Short note

Abies cuitlahuacii sp. nov., a mummified late Quaternary fossil wood from Chalco, Mexico

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ABSTRACT

A fragment of mummified wood collected from a Quaternary sedimentary sequence of Lake Chalco, Central Mexico, in the depocenter of the Basin (19°15′26″N, 98°58′32″W), has anatomical characteristics of *Abies*. Identification is based on the presence of a warty layer in the walls of the tracheids, prismatic crystals in ray cells, taxodioid pits in the cross-fields, and lack of ray tracheids and normal intercellular canals, among other well-preserved characteristics. This specimen represents the first macrofossil evidence of the genus in this region and suggests that by the late Quaternary it was already established in the surroundings of Lake Chalco, and most probably in what is now central Mexico. Unfortunately, as with morphological and genetic characteristics, the anatomical attributes of the wood of the genus have not been useful for the delimitation of species. Most wood characteristics have been considered of little diagnostic value. However, comparison of available anatomical descriptions of fossil and living species highlight differences among them, even with *Abies religiosa* wood, which is the closest species to Lake Chalco. Other characteristics or plant organs are needed to assemble a whole plant that can be used to establish phylogenetic relationships and clarify the evolutionary history of the genus. Meanwhile this wood is assigned to a new fossil taxon, *Abies cuitlahuacii* Cevallos-Ferriz, Ríos-Santos & Lozano-García.

Keywords: mummified wood, Lake Chalco, anatomical characteristics, late Quaternary, *Abies cuitlahuacii*.

RESUMEN

Un fragmento de madera momificada recolectada de una sección de una secuencia sedimentaria del Lago de Chalco, en el centro de México, en particular en el depocentro de la Cuenca (19°15'26" N, 98°58'32" W), tiene características anatómicas de Abies. Esto se basa en la presencia de una capa verrugosa en las paredes de las traqueidas, cristales prismáticos en las células radiales, punteaduras taxodioides en los campos de cruce y ausencia de traqueidas radiales y canales normales, entre otras características bien preservadas. Este especímen representa la primera evidencia con macrofósil del género en esta región y sugiere que para el Cuaternario tardío ya estaba establecido el género en los alrededores del Lago de Chalco y por lo tanto, en lo que hoy es el centro del país. Desafortunadamente, como ocurre con los caracteres morfológicos y genéticos, los atributos anatómicos de la madera del género tampoco han sido útiles para la delimitación de especies, ya que la mayoría de ellos son considerados poco diagnósticos. Sin embargo, en este estudio se hicieron comparaciones con maderas de especies fósiles y vivas disponibles, y en todas se encontraron diferencias anatómicas para con el ejemplar fósil, incluso con la madera de Abies religiosa que es la especie que tiene distribución más cercana al Lago de Chalco. En espera de que sean propuestos otros caracteres o estudios integrales de ellos que sirvan como auxiliaries para la delimitación de los miembros que constituyen al género, o de hallar otros órganos fósiles en el área de estudio que complementen la identificación aquí presentada, esta madera es asignada a una especie nueva, Abies cuitlahuacii Cevallos-Ferriz, Ríos-Santos & Lozano-García.

Palabras clave: madera momificada, Lago de Chalco, características anatómicas, Cuaternario tardío, Abies cuitlahuacii.

1. Introduction

The basin of Mexico is located in the geological province of the Trans-Mexican Volcanic Belt (TMVB), a continental arc active since the middle Miocene (Gómez-Tuena *et al.*, 2005). Recent studies documented that the basin was closed *ca.* 1.2 Ma ago (Arce *et al.*, 2013) leading to the development of a lacustrine system. This lake system reached an area of 1689 km^2 by the 14th century (Ruiz-Angulo and López-Espinosa, 2015). Part of this system corresponds to the modern Lake Chalco (19°15′26″N, 98°58′32″W, 2230 meters above sea level (masl)). The lake has an area of 1100 km^2, of which approximately 240 km^2 correspond to the lacustrine plain. The environmental history of the area is archived and has been disentangled from the late Quaternary sedimentary rocks of Lake Chalco (Table 1; Lozano-García *et al.*, 1993; Urrutia-Fucugauchi *et al.*, 1995; Caballero and Ortega, 1998; Ortega-Guerrero *et al.*, 2000, 2017; Lozano-García *et al.*, 2015). The previous studies demonstrated that temperate forests make up the dominant vegetation types of Central Mexico's mountains today. These forests consist of *Pinus* L. 1753, *Pinus-Quercus* L. 1753, *Abies*, and/or *Juniperus* L. 1753, and developed within elevations that range from 1500 to 4000 m. *Abies* forests are restricted to humid areas such as glens between 2600 and 3600 m and temperatures between 7 and 17°C; however, they are sometimes intermixed with pine-oak forests, although they may form pure stands. These forests are located in the southern portion of the Basin of Mexico.

