

Three new Cenomanian conifers from El Chango (Chiapas, Mexico) offer a snapshot of the geographic mosaic of the Mesozoic conifer decline

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Cenomanian conifers of El Chango

Abstract

Premise of study: “El Chango” is a recently discovered quarry that contains extremely well preserved fossils. The Cenomanian age of the locality corresponds to a time when the global flora was transitioning from gymnosperm- to angiosperm-dominated, yet conifers predominate in this locality. These fossils thus provide a rare opportunity to understand the replacement of conifers by angiosperms as the dominant group of plants.

Methods: We collected material from El Chango in annual expeditions (2010 to 2014). We selected the three most abundant and best preserved conifer morphotypes and conducted a total-evidence (i.e., including molecular and morphological data) phylogenetic analysis of a sample of 72 extant conifer species plus the three fossils. We use these results to inform our taxonomic decisions.

Results: We obtained four equally most-parsimonious trees (consistency index = 44.1%, retention index = 78.8%). Despite ambiguous relationships among some extant taxa, the three fossil conifers had the same phylogenetic position in all four most-parsimonious trees; we describe these species as new: *Sequoiadendron helicalancifolium* sp. nov. (Cupressaceae), and *Microcachrys rhomboidea* sp. nov. and *Dacrydium bifoliosus* sp. nov. (Podocarpaceae). The ecosystem is interpreted as a coastal humid mixed forest.

Conclusions: Our findings contribute to the understanding of Cenomanian equatorial regions, and support the hypothesis of a geographically and ecologically structured “rise of angiosperms”, with conifers remaining dominant in brackish-water and angiosperms becoming dominant in freshwater-ecosystems. These fossils fill in gaps in the evolutionary history of lineages like *Microcachrys*, which we demonstrate occurred in the Northern hemisphere before becoming restricted to its current range (Tasmania).

Keywords: fossils, Cretaceous, Cenomanian, Cupressaceae, *Dacrydium*, *Microcachrys*, Podocarpaceae, conifer phylogeny, *Sequoiadendron*

Resumen

Premisa del estudio: “El Chango” es una cantera recientemente descubierta que contiene fósiles extremadamente bien preservados. Su edad Cenomaniana corresponde al momento en que la flora global pasaba de ser dominada por gimnospermas a ser dominada por angiospermas, aún así las coníferas son el grupo dominante en esta localidad. Estos fósiles ofrecen una rara oportunidad para estudiar el remplazamiento de las coníferas por angiospermas como el grupo dominante de plantas.

Métodos: Colectamos material de El Chango en expediciones anuales (2010 a 2014). Seleccionamos los tres morfotipos de coníferas más abundantes y mejor preservados. Realizamos un análisis filogenético de evidencia total (i.e., incluyendo datos moleculares y morfológicos) de una muestra de 72 coníferas actuales más los tres fósiles. Utilizamos estos resultados para tomar nuestras decisiones taxonómicas.

Resultados: Obtuvimos cuatro árboles igualmente más parsimoniosos (índice de consistencia de 44.1 %, índice de retención de 78.8 %). A pesar las relaciones filogenéticas ambiguas entre algunos taxones actuales, las tres coníferas fósiles tuvieron la misma posición en los árboles más parsimoniosos. Describimos tres especies nuevas: *Sequoia-dendron helicalancifolium* sp. nov. (Cupressaceae), *Microcachrys rhomboidea* sp. nov. (Podocarpaceae) y *Dacrydium bifoliosus* sp. nov. (Podocarpaceae). Interpretamos la vegetación asociada a El Chango como un bosque costero húmedo.

Conclusiones: Nuestros resultados contribuyen al entendimiento de las regiones ecuatoriales del Cenomaniano, y apoyan la hipótesis de que “la emergencia de las angiospermas” fue geográfica- y ecológicamente estructurada; las coníferas permaneciendo como dominantes en ambientes de agua salobre y las angiospermas volviéndose dominantes en ambientes de agua dulce. Estos fósiles llenan vacíos en la historia evolutiva de linajes como *Microcachrys*, el cual demostramos que existió en el hemisferio norte antes de volverse endémico de Tasmania.

