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Palynomorph assemblages of the Cuayuca Formation (Paleogene), Puebla, southern Mexico. Part 1: trilete spores, monolete spores and gymnosperm pollen

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Abstract. This publication presents the systematics of monolete and trilete spores, and polyplicate, inaperturate and bisaccate pollen grains recovered from outcrops of the Cuayuca Formation, State of Puebla, southern Mexico. Species belonging to the following genera are described and illustrated: *Cicatricosisporites, Deltoidospora, Foveotriletes, Leptolepidites, Lusatisporis, Retitriletes, Stereigranisporis, Verrucingulatisporites, Polypodiisporites, Pinuspollenites, Pityosporites, Ephedripites*, and *Cupressacites*. Pteridophytes and bryophytes spores constitute 13.5% of the assemblages and gymnosperms 7.3%. Angiosperms, to be discussed on later papers, dominate the assemblage.

Resumen. ASOCIACIÓN PALINOLÓGICA DE LA FORMACIÓN CUAYUCA (PALEÓGENO), PUEBLA, SUR DE MÉXICO. PARTE I: ESPORAS TRILETES, ESPORAS MONOLETES Y POLEN DE GIMNOSPERMAS. Esta publicación presenta la sistemática de esporas monolete y trilete, y granos de polen poliplicados, inaperturados y bisacados recuperados de secciones estudiadas correspondientes a la Formación Cuayuca, aflorantes al sur de México, estado de Puebla. Se describen e ilustran especies pertenecientes a los géneros: *Cicatricosisporites, Deltoidospora, Foveotriletes, Leptolepidites, Lusatisporis, Retitriletes, Stereigranisporis, Verrucingulatisporites, Polypodiisporites, Pinuspollenites, Pityosporites, Ephedripites* y *Cupressacites*. Las pteridofitas y briofitas constituyen el 13.5% del total de la palinoflora estudiada y las gimnospermas el 7.3%. Las angiospermas, que serán discutidas en trabajos posteriores, dominan las asociaciones.

Key words. Palynology. Systematic descriptions. Tertiary. Cuayuca Formation. Paleogene. Mexico.

Palabras clave. Palinología. Descripciones sistemáticas. Terciario. Formación Cuayuca. Paleógeno. México.

Introduction

The Cuayuca Formation is characterized by continental lacustrine sedimentary deposits. Fries (1966) studied the geology of this area and divided the formation into three members which include siliciclastic (conglomerate to siltstones), carbonate (limestone, chert, marl) and sulphate (gypsum) lithofacies. He assigned the formation to the Miocene - Pliocene on the basis of weak stratigraphic relationships with other units (figure 1). However, the lack of microfossils and radiometric dating at that time made it difficult to determine its precise age. Ramírez-Arriaga and Martínez-Hernández (2003) proposed a Late Eocene-Early Oligocene age for the Cuayuca Formation based on the initial palynological results and its correlation with other Tertiary assemblages.

A systematic study of the palynological contents of Cuayuca Formation is presented for five evaporitic sections near the village of Cuayuca (18º32'52''N; 18º36'W) and three, at Izúcar de Matamoros locality (18º36'41''N; 98º29'23''W), state of Puebla, southern Mexico (figure 2). This study is part of the doctoral thesis of one of the authors (E. Ramírez-Arriaga) and its main objective is to give a suitable chronostratigraphic assignment of the Cuayuca Formation and to correlate these new results with those published for central Mexico (Martínez-Hernández and Ramírez-Arriaga, 1999).

The Cuayuca Formation yielded a diverse and well preserved terrestrial palynoflora consisting mainly of pollen grains of angiosperms and gymnosperms and pteridophyte and bryophyte spores. A systematic treatment will be presented in several contributions to show the diversity of the palynological assemblages. This first one comprises the taxonomic descriptions of trilete spores, monolete spores and gymnosperm pollen grains.

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Materials and methods

A total of forty nine samples from eight sections were collected and twenty one of them yielded palynomorphs. All samples were processed by standard methods and slides are housed at the Laboratory of

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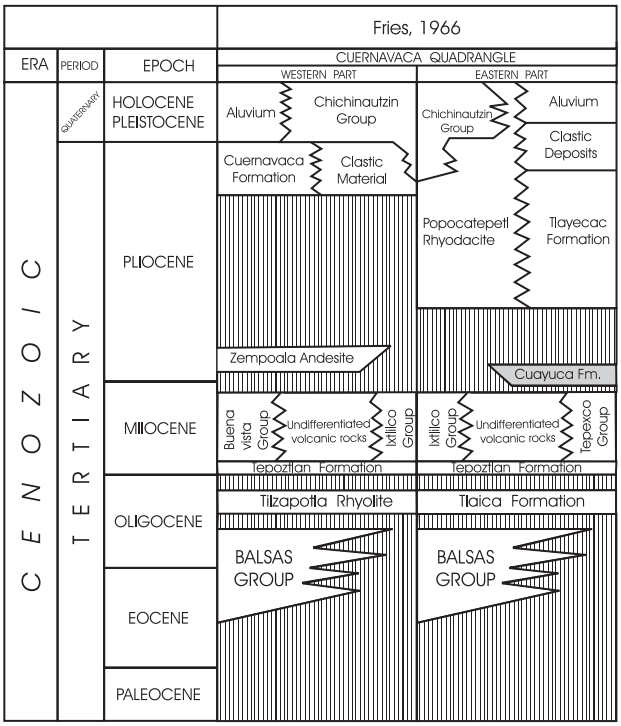


Figure 1. Old regional stratigraphic arrangement (Fries, 1966). Note that the position of Cuayuca Formation is in discussion based on new chronostratigraphic re-assignation of the underlying strata and recent palynostratigraphic results (Ramírez-Arriaga and Martínez-Hernández, 2003)/*Antiguo esquema estratigráfico regional (Fries, 1966). Nótese que la posición de la Formación Cuayuca está en discusión a partir de las nuevas asignaciones cronoestratigráficas de los estratos infrayacentes y los recientes resultados palinoestratigráficos (Ramírez-Arriaga y Martínez-Hernández, 2003).*

Palynology of the Institute of Geology, Universidad Nacional Autónoma de México (UNAM).

The geologic columns of the eight sections studied and the stratigraphic position of each collected sample are shown in figures 3 and 4. The designation of samples corresponds to the system used for palynologic fossil collections (Pb) of the Institute of Geology, Universidad Nacional Autónoma de México.

The study and the description of the specimens were made with a Zeiss photomicroscope. The terminology of Punt *et al.* (1994) is followed for sculpture and exine morphology. Erdtman's (1952) terminology is used for exinal layers. Bisaccate pollen grains were measured according to Kapp *et al.* (2000). Finally, occurrences of taxa are assigned following a semi-quantitative classification: single or unique (one specimen only); rare (2-4); common (5-20); frequent (21-70); abundant (70-120) and dominant (>120 specimens); modified from El Beialy (1998).