Several studies (Lozano-García and Ortega-Guerrero, 1994; Lozano-García *et al.*, 1993; 1998; Lozano-García, 1996; Torres-Rodríguez *et al.*, 2015) have documented changes in the composition of communities in response to late Pleistocene climatic changes. They are based on the presence of open *Pinus* forests during cold periods, such as the last glacial maximum, where temperatures were reduced by 6 to 8°C relative to the pre-glacial period (Vázquez-Selem and Heine, 2011; Correa-Metrio *et al.*, 2013). As the climate warmed at the beginning of the Holocene, pollen records show an increase in the associated *Abies* Mill. 1754 forest communities due to the increase in humidity in the area (Lozano-García *et al.*, 1993; Lozano-García and Ortega-Guerrero, 1994, 1998; Lozano-García, 1996; Torres-Rodríguez *et al.*, 2015).

The climate corresponding to the great majority of the modern forests of these species in Mexico, according to the classification of Köppen (1948), is Cw (dry winter). The geological substrates in which these forests developed are varied. The most predominant ones are those of volcanic origin, mainly andesites and basalts (Rzedowski, 2006).

Xiang *et al.* (2007) proposed that *Abies* originated during the Cretaceous. However, more recent molecular and biogeographic studies have estimated its origin in the Eocene, possibly in western North America, or in North America and East Asia when these were connected via the Bering Land Bridge (Xiang *et al.*, 2015).

There is no macrofossil evidence of *Abies* in the fossil record in Mexico. However, there is a palynological record of the genus in the Pliocene from Paraje Solo, Veracruz (Graham, 1976, 1999). The palynological record of the area, including older Cenozoic strata in the same geographic region, strongly suggests that *Abies* and probably other conifer pollen grains were dispersed from the north (Graham, 1999). These data, coupled with the existing diversity of the genus in this part of the North American continent, suggest a rapid diversification shortly after their establishment (Aguirre-Planter *et al.*, 2012). A similar history was proposed by Huerta-Vergara (2014) for *Pinus* in Mexico suggesting its relatively recent establishment in the region.

Although little is known about the fossil record of *Abies* in Mexico, the Pliocene has been proposed as the time of its arrival to the area. This is based on palynological records and the discussion of plant communities where *Abies* has been found, especially in high latitude North America (Graham, 1999). At that time, it formed part of lowland forests of mixed conifers and broadleaf deciduous trees

Table 1. Fir species distributed in Mexico (Farjon 2010).

Species	Varieties	Distribution
Abies concolor (Gordon) Lindl. *ex* Hildebr.		Mexico: Baja California, Chihuahua y Sonora; USA: from Oregon to Idaho through the Rocky Mountains and the California and Arizona Hills.
A. durangensis Martínez	*A. durangensis* Martínez var. *durangensis*	Chihuahua, Durango, Northern zones of Jalisco and Sinaloa.
	A. durangensis var. *coahuilensis* (I.M. Johnst.) Martínez	Coahuila
A. guatemalensis Rehd.	*A. guatemalensis* Rehd. var. *guatemalensis*	Mexico: from Chiapas to Nayarit and Tamaulipas; El Salvador; Western Guatemala; and Honduras.
	A. guatemalensis Rehd. var. *jaliscana* Martínez	Jalisco
A. hickelii Flous & Gaussen	*A. hickelii* Flous Gaussen var. *hickelii*	Chiapas, Guerrero and Oaxaca.
	A. hickelii Flous & Gaussen var. *oaxacana* (Martínez) Farjon & Silva	Guerrero and Oaxaca
A. hidalgensis Debreczy, Rácz & Guízar		Hidalgo
A. religiosa (Kunth) Schltdl. & Cham.		High zones of Central and Southern Mexico; Western Guatemala.
A. vejarii Martínez	*A. vejarii* Martínez var. *vejarii,*	Oriental Sierra Madre in Coahuila, Nuevo León and Tamaulipas.
	A. vejarii Martínez var. *macrocarpa* Martínez	Coahuila (Mesa de las Tablas) and Nuevo León (Cerro Potosí).
	A. vejarii Martínez var. *mexicana* (Martínez) T.S. Liu	Southeastern Coahuila and Nuevo León (Sierra Santa Catarina).

adjacent to coastal mangroves. This contrasts with the extant distribution of the plants that formed these types of vegetation. While mangroves grow at sea level next to tropical floras, more temperate elements establish their distribution high in the mountains (Graham, 1976). In contrast, molecular studies have proposed that the origin of Mesoamerican firs (a group with species from southwestern North America of sections Oiamel and Grandis; Farjon and Rushforth, 1989) dates from late Paleocene and early Miocene, after a few southward expansions that these groups probably followed through the mountain chains of western North America (Aguirre-Planter *et al.*, 2012).

