerp *et al.* (1990), Mapes and Rothwell (1991), Hernandez-Castillo *et al.* (2001), and Hernandez-Castillo (2005).

Calnalia hidalguensis have simple leaves on penultimate shoots that contrast with taxa bearing forked penultimate leaves (Table 2). The presence or absence of simple or forked leaves on penultimate shoots is used to distinguish taxa and heterophylly in conifers (Hernandez-Castillo *et al.*, 2001). This is important because some of these conifers display different types of heterophylly, suggesting different tree architectural types, similar to those found in living conifers (Rothwell and Mapes, 2001; Hernandez-Castillo *et al.*, 2003; Hernandez-Castillo, 2005). Plagiotropic branches of

Table 2. Comparison of leaves of ultimate order shoots of *Calnalia hidalguensis* gen. nov. et sp. nov. and other Lebachoid Paleozoic walchian conifers.

Species/ Characters	Leaves of ultimate order					*Heterophylly	
	Length (mm)	Width (mm)	Shape (face view)	Shape, (side view)	Angle of Divergence		
					Base	Apex	
<i>Calnalia hidalguensis</i>	1.3-2.9	0.4-0.9	Nt, Li	Sc, Sss	17-39	16-39	Absent?
¹ <i>Emporia lockardii</i>	1.7-5.0	0.4-1.16	Nt, Li	Sc, Sss	26-63	28-69	Present
² <i>Emporia cryptica</i>	<i>1.2-2.7</i>	0.3-1.2	Nt, Li	Sss, Sc, Sp	30-64	27-70	Present
² <i>Emporia royalii</i>	1.6-4.5	0.6-1.7	Nt, Li	Sc, Sss	24-57	21-61	Present
³ <i>Lebachia americana</i>	2-4.5	0.7-1.5	St, Sl,	Sc, Sss	15-85	-65	<i>Absent</i>
³ <i>Lebachia angustifolia</i>	5-8	<i>0.5-0.7</i>	<i>Nt, Li, St</i>	Sc, Sss	oct-20	-30	<i>Absent</i>
⁴ <i>Lebachia garnettensis</i>	4.0-7.0	0.4-1.4	Nt, Li	Sc, Ss	35-70	?	<i>Absent</i>
⁵ <i>Lebachia goeppertiana</i>	1.9-5.8	<i>0.4-0.6</i>	<i>Nt, Li, Sl</i>	<i>Sc, Sss, Sp</i>	19-55	26-70	Absent?
⁵ <i>Lebachia mucronata</i>	1.5-4.7	1.0-2.1	Sl, St	Sc, Sp	30-45	35-90	<i>Absent</i>
⁵ <i>Lebachia parvifolia</i>	2.8-5.0	<i>0.5-1.2</i>	<i>Nt, Li, St</i>	Sc, Sss	21-60	<i>19-37</i>	Present
⁵ <i>Lebachia piniformis</i> var <i>solmsii</i>	2.2-6.3	0.4-1.2	Nt, Li	Sc, Sss	24-55	28-66	<i>Absent</i>
⁶ <i>Otovicia hypnoides</i>	1.5-4.0	<i>0.2-0.5</i>	Nt, Li	Sc	35-90	35-?	Present
⁷ <i>Thucydia mahoningensis</i>	3-6	<i>0.4-1.0</i>	Nt, Li	Sc, Ss	22-57	21-54	<i>Absent</i>
⁸ <i>Utrechitia floriniformis</i>	9-13	<i>0.4-0.6</i>	Nt, Li	Sc, Ss	?	30	Present

Character combinations that differ from those of *C. hidalguensis* are recorded in bold face type and overlapping characters are recorded in italics. Modified from Hernandez-Castillo *et al.*, 2001. ¹ Hernandez-Castillo, 2005; Mapes and Rothwell, 1984, 1991. ² Hernandez-Castillo, 2005. ³ Florin 1938-45. ⁴ Emended by Winston (1984). ⁵ Florin 1938-45. ⁶ Kerp *et al.*, 1990; Florin (1938-45). ⁷ Hernandez-Castillo *et al.*, 2001. ⁸ Florin 1938-45; Mapes and Rothwell, 1991. Leaf shape abbreviations: Li = Linear, Nt = Narrowly triangular, Sc = Slightly concave, Sl = Slightly lanceolate, Sp = Spreading (extending nearly to the horizontal), Slp = Slightly spreading (not necessarily extending nearly to the horizontal plane), Ss = S-shaped, Sss = Slightly S-shaped, St = Sub-triangular. * Heterophylly is based on differences in the shape of leaves, where two distinctive types of leaves are known (Hernandez-Castillo *et al.*, 2001).