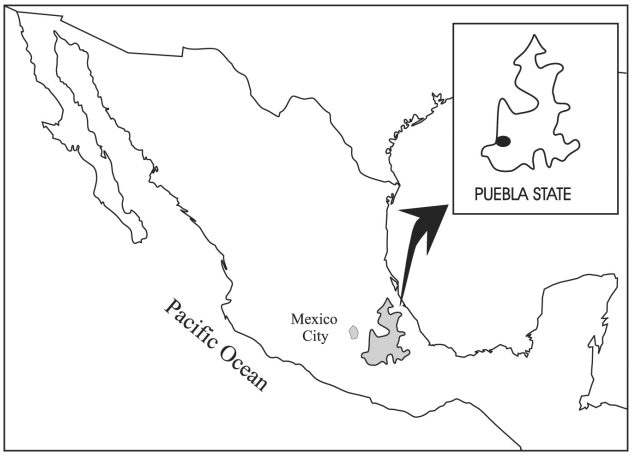
A paleofloristic reconstruction of the Tertiary of Mexico will be possible, by determining the botanical affinities of the palynomorphs to the extant for Paleogene plant microfossils.

Taxonomic list

Taxa are presented in alphabetic order under each category, emphasizing with an asterisk those taxa which are described in this paper.

a. Pteridophytes and Bryophytes
a.1. Trilete spores

**Cicatricosisporites dorogensis* Potonié and Gelletich 1933 (figures 5.A-C)
**Deltoidospora* sp. (figure 5.I)
**Foveotriletes* sp. (figures 5.D-F)
**Leptolepidites* sp. (figure 5.J)
**Lusatisporis dettmannae* (Drugg) Srivastava 1972 (figures 5.G-H)
**Retitriletes* sp. (figure 6.A)
**Stereigranisporis* aff. *granula* (Krutzsch and Sontag) Kedves and Russell 1982 (figures 6.B, C, E)
**Verrucingulatisporites* sp. (figure 6.F)



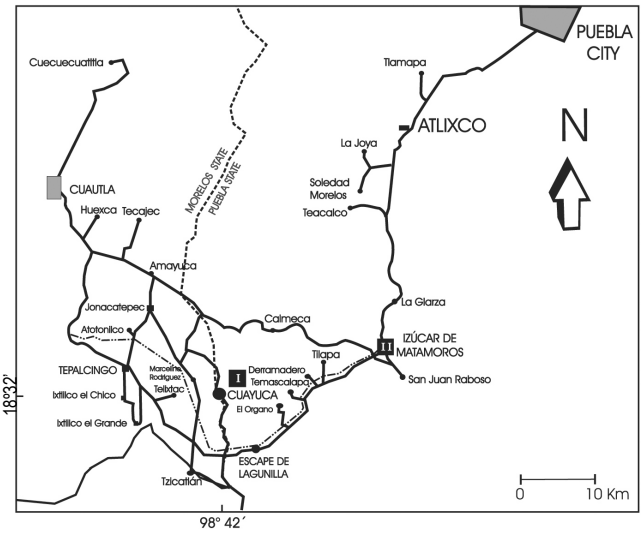


Figure 2. Location map of the studied area showing the sampled sections, State of Puebla, Mexico. **I,** Principal section, sections "A" and "B", Tzompahuacan and Lagunilla (all of them near Cuayuca village). **II,** Section "H", section "F" and second section at Izúcar de Matamoros/ *Mapa de ubicación del área estudiada mostrando las secciones muestreadas, Estado de Puebla, México.* ***I,*** *Sección Principal , sección "A" y "B", Tzompahuacan y Lagunilla (todas en cercanías del poblado de Cuayuca).* ***II,*** *Sección "H", sección "F" y segunda sección de Izúcar de Matamoros.*

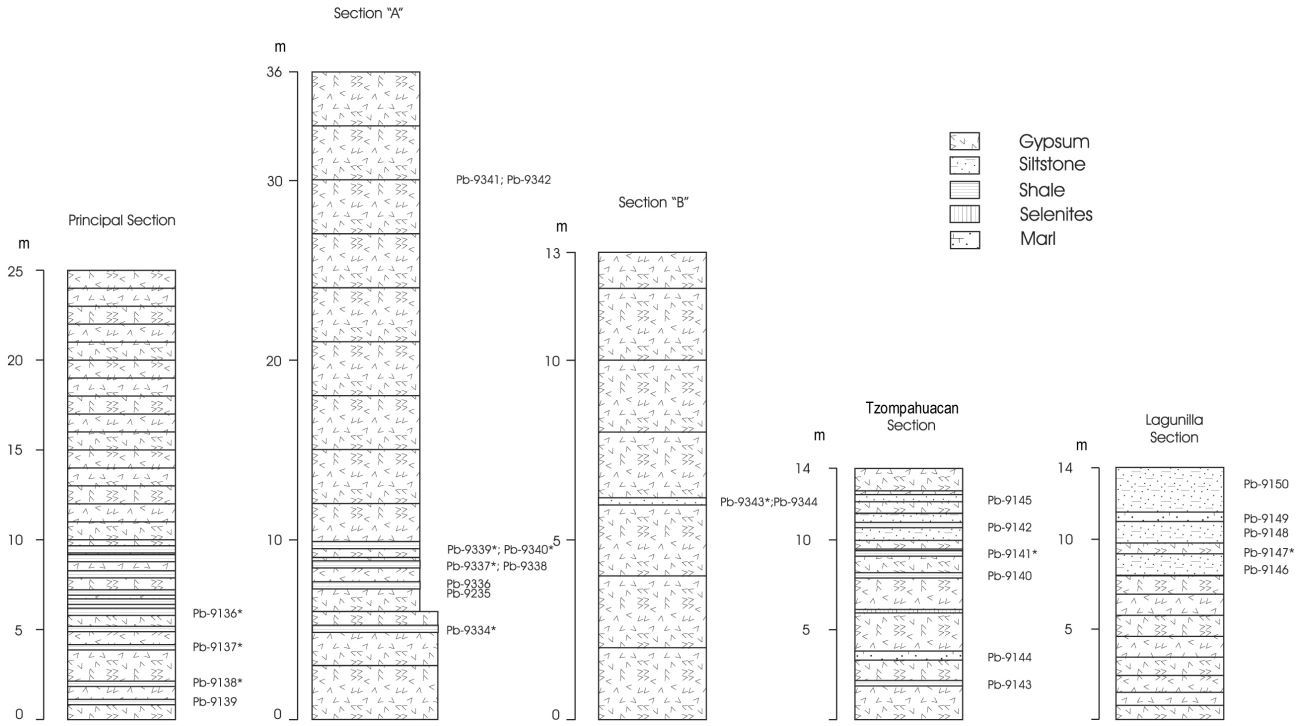


Figure 3. Stratigraphic sections of Cuayuca Formation near Cuayuca village/*Secciones estratigráficas de la Formación Cuayuca en cercanías del poblado de Cuayuca.*

a.2. Monolete spores

Laevigatosporites sp.
* *Polypodiisporites* cf. *favus* (Potonié) Potonié 1956 (figure 6.D)
**Polypodiisporites* sp. 1 (in this paper) (figure 6.H)

b. Gymnosperm pollen
b.1. Bisaccates

Piceapollis sp.
**Pinuspollenites* sp. (figure 6.J)
**Pityosporites* sp. (figure 6.I)

b.2. Poliplicates

**Ephedripites* (*Distachyapites*) *claricristatus* (Shakhmundes) Krutzsch 1970 (figures 6.K-L)
**Ephedripites* aff. *krempii* Kedves 1997 (figure 6.P)
**Ephedripites* aff. *viesenensis* Krutzsch 1961 (figures 6.N-O)
**Ephedripites* sp. 1 (in this paper) (figure 6.G)

b.3. Inaperturates

* *Cupressacites* spp. (figure 6.M)

Systematic descriptions

Trilete spores

Genus ***Cicatricosisporites***
Potonié and Gelletich 1933

Type species. *Cicatricosisporites dorogensis* Potonié and Gelletich 1933.