2. Methodology

The drilling of the sedimentary sequence of Chalco was in the depocenter of the basin (19°15′26″N, 98°58′32″W). Three parallel cores were drilled with the aim of retrieving the entire sequence. The three wells are: well A (10 to 420 m), well B (6 to 310 m), and well C (10 to 300 m and 409 to 520 m). The upper 300 m of lacustrine sediments were recovered with a percussion HQ system with diamond drill in section lengths of 1.5 m (Lozano-García *et al.*, 2017). The documentation and description of the sequences were performed at the University of Minnesota

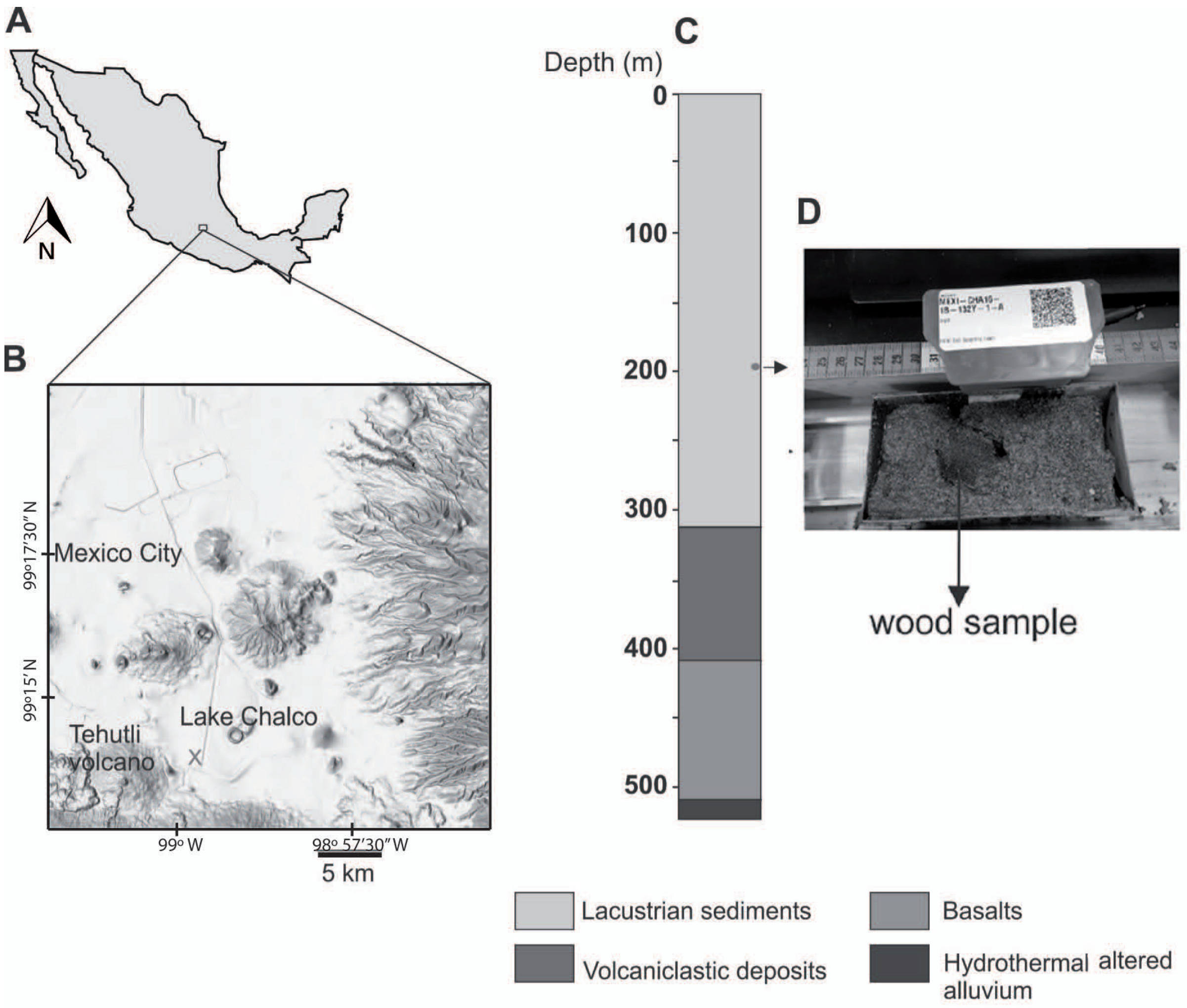

Figure 1 Location map. A. Basin of Mexico. B. Lake Chalco Basin of Mexico (19°15'N, 98°58'W, 2230 masl). X indicates the drilling site. C. Simplified and combined stratigraphic column of wells A and B (Bücker *et al.*, 2017; Lozano-García *et al.*, 2017). D. Specimen of the wood recovered in section 1B-132 of well B.

Lacustrine Core Facility (LacCore) and included the measurement of magnetic susceptibility and gamma density with a Geotek Multi-Sensor Core Logger. Once open, the sections were described and photographed with a DMT CoreScan digital linescan camera. During the description process of sequence B corresponding to a depth of 198.5 m, a piece of wood embedded in volcanic ash was recovered (Figure 1).