C. hidalguensis display penultimate order shoots bearing leaves that are most similar to those of *Lebachia piniformis* var. *solmsii* Florin (Table 2). Unfortunately, not many penultimate order leaves have been found, which prevents us from more comprehensive comparisons to the very few walchian species with well-preserved penultimate leaves.

Shoots, of ultimate order, bear some of the smallest leaves found among walchian conifers of Europe and North America (Table 3). Leaves range from 1.3 to 3.2 mm long and fall within the ranges of variation of species such as *Emporia lockardii* (Mapes & Rothwell) Mapes & Rothwell, two new *Emporia* species, *Emporia cryptica* and *Emporia royalii*, from the Hamilton Quarry (Hernandez-Castillo et al., 2009b, 2009c), *Lebachia goeppertiana* Florin, *Lebachia mucronata* Florin, and *Otovicia hypnoides* Kerp, Poort Swinkels & Werver (Table 3). In contrast, other euramerican conifers, such as *Lebachia americana* Florin, *Lebachia angustifolia* Florin, *Lebachia garnettensis* (Florin) Winston, *Thucydia mahoningensis* Hernandez-Castillo, Rothwell and Mapes, and *Utrechtia floriniformis* Mapes and Rothwell, display larger leaves than those of *Calnalia* (Table 3). Angles of insertion of leaves, in most euramerican taxa, either overlap or are greater than those of *Calnalia* (Table 3). Therefore, no other previously described walchian conifer morphotaxa have leaves with same ranges of variation as those recorded for *Calnalia hidalguensis*.

5.2. Conifer morphotaxa

Traditionally, Paleozoic conifer remains based on isolated lateral branches, shoots with leaves, and cones have been described as form-genera and now designated as morphotaxa (Stewart and Rothwell, 1993; Greuter et al., 2000; McNeill et al., 2006; Table 1). According to the ICBN (Vienna Code), “a morphotaxon is defined as a fossil taxon which, for nomenclatural purposes, comprises only the one part, life-history stage, or preservational state represented by the corresponding nomenclatural type” (McNeill et al., 2006). Therefore, the new Mexican conifer conforms to the concept of a new morphotaxon for walchian conifers represented by two orders of lateral branches with attached leaves.

Most Paleozoic conifer morphotaxa lack familial affinities due to broad and/or overlapping ranges of morphological and cuticular variation of leaves and leaf-like structures such as, pollen cone microsporophylls, ovulate cone bracts and sterile scales (Hernandez-Castillo et al., 2001; 2009b). Species identification, including familial affinities among these conifers, are controversial due to these overlapping ranges of variation and the absence of organic connections (Hernandez-Castillo et al., 2001; Rothwell et al., 2005; Hernandez-Castillo, 2005). The lack of unequivocal sets of diagnostic characters, used to characterize and distinguish walchian conifer species, has prompted different approaches to solving Paleozoic conifer systematics. Hence, each approach creates different

classifications with alternative morphotaxa (Table 1; Visscher et al., 1986; Mapes and Rothwell, 1991).

Traditional approaches allow workers to describe conifer remains based on conventional morphological and/or cuticular characters (Florin, 1927, 1938-45; Clement-Westerhof, 1984, 1987, 1988; Visscher et al., 1986; Kerp et al., 1990). However, these approaches fail to acknowledge and deal with known broad ranges of variation within and among walchian conifer species (Hernandez-Castillo et al., 2001; Hernandez-Castillo, 2005). A third approach proposed by Mapes and collaborators allows us to accurately correlate different conifer organs in order to reconstruct new conifer plants and survey known ranges of variation (Rothwell and Mapes, 2001; Hernandez-Castillo et al., 2001; Hernandez-Castillo et al., 2003). Nevertheless, this approach requires of dozens or hundreds of conifer remains.

Due to the small amount of fossil conifer specimens and poor preservation (no cuticles), we decided to use a combination of techniques from previous approaches, where few specimens are described using conventional morphological characters (i.e., Florin and Clement-Westerhof) and their ranges of variation (Hernandez-Castillo, 2005), by surveying fourteen morphological characters of branches and leaves and comparing them to previously described species (Hernandez-Castillo and Silva-Pineda, 2009). This will permit employing a combination of approaches and preparing our material for future comparisons with the best-known and reconstructed walchian conifers from Euramerica.

Calnalia hidalguensis lateral branches and leaves are some of the smallest ever found among walchian conifers (Table 1). Comparisons to previous taxa suggest that both shape and size of *Calnalia* branches relate to apical and medium-size branches of young or juvenile walchian and araucarian trees (Hernandez-Castillo et al., 2003, 2008, 2009). This assumption is supported by the lack of a) fully developed oblong-shaped lateral branches (basal and/or mature branches); b) narrowly oblong-shaped branches (most apical branches), and c) reproductive structures, as seen in most previously described morphotaxa and newly reconstructed Paleozoic conifers (Florin, 1938-45; Clement-Westerhof, 1994; Mapes and Rothwell, 1991; Hernandez-Castillo et al., 2003, 2008, 2009a, 2009c; Looy, 2007).