Cicatricosisporites dorogensis
Potonié and Gelletich 1933
Figures 5.A-C

Studied material. Section: "F" of "Izúcar de Matamoros". Samples: Pb-8870(6A): 106.5/16, 97.5/19, 93.2/17.6, 100.9/16.6; Pb-8870(1A): 86.8/14.6, 94.6/19.8, 96.5/8.7; Pb-8869(19): 107.1/8.7, 99.2/2.2, 104.6/20.5, 104.6/19.6, 107.5/7.7; Pb-8869(8): 101.7/13, 107.9/14.8.

Description. Monad, heteropolar, radiosymmetric. Trilete, amb subtriangular with rounded apices. Laesurae 3/4 or more of spore radius. Exine 2.6-4 µm thick; sculpture canaliculated or cicatricose comprising one set of parallel muri in distal view and 3 sets of parallel muri in proximal view. Muri sinuous 3.8 µm (1.6-5 µm) thick and sometimes anastomosed. There are also spores with degradated sporoderm that appear foveolate with a thinner exine (1.6 µm thick).
Dimensions. Equatorial axis = 59.2 µm (31.2-77 µm) based on 15 specimens.
Occurrence. Common (Pb-8869; Pb-8870).
Previous records. Mexico-Middle Eocene, San Ignacio and Colombia, Tamaulipas (Martínez-Hernández *et al*., 1980); Eocene-Oligocene, Esperanza Group, Chiapas (Tomasini-Ortiz and Martínez-Hernández, 1984). From Miocene, Chiapas, Palacios and Rzedowski (1993) found different types of *Cicatricosisporites*, two of them probably similar to the Cuayuca Formation specimens (unfortunately they

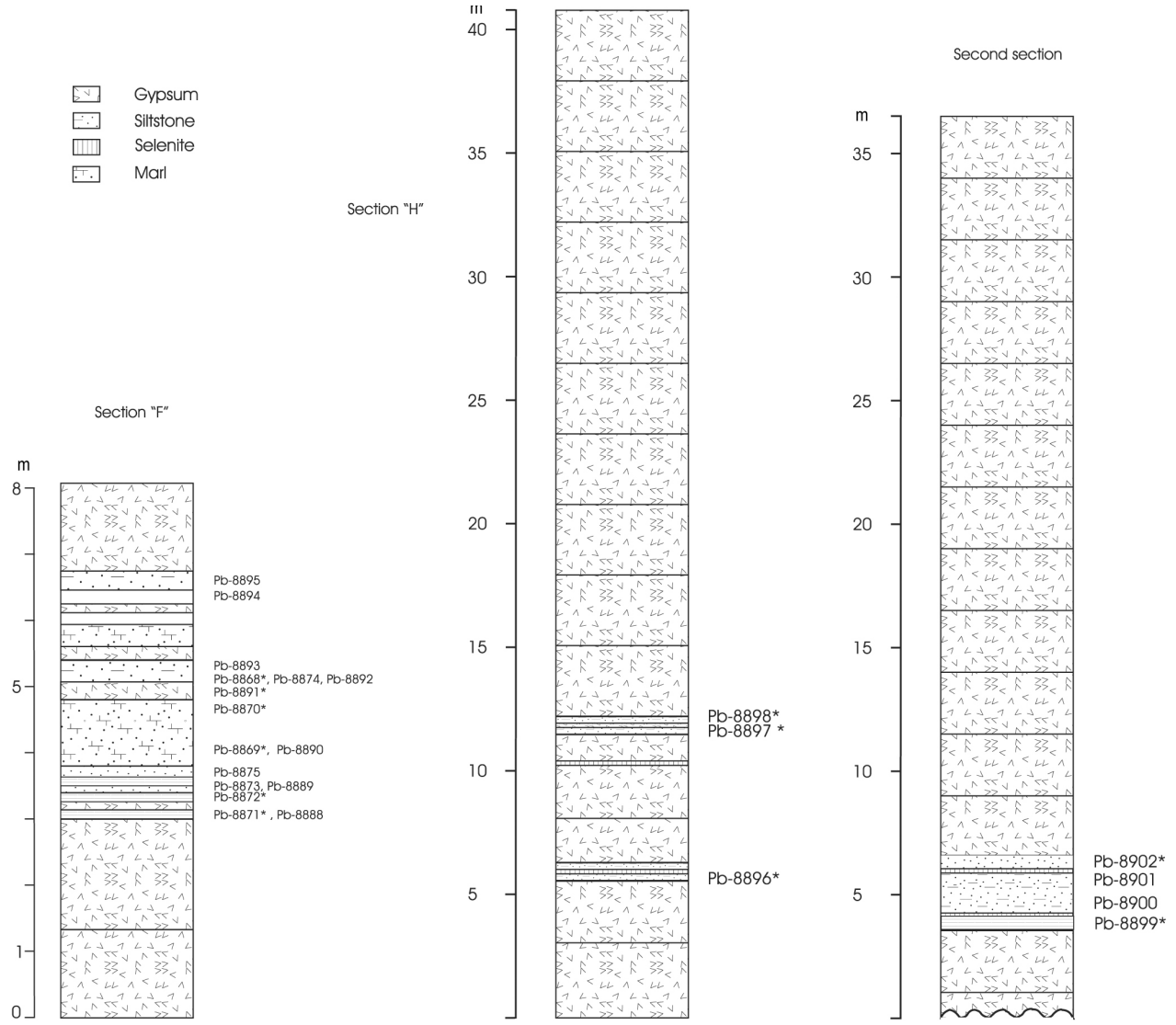


Figure 4. Stratigraphic sections of Cuayuca Formation at Izúcar de Matamoros/*Secciones estratigráficas de la Formación Cuayuca en Izúcar de Matamoros*.

are not clearly illustrated). North America-*C. dorogensis* was recorded from the Late Paleocene, Silverado Formation from California (Gaponoff, 1984), found it at Rockdale lignite (Elsik, 1968), Middle Eocene, Claiborne Group, Texas (Elsik, 1974); Late Eocene Jackson Group, Mississippi and Alabama (Frederiksen, 1980). South America-Middle Eocene to Oligocene, Brasil (Regali, *et al*., 1974; Lima *et al*., 1991). Europe - Late Paleocene into Eocene, Hungary (Potonié and Gelletich, 1933); Early Eocene, Belgium (Krutzsch and Vanboorne, 1977); Middle Eocene, Messel near Darmstadt (Thiele-Pfeiffer, 1988).