Eight slides were obtained with the conventional thin-section technique oriented on the three cutting planes of the wood. The observation of the anatomical characteristics was done with a Carl Zeiss Primo Star optical microscope and the photographs of the characteristics were obtained with a Canon PowerShot A640 camera. Anatomical descriptions follow Baas *et al.* (2004), García-Esteban *et al.* (2002), and Barefoot and Hankins (1982). As for the quantitative traits, 30 measurements for each attribute were obtained. However, ray height is based on 100 measurements. It should be emphasized that both the observations and the measurements of attributes were made from the early wood. Values are expressed as average (minimum-maximum), or in sporadic cases, with the intention of better expressing their distribution, as minimum-average-maximum (occasional maximum). Identification of the sample is based on the already mentioned literature, but additional works were consulted for important taxonomical decisions (*e.g.*, Greguss, 1955; García-Esteban *et al.*, 2004, 2009; Samerikova and Semerikov, 2014).

3. Results

3.1. SYSTEMATICS

Family Pinaceae Spreng. *ex* F. Rudolphi, 1830.
Genus *Abies* Mill., 1754.
Species *Abies cuitlahuacii*, Cevallos-Ferriz, Ríos-Santos & Lozano-García.

Etymology: The specific epithet honors Cuitláhuac, the penultimate "Huey Tlatoani"; a Nahuatl expression that refers to governors of the triple alliance (Tenochtitlán-Texcoco-Tlacopan) of the regions where the lake system occurred.
Repository: Paleontological Collection of the Instituto de Geología, Universidad Nacional Autónoma de México, Mexico.
Holotype: IGL-CHA16-B: 1-8.
Number of specimens examined: 1.
Thin-sections: 8.
Location: Lake Chalco.
Coordinates: 19°15′26″N, 98°58′32″W.
Hole: CHA-SEQ-2016-B.
Depth: 198.5 m.
Age: *ca.* 200000 yrs (Pleistocene; estimation based on previous studies in lake Chalco (Torres-Rodríguez *et al.*, 2015; Ortega-Guerrero *et al.*, 2017).
Diagnosis: Pycnoxilic wood with distinguishable growth ring boundaries; tracheid walls with warty layer, trabecula and uniseriate abietinean bordered pits on radial and tangential walls; bordered pits occasionally with torus extension; axial parenchyma with brown contents, nodular transverse end walls, and tangentially zonate arrangement; uniseriate and partially biseriate rays, 19.5 – 25(37) cells high, ray parenchyma cells with pitted horizontal walls, nodular end walls, brown contents and prismatic crystals in their lumens, occasionally irregularly shaped parenchyma cells; taxodioid cross-fields pits, with 1 – 2 pits per cross-field and average diameter of 4.6 × 3 µm; resin canals and ray tracheids absent.
Description: Mummified wood fragment 1.5 cm in diameter by 2 cm in length, with distinguishable growth ring boundaries with normal abrupt transition (Figure 2A). The late wood consists of approximately 6 to 27 rows of tracheids. The tracheids have quadrangular outlines in cross section (Figure 2B) and on average there are 2090 tracheids/mm^2. The radial and tangential diameters of the early wood tracheids is 20 (16 – 29) µm and 21.6 (17 – 30) µm, respectively. In the lumen trabeculae (Figure 3H) can be observed sporadically. The walls of tracheids are 2 µm thick on average and have a warty layer (Figure 2D). The radial walls of the tracheids have abietinoid bordered pits arranged in a single series (Figure 2E), with circular contours and openings, diameter of 13.8 (12.5 – 15) µm and with extended torus (Figure 2F); the tangential walls have the same type of bordered pits, but unlike the bordered pits on the radial walls, they are more sporadic and slightly smaller in diameter, 10.7 (8 – 13) µm (Figure 3G). Axial parenchyma cells have a tangentially zoned arrangement, particularly in the transition from the early to the late wood (Figure 2A); parenchyma cells have obscure contents (Figure 2B) and nodular transverse walls (Figure 3I). The rays are uniseriate (Figure 3E) and sometimes partially biseriate (Figure 3F); their height varies from 1 – 9.5 – 25 (37) cells and their frequency is 9.2 rays/mm; they are composed of rectangular parenchyma cells (Figure 2C and G) with occasional irregular formed cells in the ray margins (Figure 2H). Ray parenchyma cells have pitted horizontal walls (Figure 2G), nodular end walls (Figure 2H), brown contents (which could be some type of resin, Figure 2B), and furthermore rarely indentures (Figure 3A) and crystals (Figure 3B). One or occasionally 2 taxodioid pits present per cross-field, with an average diameter of 4.6 × 3 µm (Figure 3C and D). The wood lacks resin canals and radial tracheids.