Calnalia is here represented by a small sample of young branches and leaves with unique ranges of morphological variation that do not correspond to any known walchian conifer, and as such deserves to be placed in its own genus and species. The use of previously assigned morphotaxa names is not recommended for newly discovered species with distinct ranges of morphological variation if 1) the taxon is undoubtedly correlated to unknown and/or overlapping ranges of morphological variation (e.g., *Walchia*); and 2) if the taxon is in conflict with current classifications (Visscher, et al., 1986; Mapes and Rothwell, 1991; Hernandez-Castillo et al., 2001). This approach prevents us from using ambiguous morphotaxa names that

Table 3. Current conifer classification approaches used to describe early conifers and recognized morphotaxa.

Approach	Taxa
Florin	Walchiaceae
	<i>Ernestiodendron</i> Florin (Florin)
	<i>Gomphostrobus</i> Florin
	<i>Lecrosia</i> Florin
	<i>Walchia</i> Sternberg
	<i>Walchiostrobus</i> Florin
	<i>Walchianthus</i> Florin
	Walchiaceae
	<i>Ernestiodendron</i> Florin (Florin)
	<i>Feysia</i> Broutin & Kerp
Clement-Westerhof and colleagues *Morphotaxa assign to Walchiaceae	<i>Gomphostrobus</i> Florin
	<i>Lecrosia</i> Florin,
	<i>Moyliostrobus</i> Miller & Brown
	<i>Otovicla</i> Kerp, Poort Swinkels & Verweer
	<i>Ortiseia</i> Clement-Westerhof
	<i>Walchia</i> Sternberg
	Majoniaceae
	<i>Dolomitia</i> Clement-Westerhof
	<i>Majonica</i> Clement-Westerhof
	<i>Pseudovoltzia</i> Florin
Mapes, Rothwell, Hernandez-Castillo and Stockey	Ullmaniaceae
	<i>Ullmania</i> Goeppert
	Morphotaxa
	<i>Cassinia</i> Freytet, Kerp & Broutin
	<i>Culmitzchia</i> Ullrich *
	<i>Hermitia</i> Visscher et al. <i>emend</i> Broutin & Kerp
	<i>Thuringiostrobus</i> Kerp & Clement-Westerhof
	<i>Walchianthus</i> Florin
	<i>Walchiostrobus</i> Florin *
	Walchian Voltziales
	<i>Ernestiodendron</i> Florin (Florin)
	<i>Thucydia</i> Hernandez-Castillo, Rothwell & Mapes
	Lebachoid Walchians
	<i>Barthelia</i> Rothwell & Mapes
	<i>Emporia</i> Mapes & Rothwell
	<i>Hanskerpia</i> Rothwell, Mapes & Hernandez-Castillo
	<i>Otovicla</i> Kerp, Poort Swinkels & Verweer
	<i>Utrechtia</i> (Mapes & Rothwell) Rothwell & Mapes
	Voltzian Voltziales
	<i>Aethophyllum</i> Brongniart
	<i>Dolomitia</i> Clement-Westerhof
	Lebowskia Looy
	<i>Majonica</i> Clement-Westerhof
	<i>Ortiseia</i> Clement-Westerhof
	<i>Voltzia</i> (Bischoff) Geinitz, Schweitzer
	Angaran Voltziales
	<i>Concholepis</i> Meyen
	<i>Kungurodendron</i> Florin
	<i>Timanostrobus</i> Florin
	Gondwanan Voltziales
	<i>Ferugliocladius</i> (Feruglio) Archangelsky & Cuneo
	<i>Genoites</i> Feruglio
	Euroamerican morphotaxa
	<i>Cassinia</i> Freytet, Kerp & Broutin
	<i>Culmitzchia</i> Ullrich
	<i>Cyparissidium</i> Heer
	<i>Feysia</i> Broutin & Kerp
	<i>Gomphostrobus</i> Florin
	<i>Lecrosia</i> Florin
	<i>Moyliostrobus</i> Miller & Brown
	<i>Pseudovoltzia</i> Florin
	<i>Quadrocladus</i> Mädlar
	<i>Steirophyllum</i> Eichwald
	<i>Walchia</i> Sternberg
	<i>Walchianthus</i> Florin
	<i>Walchiostrobus</i> Florin
	Eurasian morphotaxa
	<i>Buriadia</i> (Seward & Sahni) Pant
	Angaran morphotaxa
	<i>Sashinia</i> Meyen
	<i>Dvinostrobus</i> Gomankov & Meyen
	<i>Taxodiella</i> Zalesky