Botanical affinity. Related to *Anemia mexicana* Klotzsch and *A. dregeana* Kze. Canaliculated sculpture occurs in the subgenera *Coptophyllum* and *Anemirhiza* (Dettmann and Clifford, 1992).

Genus ***Deltoidospora*** Miner 1935

Type species. *Deltoidospora halli* Miner 1935.

Deltoidospora sp.
Figure 5.I

Studied material. Sections "A", "B" and principal section of Cuayuca; "F" and "H" of Izúcar de Matamoros. Samples: Pb-9334(4): 96.2/7, 100.7/10.3, 96.9/12.2, 97/12, 98.7/12.5, 98.7/12.5, 105.1/13.2, 95.8/15.2, 95.9/15.9, 104.2/16.4, 91.2/16.3, 94.4/18, 96.5/18.9, 93.2/9.3, Pb-9340, Pb-9343, Pb-9136, Pb-9138, Pb-8869, Pb-8898, Pb-8897, Pb-8896.

Description. Monad, heteropolar, radiosymmetric. Trilete, amb subtriangular with rounded apices. Laesurae 3/4 or more of spore radius. Exine 0.5-1 µm thick, psilate and usually folded.

Dimensions. Equatorial axis= 43.3 µm (36-58 µm), based on 15 specimens measured.
Occurrence. Unique (Pb-8897, Pb-9136); rare (Pb-9343, Pb-9138); frequent (Pb-9334, Pb-9340); common (Pb-8896, Pb-8898, Pb-8870).
Previous records. This genus is of worldwide distribution during the Mesozoic and Cenozoic.

Mexico-Late Eocene into Early Oligocene, Pie de Vaca Formation, Puebla (Martínez-Hernández and Ramírez-Arriaga, 1999); Early Eocene-Early Oligocene age of La Trinidad and La Quinta Formations (Tomasini-Ortiz and Martínez-Hernández, 1984); Oligocene-Miocene, La Quinta Formation (Biaggi, 1978); Middle to Late Miocene, Ixtapa Formation, Chiapas (Martínez-Hernández, 1992); Miocene, Pichucalco, Chiapas (Palacios and Rzedowski, 1993).
Botanical affinity. Cyatheaceae

Genus Foveotriletes van der Hammen 1955 *ex* Potonié 1956

Type species. *Foveotriletes scrobiculatus* Potonié 1956.

Foveotriletes sp.
Figures 5.D-F

Studied material. Section: "A" of Cuayuca. Sample: Pb- 9334 (4): 92.5/13.2.

Description. Monad, heteropolar, radiosymmetric. Trilete, amb triangular with rounded apices, margin lobate. Laesurae 3/4 or more of spore radius. Exine 1.6-2.4 µm thick, heterofoveolate; in distal face the biggest foveolae 2.4-4 µm in diameter, sometimes two or three foveolae are grouped and surrounded by small ones, with 0.8 µm in diameter or less. At proximal face one to five foveolae 0.8-2.4 µm in diameter are clustered.
Dimensions. Equatorial axis= 40 µm (one specimen measured).
Occurrence. Unique (Pb-9334).
Comparison. *Foveotriletes* sp. is different from *F. verrucosus* from the Late Oligocene-Early Miocene of New Zealand because the latter has a exine of 3-5,5 µm, foveolae up to 9 µm wide in distal view and a distinctive verrucate proximal side (Pocknall and Mildenhall, 1984).
Previous records. Mexico-Oligocene into Miocene, La Quinta Formation, Chiapas (Biaggi, 1978); Pliocene, Paraje Solo Formation, Veracruz (Graham, 1979).
Botanical affinity. Related with *Sphaeropteris* or *Trichipteris* (Graham, 1979).

Genus *Leptolepidites* Couper 1953

Type species. *Leptolepidites verrucatus* Couper 1953.

Leptolepidites sp.
Figure 5.J

Studied material. Sections: "A" of Cuayuca, Tzompahuacan and "F" of Izúcar de Matamoros. Samples: Pb-9334, Pb-9141, Pb-8870, Pb-8869(19NF): 96.4/4.4, 99.6/4, 115.7/6.6, 115/14.9, 97/18.5, 111.3/17, 107.2/11.5, 111.7/10.5, 101.2/10.3, 109.6/9.8, 107.3/7.4, 111.3/2.3, 99.4/14.8.

Description. Monad, heteropolar, radiosymmetric. Trilete, amb triangular with rounded apices, margin lobate. Laesurae 2/3 of spore radius. Exine 1.6-3.2 µm thick, heteroverrucate in proximal and distal pole, verrucae with diameter of 0.8-3.2 µm. Scultural elements lightly smaller in proximal face.
Dimensions. Equatorial axis= 30.7 µm (22.4-36.8 µm) based on thirteen specimens measured.
Occurrence. Single (Pb-9141); rare (Pb-9334); frequent (Pb-8869, Pb-8870).
Botanical affinity. Spores of the genus *Leptolepidites* are related to the families Lycopodiaceae/Selaginellaceae.

Genus *Lusatisporis* Krutzsch, 1963

Type species. *Lusatisporis punctatus* Krutzsch 1963.

Lusatisporis dettmannae (Drugg) Srivastava 1972
Figures 5.G-H

Studied material. Sections: "A" of Cuayuca and "H" of Izúcar de Matamoros. Samples: Pb-9334(4): 104.4/13.3, 103.2/17.7, 103.2/15, Pb-9340(1): 99.4/7.7, Pb-8898.

Description. Monad, heteropolar, radiosymmetric. Trilete, amb subtriangular with rounded apices. Exine 0.8 µm thick. Laesurae extending to flange with lips. Flange membranous and granular, formed by the separation of the exoexine from the intexine at the equator of 4-5 µm wide.
Dimensions. Equatorial axis= 42 µm (38-48 µm) based on four specimens measured including flange.
Occurrence. Single (Pb-8898); rare (Pb-9334); common (Pb-9340).
Botanical affinity. Related to the genus *Selaginella.*
Previous records. Mexico-Late Eocene into Early Oligocene, Pie de Vaca Formation, Puebla (Martínez-Hernández and Ramírez-Arriaga, 1999).

Genus *Retitriletes* Pierce *emend.* Döring, Krutzsch, Mai and Schulz in Krutzsch 1963

Type species. *Retitriletes globosus* Pierce 1961.