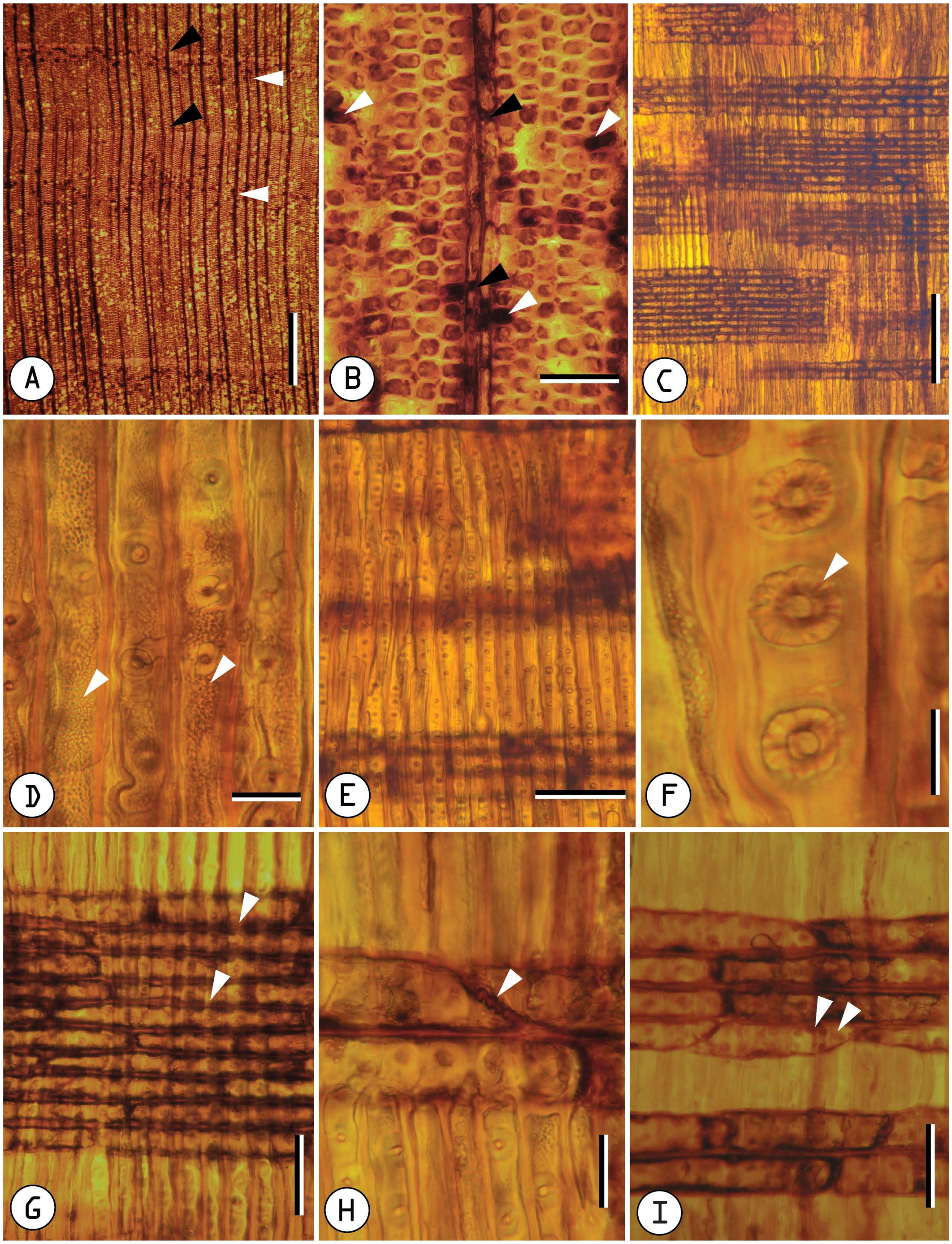

Figure 2 Photomicrographs of *Abies cuitlahuacii*. TR. A. Distinguishable growth ring boundaries generally with abrupt transition (black arrows). Axial parenchyma tangentially zoned (white arrows). Scale bar = 1 cm. B. Tracheids of quadrangular outlines. Axial parenchyma (white arrows) and ray parenchyma cells (black arrows) with brown contents. Scale bar = 65 µm. C. Overview of the radial section. Rays composed exclusively of radial parenchymal cells. Scale bar = 200 µm. D. Radial walls of tracheids with warty layer (arrows). Scale bar = 20 µm. E. Tracheids with abietinean radial pitting. Scale bar = 100 µm. F. Bordered pits with their torus extensions (arrow). Scale bar = 15 µm. G. Ray parenchyma cells with horizontal pitted horizontal walls (arrows). Scale bar = 60 µm. H. Radial parenchymal cells with nodular axial walls (arrow). Scale bar = 20 µm. I. Ray parenchyma cell with abnormal shape in the margin of a ray (arrow). Scale bar = 40 µm.