Walchian, Lebachoid, Voltzian, Gondwanan and Angaran Voltziales are clades names derived from phylogenetic analyses (Rothwell *et al.*, 2005). Generic names from: Seward and Sahni, (1920), Florin (1927, 1938-45), Schweitzer (1963, 1996), Pant (1982), Clement-Westerhof (1984, 1987), Winston (1984), Visscher *et al.* (1986), Archangelsky and Cuneo (1987), Meyen (1987, 1997), Kerp and Clement-Westerhof (1991, 1996), Mapes and Rothwell (1991), Freytet *et al.* (1996) Kerp *et al.* (1996), Hernandez-Castillo *et al.* (2001; 2009a-c), Rothwell and Mapes (2001), Rothwell and Mapes (2001, 2003), Hernandez-Castillo (2005), Looy 2007.

would lead to more confusing walchian conifer species concepts.

5.3. Permian outcrops and conifers of Mexico.

Walchia hidalguensis is the first species of conifer fossils to be described from the Permian of Mexico and its general features resemble most closely Euramerican Lebachiod conifers. In addition, *Walchia* expands the present distribution for walchian conifers in North America. Typical Lebachiod conifers (Rothwell *et al.*, 2005) have been described and reconstructed from the Upper Carboniferous to the Late Permian of Europe and North America. However, additional records have been found in North Africa and the Middle East (El Wartiti *et al.*, 1986; Broutin *et al.*, 1986, 1998; Berthelin *et al.*, 2003), and new sites in Texas (USA) and Blanz (France) (Bercovici and Broutin, 2007; Looy, 2007), therefore expanding the geographic distribution of Lebachiod walchians at the end of the Paleozoic (Florin, 1938-45; Rothwell, 1982; Mapes and Rothwell, 1984; Rothwell *et al.*, 1997).

Walchian fossils have been collected from sediments that currently are located in central Mexico, but this region was once part of the southern most region of the Sierra Madre terrane (Rosales-Lagarde, 2002; Centeno-García, 2005). The Sierra Madre terrane was part of the Oaxaquia block along with Coahuila terrane. It is believed that the Oaxaquia block was part of Gondwana until it collided with North America at the Carboniferous-Permian boundary (Pindell, 1985; Centeno-García, 2004, 2005). Different models are now trying to explain this accretion process and posterior formation of the Mexican paleogeographic regions (Pindell, 1985; Ortega-Gutierrez *et al.*, 1995; Dickinson and Lawton, 2001). One of the models with the strongest evidence (Pindell's model) relies on strong faunal associations during the Mississippian among the Coahuila and Sierra Madre terranes, and the mid-continent province in North America (Stewart *et al.*, 1999; Navarro-Santillán *et al.*, 2002; Centeno-García, 2005), suggesting that these terranes were part of the North American Craton at the end of the Paleozoic. The presence of *Calnalia* and other taxa yet to be described in the Sierra Madre terrane reinforces this model. Preliminary surveys of at least six localities in the Tuzancoa Formation suggest similarities with Permian floras of Texas (DiMichele *et al.*, 2000, 2001). Furthermore, walchian conifer remains found in Texas resemble typical Lebachiod conifers and Walchian Voltziales (DiMichele *et al.*, 2000, 2001; Looy, 2007, 2007a). Some of these Texan conifers resemble branches/leaves of *Calnalia*, while others resemble typical branches/leaves and cones of Upper Permian Majonicaceae conifers (Looy, 2007). These facts add more evidence of the presence of an arc found along the Coahuila and Sierra Madre terranes (Oaxaquia block) that connected Texas to these Mexican terranes by the early Permian (Centeno-García, 2005).

Calnalia is the first species to be described from a series of new localities in the early Permian of Mexico. Together with several localities in the states of Chihuahua, Chiapas, Coahuila, Guerrero, Puebla, Sonora and Veracruz, conform an ample suite of early Permian outcrops throughout Mexico. Many of these localities yield conifer remains that conform to typical walchians, thus increasing the paleo-distribution of these conifers during the early Permian. Thus far, most localities with plants seem to be correlated to localities with fusulinids in the North, Central and South regions of Mexico (Vachard *et al.*, 2000), adding another component to the depositional and taphonomic processes regarding walchian conifers in Mexico. This presents the urgent need of producing more multi-disciplinary research to assess and correlate late Permian localities in Mexico. Furthermore, geological, geochemical, paleontological, sedimentological, and stratigraphical data needs to be gathered, organized and compared to previous hypotheses that could explain the origin and evolution of blocks, terranes, faunas, and floras in Mexico. *Calnalia hidalguensis* represents the first step in this direction and the beginning of new paleobotanical research into the Paleozoic of Mexico.

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