Retitriletes sp.
Figure 6.A

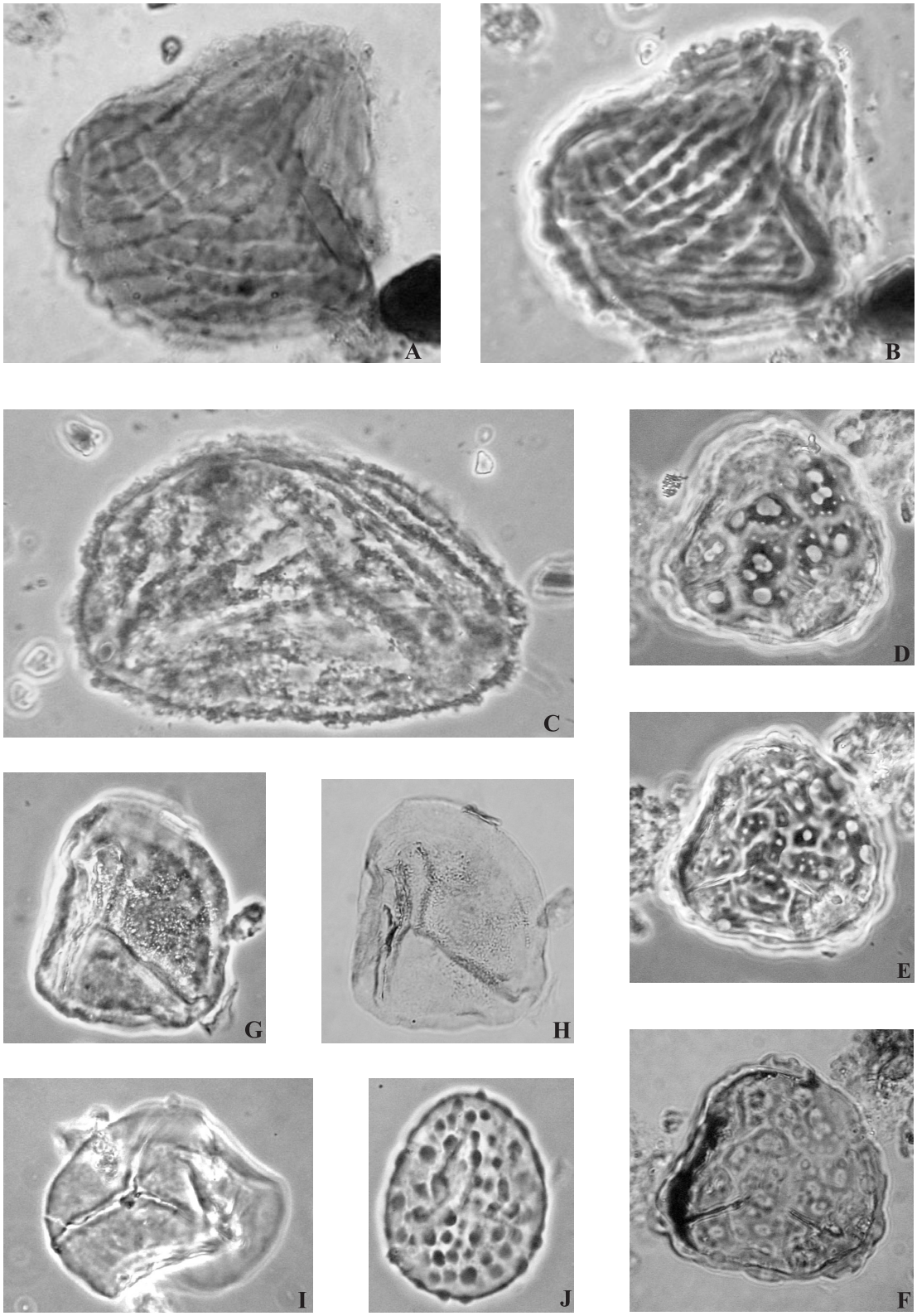


Figure 5. All figures X 1000/*Todas las figuras ampliadas X 1000.* **A-C,** ***Cicatricosisporites dorogensis*** Potonié and Gelletich. **A-B,** Pb-8870(6): 106.5/16 IGLUNAM. **C,** Pb-8869: 92.1/11.5 IGLUNAM. Spore with degradated sporoderm/*espora con esporodermo degradado.* **D-F,** ***Foveotriletes*** sp. Pb-9334(4): 92.5/13.2 IGLUNAM. **D,** distal face/*cara distal*; **E,** proximal face/*cara proximal and* **F,** optical photomicrograph/*corte óptico;* **G-H,** ***Lusatisporis dettmannae*** (Drugg) Srivastava. Pb-9334(4): 104.4/13.3 IGLUNAM. **I,** ***Deltoidospora*** sp. Pb-9334(4): 96.2/7 IGLUNAM. **J,** ***Leptolepidites*** sp. Pb-8869 (8A): 115.7/6.6 IGLUNAM.

Studied material. Section: "A" of Cuayuca, Tzompahuacan. Samples: Pb-9334(4): 103/13.4, 100.5/15.8, 100.5/18.3, 101.6/20.7, Pb-9334(5): 106.7/15.8, Pb-9141.

Occurrence. Common (Pb-9334).
Description. Monad, heteropolar, radiosymmetric. Trilete, amb subtriangular with rounded apices. Exine 2 µm thick, reticulate at the proximal and distal face. Lumina 2-4 µm in diameter and muri 0.8-1 thick. Laesurae 2/3 of spore radius.
Dimensions. Equatorial axis= 68.9 µm (59-84 µm) based on five specimens measured.
Previous records. Mexico-Late Eocene into Early Oligocene, Pie de Vaca Formation, Puebla (Martínez-Hernández and Ramírez-Arriaga, 1999).
Botanical affinity. Comparable with certain spores of Lycopodiaceae family.

Genus ***Stereigranisporis*** (Krutzsch) Kedves 1982

Type species. *Stereigranisporis granula* (Krutzsch and Sontag) Kedves 1982 (in Kedves and Russell 1982) ibid. *Stereisporites* subgenus *Stereigranisporis granulus* Krutzsch and Sontag 1963 (in Krutzsch 1963).

Stereigranisporis aff. ***granula*** (Krutzsch and Sontag) Kedves 1982
Figures 6.B, C, E

Studied material. Sections: Tzompahuacan and "F" of Izúcar de Matamoros. Samples: Pb-8869(8): 100.3/2,109.8/9.4, 106.4/17.4, 107.8/14, 108.8/6.2, Pb-9141.

Description. Monad, heteropolar, radiosymmetric. Trilete, amb subtriangular often with rounded thickened at the radial corners, but the corners are angular. Laesurae 3/4 or more of spore radius. Exine 1.6-2.4 µm thick; sculpture verrucate in proximal and distal face. Verrucae from 0.5-2 µm, that make the outline sinuous.
Dimensions. Equatorial axis= 20.4 µm (16.8-27.2 µm) based on 10 specimens measured.
Occurrence. Unique (Pb-9141); abundant (Pb-8869); dominant (Pb-8870).
Remarks. *S.* aff. *granula* and *S. granula* have similar dimensions although *S.* aff. *granula* could be smaller than *S. granula* and they exhibit a verrucose sculpture that overlaps onto and spreads over the proximal face showing a weakly differentiated contact area.
Previous records. Mexico-Eocene, Claiborne Formation, Tamaulipas (Martínez *et al.*, 1980).
Botanical affinity. Bryophyta.