4. Discussion and conclusion

4.1. COMPARISON WITH EXTANT PLANTS

The anatomical structure of the wood of Pinaceae is unique for having attributes that are not normally present in other conifer families. These unique attributes have been recognized as anatomical apomorphic characteristics among living conifers. These include: normal resin canals, pinoid, window or piceoid cross-field pits, and radial tracheids, among others (Greguss, 1955). However, of all the genera that make up Pinaceae, *Pseudolarix* Gordon, 1858, *Keteleeria* Carrière, 1866, and *Abies* (three of the six circumscribed genera in the subfamily Abietoideae Pilg.; Farjon, 2010) have simpler structure (Greguss, 1955) and more similar anatomy to the wood described in this study. Moreover, *Pseudolarix* lacks the warty layer on the walls of its tracheids (García-Esteban *et al.*, 2009) and has a larger number of pits (3 – 6) per cross-field (Greguss, 1955). Also, *Keteleeria* is distinguished by having axial resin canals (García-Esteban *et al.*, 2009), which prevents the association of Chalco wood with this genus. Therefore, the wood described in this contribution is included in *Abies* because both share the warty layer in the walls of the tracheids, prismatic crystals in ray parenchyma cells, and taxodioid cross-field pitting (Greguss, 1955; García-Esteban *et al.*, 2009). However, in previous anatomical studies (*e.g.*, García-Esteban *et al.*, 2002, 2004), *Abies* woods have been described with cross-field pitting with piceoid pits. In addition to the characteristics mentioned above, there are others that were observed in the fossil wood that reinforce its identification despite not being completely diagnostic for *Abies*. Among them are the exclusively uniseriate abietinoid bordered pits on the radial and tangential walls of the tracheids, with bordered pits with torus extensions; tangentially zoned axial parenchyma with nodular transverse walls; uniseriate to partially biseriate rays; ray parenchyma with pitted horizontal and nodular end walls; and finally a lack of radial tracheids and normal resin canals (Barefoot and Hankins, 1982; García-Esteban *et al.*, 2002, 2004, 2009; Baas *et al.*, 2004; Samerikova and Semerikov, 2014).

According to García-Esteban *et al.* (2009), there are no qualitative anatomical differences that can be used to separate species of this genus. In fact, this has also been observed with morphological and genetic characters (Martínez-Méndez *et al.*, 2016). Thus, delimitation of species of this genus has proved so difficult that there is no consensus on how many species actually exist (Strandby *et al.*, 2009; Martínez-Méndez *et al.*, 2016). Particularly, the Mesoamerican firs probably are still in a gray zone of speciation (*sensu* de Queiroz, 1998, 2005), where due to the recent time of separation of the populations, the reciprocal monophyly is incomplete and populations have not yet formed phenotypically and ecologically distinguishable or diagnosable groups (Martínez-Méndez *et al.*, 2016). This situation supports that the assignment of this fossil wood to a living species is complicated. Although this fossil wood is similar to the wood of *Abies religiosa*, (Kunth) Schltdl. & Cham., 1830, a species whose geographical distribution is the closest to the locality where the fossil wood was collected (less than 20 km from Mexico City), some characteristics in the extant plants were not observed in the wood from Chalco. These are, helical thickenings in the tracheids, biseriate bordered pits, bars of Sanio, piceoid pits in the cross-fields, and lower rays with a maximum of 6 cells high (García-Esteban *et al.*, 2002, 2004, 2009). There are no studies describing the wood anatomy of most of the Mesoamerican fir species. Exceptions are *Abies guatemalensis* Rehd., 1939 and *Abies concolor* (Gordon) Lind. *ex* Hildebr., 1861. The first one can be distinguished from this fossil wood by having xylem with biseriate bordered pits, bars of Sanio, 1 – 4 piceoid pits per cross-field, and the absence of torus extensions; while the second one generally has lower rays (1 – 4 (12) cells), marginal axial parenchyma, and piceoid cross-field pits. Despite

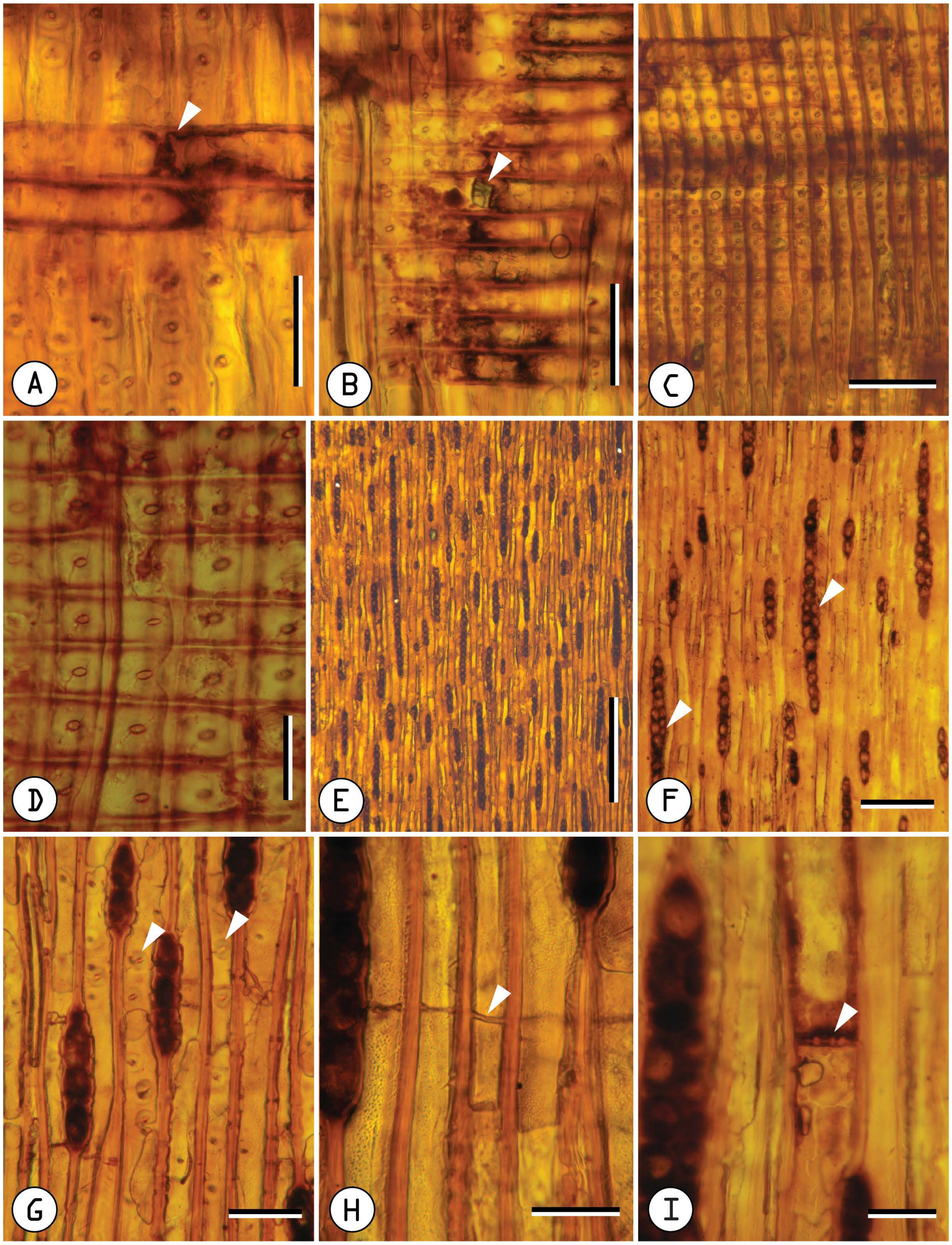

Figure 3 Photomicrographs of *Abies cuitlahuacii.* RA. A. Ray parenchyma cell with radial indentures (arrow). Scale bar = 40 µm. B. Ray parenchyma cell with a quadrangular crystal (arrow). Scale bar = 50 µm. C. Overview of the cross-fields. Scale bar = 80 µm. D. Taxodioid pits in cross-fields. Scale bar = 35 µm. TA. E. Uniseriate rays. Scale bar = 200 µm. F. Partially biserial rays (arrows). Scale bar = 100 µm. G. Bordered pits on tangential walls of tracheids (arrows). Scale bar = 40 µm. H. Tracheids with trabeculae (arrow). Scale bar = 40 µm. I. Axial parenchyma cells with nodular transverse walls (arrow). Scale bar = 20 µm.

these differences *A. concolor* has wood with greater similarity to the fossil wood, probably because it has been considered a species more divergent within the Mesoamerican firs (Aguirre-Planter *et al.*, 2012; Martínez-Méndez *et al.*, 2016).

4.2. COMPARISON WITH FOSSIL WOODS

The record of fossil woods related to *Abies* is not extensive and is restricted to *Abietoxylon* Houelbert, 1910 and *Abies* Mill, 1754. In North America, *Abietoxylon koreanoides* Roy & Hill, 1972 and *Abietoxylon traumatiductus* Roy & Hill, 1972 were described from the Beaufort Formation (Miocene – Early Pliocene) in northwest Banks Island in the Canadian Arctic Archipelago. *Abies firmoides* Watari, 1956 was described from deposits of the lower Oligocene of Japan. *Abies chavchavadzeae* Blokhina & Bondarenko, 2008 was described along with *Abies* aff. *sachalinenses* from the lignite field of Pavlovka in the Primorskii Region, Pliocene of Russia. *Abietoxylon shakhtnaense* Blokhina, 2010 has also been reported from Russia, but in deposits of the upper Oligocene – lower Miocene in the east of Sakhalin. Finally, the wood of *Abietoxylon faudense* Houlbert, 1910 was described from Faluns Formation, Miocene of Touraine, France.

Abietoxylon koreanoides is distinguished from the Chalco wood based on lower rays (2 – 8 (10) cells high), more piceoid to taxodioid pits per cross-field (2 – 4), and lack of bordered pits on tracheids tangential walls (Roy and Hill, 1972). *Abietoxylon traumatiductus* differs from the Mexican wood because it has traumatic resin canals, relatively lower rays (2 – 12 (15) cells), occasional helical thickenings in tracheids of early wood, axial parenchyma with smooth transverse walls, and a greater number of taxodioid pits per cross-field (2 – 4; Roy and Hill, 1972). *Abies firmoides*, in contrast to *Abies cuitlahuacii*, has biseriate bordered pits with bars of Sanio (or crassulae), and axial parenchyma with smooth and nodular transverse end walls, as well as a greater number of pits per cross-field (2 – 5; Watari, 1956). *Abies chavchavadzeae* unlike the Chalco wood has uniseriate and biseriate bordered pits, bars of Sanio associated with biseriate bordered pits, higher rays (1 – 51 cells), and greater number of taxodioid pits per cross field (1 – 3 (4); Blokhina and Bondarenko, 2008). *Abietoxylon shakhtnaense* is distinguished from the new wood because it has higher rays 1 – 30 (50 – 60), greater number of taxodioid pits per cross-field (1 – 3 (4), occasionally biseriate bordered pits, and traumatic resin canals (Blokhina, 2010).