Género ***Verrucingulatisporites*** Kedves 1961

Type species. *Verrucingulatisporites verrucatus* Kedves 1961.

Verrucingulatisporites sp.
Figure 6.F

Studied material. Section: "F" of Izúcar de Matamoros. Sample: Pb-8869(8A): 94.6/4.2, Pb-8869(19): 116.4/11.7, 113.6/8.5, 99.8/6.6, 104.7/21.

Description. Monad, heteropolar, radiosymmetric. Trilete, amb triangular with rounded apices. Exine 1.2 µm thick with cingulum verrucate of 4 µm thick. Distal face with verrucae from 2.4 to 3.4 wide and verrucae from the proximal face of 1.6 µm wide, some specimens present microechinae. Laesura undulate extending to the equator.
Dimensions. Equatorial axis= 24.1 µm (16.8-28.8 µm) based on five specimens measured.
Occurrence. Common (Pb-8869); frequent (Pb-8870)
Previous record. Miocene, Pichucalco, Chiapas (Palacios and Rzedowski, 1993).
Botanical affinity. Related with some species of *Pteris*.

Monolete spores

Genus ***Polypodiisporites*** Potonié 1931 in Potonié and Gelletich 1933 *ex* Potonié 1956

Type species. *Polypodiisporites favus* Potonié 1931 *ex* Potonié 1956.

Polypodiisporites cf. ***favus*** (Potonié) Potonié 1956
Figure 6.D

Studied material. Sections: "A" and "B" of Cuayuca; "F" of Izúcar de Matamoros. Samples: Pb-9340(1): 99.1/12.7; Pb-9334(4): 99/10.4, 96.1/16.3, 106.6/9.3, 104.1/22.3, Pb-9343

Description. Monad, heteropolar, bilateral symmetry. Monolete, bean shape. Exine 1-2 µm thick, verrucate with negative reticula. Verrucae with diameter between 0.8 to 3 µm. Laesurae 3/4 or more of spore length.
Dimensions. Major equatorial axis= 50.4 µm (42-58 µm), minor equatorial axis= 34 µm E.P.= 30.3 µm (26-35 µm) based on five specimens measured.
Occurrence. Rare (Pb-9340, Pb-9334, Pb-9343).
Remarks. *Polypodiisporites* cf. *favus* is similar to *P. favus*, in some characteristics such as negative reticulum and size spore, in contrast *P. favus* has an outline clearly undulating due to verrucae, while *Polypodiisporites* cf. *favus* has small flat verrucae showing an slightly undulating outline. A similar taxon (*Polypodiisporites* cf. *P. favus* in Tomasini and Martínez-Hernández, 1984) was reported for the upper Oligocene, Chiapas, Mexico. It was characterized by low sculptured elements 1 to 3 µm wide.
Botanical affinity. Related to the family Polypodiaceae.

Polypodiisporites sp.1
Figure 6.H

Studied material. Section: "A" of Cuayuca. Sample: Pb-9334(4): 100.9/21.9, 90.7/19.2, 95/19.3, 98/19.1.

Occurrence. Rare (Pb-9334).
Description. Monad, heteropolar, bilateral symmetry. Monolete, bean shape. Exine verrucate to rugulate. Laesurae 3/4 or more of spore length. Rugulae of 3 µm wide and 3-8 µm in maximum length.
Dimensions. Polar axis= 25.5 µm (20-34 µm); Equatorial axis= 38.3 µm (31-45 µm) based on four specimens measured.
Remarks. *Polypodiisporites* sp.1 is different from *Polypodiisporites* cf. *favus* because the first one exhibits a verrucate-rugulate exine while *P.* cf. *favus* has a verrucate exine forming a negative reticulum. A similar material was cited as *Verrucatosporites* sp. for the Eocene of Tamaulipas, Mexico (Martínez-Hernández *et al*., 1980: fig. 5-d).
Botanical affinity. Polypodiaceae.

Pollen grains

Gymnosperms

Bisaccates

Genus ***Pinuspollenites*** Raatz 1937 ex Potonié 1958

Type species. *Pinuspollenites labdacus* (Potonié) Raatz *ex* Potonié 1958.

Pinuspollenites sp.
Figure 6. J

Principal material studied. Section: "A", "B" and principal section of Cuayuca. "F", "H" and second section of Izúcar de Matamoros. Samples: Pb-9136, Pb-9138, Pb-9340, Pb-9337, Pb-9334(4): 96.7/3.8, 103.1/5.7, 101.2/7.4, 94.1/8, 98/13.5, 97/13.7, P-9343, Pb-9147, Pb-8891, Pb-8870, Pb-8872, Pb-8871, Pb-8898, Pb-8896.

Dimensions. The specimens were measured in polar and equatorial view. At equatorial view: Height of body 27.3 µm (21.6-34 µm). Width of body 43.5 µm (32-46.4µm). Height of saccus 24.2 µm (19-30 µm). Width of saccus 20.4 µm (12-32 µm). At polar view: Length of body 37.1 µm (32-44). Width of body 42.2 µm (33-53 µm). Height of saccus 38.5 µm (32.8-42 µm). Width of saccus 24.5 µm (16.8-32 µm).
Occurrence. Unique (Pb-9337, Pb-9136, Pb-8902, Pb-8891); rare (P-9343, Pb-8897, Pb-8871); common (Pb-9147, Pb-8896, Pb-8870, Pb-8872), frequent (Pb-9138, Pb-9334, Pb-9340, Pb-8898); dominant (Pb-9138; Pb-9334, Pb-9340).
Previous records. *Pinuspollenites* is very common throughout the Tertiary. Mexico-Late Eocene into Early Oligocene, Pie de Vaca Formation, Puebla (Martínez-Hernández and Ramírez- Arriaga, 1999); Oligocene, San Gregorio Formation, Baja California Sur (Martínez-Hernández and Ramírez-Arriaga, 1996); Oligocene-Miocene, Chiapas (Langenheim et al., 1967; Biaggi, 1978); Neogene (Graham, 1975; Martínez-Hernández, 1992 and Palacios and Rzedowski, 1993).
Botanical affinity. *Pinus*.

Genus ***Pityosporites*** Seward 1914

Type species. *Pityosporites antarcticus* Seward 1914.

Pityosporites sp.
Figure 6.I

Studied material. Section: "A" of Cuayuca. Sample: Pb-9334: 108.1/5.8, 113.5/7.7, 103.6/18, 100.2/20.3, 103.2/22.8, 94.3/15.5.

Dimensions. The six specimens were measured in polar view. Length of the body 20.3 µm (14-27 µm). Width of the body 22.2 µm (15-27 µm). High of saccus 17.9 µm (12-16 µm). Width of saccus 12.9 µm (11-20 µm).
Occurrence. Common (Pb-9334).
Botanical affinity. *Pinus*.