Abietoxylon faudense Houlbert is the type species of the genus, and Philippe and Bamford (2009) reviewed the original material of this fossil taxon. Since there was no holotype assigned in the original publication, a lectotype was proposed under the name of *Abietoxylon falunense*. Since the lectotype, like the rest of the syntypes, lacked good preservation, it was not possible to identify the anatomical diagnostic characteristics for its correct identification. In fact, it was not possible to know what the diagnostic characteristics were for the genus because Houelbert (1910) never indicated them. Philippe and Bamford (2009) added that the quantitative characteristics of this type of wood are very similar to the characteristics of *Taxoxylon*, another type of wood that Huelbert (1910) described. They continued arguing that these genera, along with *Cupressoxylon* and *Juniperoxylon*, described in the same publication, probably belong to a single taxon and suggested not to use this fossil genus. The review of this taxonomic problem is beyond the scope of this paper; however, a taxonomic revision of the genus is needed. The anatomical characteristics in common between the fossil woods and that differ with the current woods are higher rays, bordered pits on the radial walls of the tracheids, traumatic canals, and axial parenchyma cells with a combination of smooth and nodular transverse end walls.

Because of the age of the fossil wood of Mexico (Pleistocene), the difficulty in identifying extant species of *Abies*, and the anatomical differences founded both in extant and fossil woods (although we do not rule out the possibility that some characteristics that we consider in anatomical comparisons are more related to the phenotypic plasticity of wood; for example, the number of pits in the cross-field and biseriate bordered pits), the new wood is recognized as a member of the genus, and as a new species, *Abies cuitlahuicii*. However, the need to find other macrofossils of this genus in the same locality to assemble them under the whole plant reconstruction hypothesis is highlighted. Moreover, new integrative studies about different characteristics of *Abies* will be necessary to do a detailed comparison that backs-up our taxonomic decision and also to know about its more precise phylogenetic relationship.

4.3. THE GENUS IN MEXICO

The new fossil, *Abies cuitlahuacii*, represents the first macrofossil of this genus in Mexico, and thus the first direct evidence of the species growing close to the area of deposition. The associated plants in the studied nuclei represent both mixed conifers and broadleaf deciduous forests, as expected, but compared with previous fossil records, *Abies cuitlahuacii* was growing at over 2000 masl.

Abies is the genus with the second highest number of species (47 spp.) of Pinaceae (Farjon, 2010). Most of the species of this family are mesophyll elements of the boreal and temperate forests of the Northern Hemisphere, which together with species of *Picea* A. Dietr., *Tsuga* (Endl.) Carrière, *Pseudotsuga* Carrière, and *Pinus* L. (subgenus Strobus) conform conifer forests in high mountain belt areas where humidity is high and constant (Semerikova and Semerikov, 2014). *Abies cuitlahuacii* probably represents a plant growing at a moment in which the genus had its greatest distributional area in Central Mexico. Flores-Mata *et al.* (1971) estimated that the *Abies* forests covered during the Pleistocene approximately 0.16% of Mexico, but this area most likely has been reduced, primarily by anthropogenic activity. This type of vegetation is represented in small patches, often restricted to a hill, a slope, or a glen, and at altitudes usually between 2400 and 3000 m (Rzedowski, 2006).

It is proposed here that *Abies cuitlahuacii* formed part of the stem group that gave rise to the extant species growing today near the area (*e.g.*, *A. religiosa*, *A. guatemalensis*, *A. hickelii*). Further studies will clarify this proposal and establish the relationship of the fossil plant with the seven fir species that grow naturally in Mexico, more than half of them with two or three varieties (Farjon, 2010; see Table 1). The appearance of *Abies* in the Pleistocene in Mexico seems similar to the proposed relatively recent history of extant *Pinus* in the area. Their history highlights the importance of geological evolution in the advancement of biodiversity in low latitude North America (Huerta-Vergara, 2014). *Abies cuitlahuacii* represents another example of the lineages that diversified as the mountain ranges develop in central Mexico, highlighting the close and important relationship of the geological and biological processes (Cevallos-Ferriz *et al.*, 2012). The inferred cycles of isolation and contact that *Abies* species experienced in this geographical region were influenced by their ecological monitoring towards temperate conditions related to phases of maximum glaciers and interglacial periods, and gradual uplift of the TMVB from the upper Miocene (Gómez-Tuena *et al.*, 2005; Bush *et al.*, 2009; Ramírez-Barahona and Eguiarte, 2013).

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