Polyplicates

Genus ***Ephedripites*** Bolkhovitina 1953

Type species. *Ephedripites mediolobatus* Bolkhovitina 1953.

Remarks. Many authors have discussed about the assigment of *Ephedra*-like dispersed pollen to the genus *Equisetosporites* or *Ephedripites*. Pocock (1964) concluded that *Equisetosporites* should be accepted for fossil pollen attributed to the family Ephedraceae. Muller (1968) considered the restriction of *Equisetosporites* only to Triassic forms similar to the type species of this genus. Frederiksen *et al.* (1983, p. 30) proposed the use of *Ephedra* for grains that are assumed to be produced by this modern genus and *Ephedripites* to those that having similar morphology to *Ephedra*, may well not belong to it. Balme (1995, p. 212) based on the ultrastructural study carried out by Zavada (1984) suggested to retain *Ephedripites* as a general category for polyplicate pollen. However, he remarked that in the absence of ultrastructural evidence, the assessment of its botanical affinity is not confident. The critera of Balme (1995) are followed in this contribution.

Ephedripites (***Distachyapites***) ***claricristatus***
(Shakhmundes) Krutzsch 1970
Figures 6.K-L

Studied material. Section: "A" of Cuayuca. Sample: Pb-9340(4): 96.6/20.5, 97.2/15.3, 92.2/14.7.

Description. Monad isopolar, radiosymmetric, prolate. Poliplicate. Exine tectate, psilate 1 µm thick. Valley with branched endofissurae. Four or five ridges with irregular edges, distance between ribs 8-12 µm.
Dimensions. Polar axis= 43 µm (38-48 µm); Equatorial axis= 20.7 µm (19-25 µm) based on four specimens measured.
Occurrence. Common (Pb-9340).
Previous records. Mexico-Late Eocene into Early Oligocene, Pie de Vaca Formation, Puebla (Martínez-Hernández and Ramírez-Arriaga, 1999). North America-Eocene to Holocene, Golf Coast (Fairchild and Elsik, 1969); Middle Eocene to Early Oligocene, Golf Coast (Frederiksen, 1988); Late Eocene, Jackson Group (Frederiksen, 1980); Middle Eocene, San Diego, California (Frederiksen *et al*. 1983). Argentina-Middle Miocene, "Serie el Yeso", San Juan province (Barreda *et al*., 1998); Early Miocene, Chenque Formation, Chubut and Santa Cruz provinces (Barreda, 1997a); Oligocene-Early Miocene, San Julián and Monte León Formations, Santa Cruz province (Barreda, 1997b, Barreda and Palamarczuk, 2000a, 2000b); Early Miocene, Chinches Formation (Ottone, *et al*., 1998).
Botanical affinity. Probably related to *Ephedra distachya L.* and *Ephedra nevadensis* S.Wats.

Ephedripites aff. ***krempii*** Kedves 1997
Figure 6.P

Studied material. Section: "A" of Cuayuca. Sample: Pb-9340(4): 89.2/19, 95.2/18.3, 99.6/16.8.

Description. Monad, isopolar, radiosymmetric, prolate. Poliplicate, amb ellipsoidal. Exine tectate-psilate 1-1.5 µm thick. Six or seven ridges with straight edges, with a distance of 4-5 µm between them.
Dimensions. Polar axis= 33.6 µm (32-35 µm); Equatorial axis= 12.6 µm (12-14 µm) based on three specimen measured.
Occurrence. Common (Pb-9340).
Remarks. *E.* aff. *krempii* has some similar characters to *E. krempii* (Kedves, 1997) like the number of ridges, the psilate exine and the thickness of the exine. Nevertheless, the distance between ridges is bigger in *E.* aff. *krempii* (4-5 µm) than in *E. krempii* (2-3.5 µm), perhaps this could be the result of a difference in the preservation.
Previous records. Mexico-Late Eocene into Early Oligocene, Pie de Vaca Formation, Puebla (Martínez-Hernández and Ramírez-Arriaga, 1999). Eocene-Oligocene, Esperanza Group, Chiapas (Tomasini-Ortiz and Martínez-Hernández, 1984). Argentina-Late Paleocene into Early Eocene, Rio Chico Formation (Lema *et al*., 1999).
Botanical affinity. *Ephedra*.

Ephedripites aff. ***viesenensis*** Krutzsch 1961
Figures 6.N-O

Studied material. Section: "A" of Cuayuca. Sample: Pb-9340(4): 90.3/16.9, 97.3/15, 100.4/15.4.

Description. Monad, isopolar, radiosymmetric, prolate. Polyplicate, amb ellipsoidal. Exine tectate-psilate 1 µm thick, the exine is thicker at the ridges. Twelve ridges with straight edges are present, with a distance of 3µm between edges.
Dimensions. Polar axis= 34 µm (29-38 µm); Equatorial axis= 17.6 µm (17-19 µm) based on three specimen measured.
Occurrence. Common (Pb-9340).
Remarks. *E.* aff. *viesenensis* shares some features with *E. viesenensis* (Kedves, 1997), as the number of the ridges, the psilate exine and the thickness. In contrast, *E. viesenensis* exhibits a shorter distance between ridges (0.7 µm) than in *E.* aff. *viesenensis* (3 µm).
Botanical affinity. *Ephedra* type.

Ephedripites sp.1
Figure 6.G

Studied material. Section: "A" of Cuayuca. Sample: Pb-9340(4): 92.4/15.7.

Description. Monad, isopolar, radiosymmetric, prolate. Polyplicate, amb ellipsoidal. Exine tectate-psilate 0.8 µm thick. Seven to eight ridges with undulate edge and distance between them of 3 µm.
Dimensions. Polar axis= 19 µm; Equatorial axis= 11 µm based on one specimen measured.
Occurrence. Unique (Pb-9340).
Remarks. *E.* sp. 1 is the shortest (respect to the polar axis) polyplicate pollen grain found in the studied assemblages and it has ondulated ridges, while *E.* aff. *viesenensis* and *E.* aff. *krempii* present almost straight ridges.
Botanical affinity. *Ephedra* type.

Inaperturates

Genus ***Cupressacites*** Bolkhovitina (1956) *ex* 1960 *emend*. Krutzsch 1971

Type species. *Cupressacites russeus* Bolkhovitina *ex* Krutzsch 1971.

Cupressacites sp.
Figure 6.M

Studied material. Sections: "B" of Cuayuca; Lagunilla and "F" of

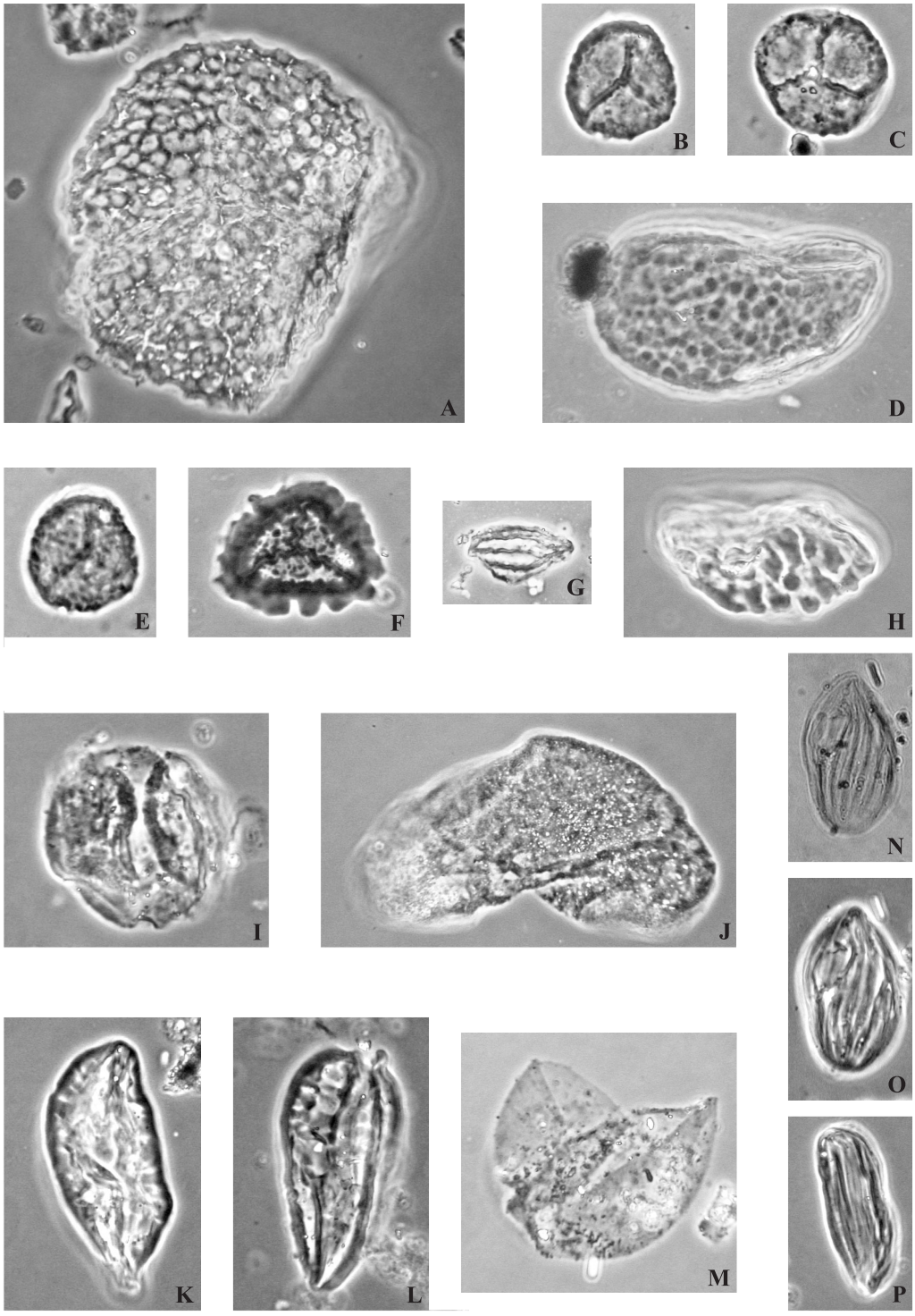


Figure 6. All figures X 1000/*Todas las figuras ampliadas X 1000.* **A, *Retitriletes*** sp. Pb-9334(4): 108.2/11.9 IGLUNAM. **B, E, *Stereigranisporis*** aff. ***granula*** (Krutzsch and Sontag) Kedves. Pb-8869(8A): 100.2/13.8 IGLUNAM. **C, *Stereigranisporis*** aff. ***granula*** (Krutzsch and Sontag) Kedves. Pb-8869(8A): 87.1/18.7 IGLUNAM. **D, *Polypodiisporites*** cf. ***favus*** (Potonié) Potonié. Pb-9334(4): 99/10.4 IGLUNAM. **F, *Verrucingulatisporites*** sp. Pb-8869(8): 4.2/94.5 IGLUNAM. **G, *Ephedripites*** sp. 1 Pb-9340(4): 92.4/15.7 IGLUNAM. **H, *Polypodiisporites*** sp. 1 Pb-9334(4): 100.5/6.3. **I, *Pityosporites*** sp. Pb-9340(1): 110.9/22.4. **J, *Pinuspollenites*** sp. Pb-9334(4): 91.4/18.8. **K-L, *Ephedripites* (*Distachyapites*) *claricristatus*** (Shakhmundes) Krutzsch. **K,** Pb-9340(4): 96.6/20.5 IGLUNAM. **L,** Pb-9340(4): 97.2/15.3 IGLUNAM. **M, *Cupressacites*** sp. Pb-9147(1): 92.8/6.6 IGLUNAM. **N-O, *Ephedripites*** aff. ***viesenensis*** Krutzch. Pb-9340(4): 90.3/16.9 IGLUNAM. **P, *Ephedripites*** aff. ***krempii*** Kedves. Pb-9340(4): 95.2/18.3 IGLUNAM.

Izúcar de Matamoros Samples: Pb-9343; Pb-8871; Pb-9147(1): 92.8/6.6.

Description. Monad, apolar, radiosymmetric. Inaperturate, tectate, supramicroverrucate. Exine 0.4- 1 µm thick.
Dimension. Diameter= 30.9 µm (29-32.8 µm) based on two specimens measured.
Occurrence. Unique (Pb-9343); rare (Pb-9147, Pb-8871).
Previous records. Mexico-Late Oligocene-Early Eocene, Pie de Vaca Formation, Puebla (Martínez-Hernández and Ramírez-Arriaga, 1999); Oligocene-Miocene, La Quinta Formation, Chiapas (Biaggi, 1978); Miocene, Pichucalco, Chiapas (Palacios and Rzedowski, 1993). Argentina-Late Miocene, Chenque Formation (Barreda, 1997a).
Botanical affinity. *Cupressus/Juniperus/Taxodium.*

Final considerations

The Cuayuca Formation provided diverse and well preserved palynological associations constituted by more than 96 taxa. The pteridophyte and briophyte spores comprised nearly 13.5 % of the total diversity and the gimnosperms only 7.3 %. Angiosperms are dominant in all the associations.

Taking into account the percentage range for each taxon within the assemblages of the different studied sections, the components of the genus *Stereisporites* were the more representative (19.7-27.8%) among the trilete spores, followed by *Cicatricosisporites dorogensis* (7.7-9.1%), *Leptolepidites* sp. (6.5-8.8%), *Deltoidospora* sp. (3.3-8.3%), and *Verrucingulatisporites* sp. (1.9-3.1%). *Pinuspollenites* (43.6-55.4%) and *Ephedripites* (3.7-13%) were the most abundant gimnosperms in nearly all the sections from Cuayuca and Izúcar de Matamoros, although *Ephedripites* was more frequent at Cuayuca sections.

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