Palabras clave: fósiles, Cretácico, Cenomaniano, Cupressaceae, Podocarpaceae, filogenia

1 INTRODUCTION

2 Despite being massively outnumbered by extant angiosperms (angiosperms account for
3 $\sim 89\%$ of extant plant species vs $\sim 0.29\%$ for gymnosperms; [Crepet and Niklas, 2009](#);
4 [Hassler, 2021](#)) conifers were dominant for the first half of the Mesozoic ([Miller, 1977](#); [Taylor](#)
5 [et al., 2009](#)). This former ecological dominance is documented in a particularly rich fossil
6 record (e.g., [Contreras et al., 2019](#); [Hernández-Castillo et al., 2014](#); [Looy, 2007](#)), which is
7 partially due to the fact that conifers have sturdy structures—i.e., cones, wood, and thick
8 leaves—that are more prone to fossilize than are the more delicate structures of other plant
9 groups. This fossil record reveals that conifers first evolved during the Carboniferous, likely
10 from an ancestor in the Cordaitales, an extinct group of seedplants ([Beck, 1988](#)). During
11 the rest of the Paleozoic, conifers increased in diversity and geographic extent, leaving
12 behind traces of lineages that are known only from the fossil record, such as the Walchian
13 and Voltzian conifers ([Looy, 2007](#); [Hernández-Castillo et al., 2014](#)). Though most of the
14 Paleozoic conifer lineages went extinct around the Permian-Triassic boundary, the groups
15 that persisted became widespread in the Mesozoic ([Beck, 1988](#); [Farjon, 2008](#)). There are
16 records of nine families of conifers in the Mesozoic, including the six extant families ([Taylor](#)
17 [et al., 2009](#)). During the Triassic and Jurassic, conifers occurred in a wide variety of habitats,
18 including some that are currently dominated by angiosperms. This diversity of habitats was
19 also associated with a diversity of life forms, such as the records of a ruderal herbaceous
20 conifer ([Rothwell et al., 2000](#)).

21 Despite the abundance of conifers in the fossil record, reconstructing their evolutionary
22 history is challenging. First, plant fossils are usually fragmentary and only in very rare cases
23 do different organs (e.g., leaves, stems, roots, reproductive structures) appear connected
24 in the fossil record. This difficulty in determining which pieces go together extends to
25 within-organ assessments—conifers, in particular, can have different types of leaves and
26 leaf arrangement (i.e., phyllotaxy) depending on the position of the branch and whether

27 or not the branch is reproductive (Hernandez, 2006; Farjon, 2008). In addition, even when
28 the whole plant can be reconstructed with some confidence, homology to features of extant
29 groups is often uncertain.

30 Another challenging aspect about understanding the history of conifers is the temporal
31 and spatial heterogeneity in the availability of fossils (Allison and Bottjer, 2011). For
32 example, areas closer to the equator tend to have thick vegetation that complicates the
33 access to fossil-bearing rock layers. Therefore, the fossil record is biased towards geographic
34 areas where rocks are exposed, like deserts or cliffs, especially those of regions with a
35 long history of paleontological exploration (Europe and North America). In Mexico, for
36 example, most of the plant fossils from the Cretaceous are from northern areas of the
37 country (Villanueva-Amadoz et al., 2014), where deserts dominate the landscape. In this
38 context, the recent discovery of a rich fossil-bearing site in Chiapas (southern Mexico) is
39 particular noteworthy as it increases our latitudinal sample of terrestrial communities in
40 the Cenomanian. Therefore, by studying the plant community of El Chango, we can obtain
41 some insight regarding the latitudinal variation of vegetation in the Cenomanian, as well as
42 particular information about the evolutionary history of individual lineages.

43 This site, named “El Chango”, is Cenomanian in age and contains extremely well
44 preserved fossils of fishes, invertebrates, angiosperms, and gymnosperms (Alvarado-Ortega
45 and Than-Marchese, 2013, 2012; Guerrero-Márquez et al., 2013; Huerta-Vergara et al., 2013;
46 González-Ramírez et al., 2013; Moreno-Bedmar et al., 2014). El Chango’s fossils offer a great
47 opportunity to expand our knowledge about Cenomanian low-latitude floras (Villanueva-
48 Amadoz et al., 2014) filling in an important gap both temporally (i.e., Cenomanian) and
49 geographically (southernmost North America). In this paper we describe three new species of
50 conifers from El Chango and infer their phylogenetic position and taxonomic affinities based
51 on a total-evidence phylogenetic analysis incorporating 72 extant conifer representatives.
52 These new species expand our records of the temporal and geographic occurrence of the

53 lineages they belong to and deepen our understanding of Cenomanian biogeographic patterns.
54 In particular, they provide insight into the identity and distribution of conifers in the middle
55 of the angiosperm rise to dominance.

56 **Geological framework**

57 El Chango is located in Chiapas, Mexico (16°34.14'N, 93°16.11'W) and belongs to the
58 Cintalapa Formation, in the Sierra Madre Group (Moreno-Bedmar et al., 2014). The
59 sediments that formed the Sierra Madre Group were deposited during the Albian-Santonian,
60 in the mid-Cretaceous, ~113 to 83.6 Mya (Steele and Waite, 1985). The rocks of El
61 Chango specifically are Cenomanian in age (100.5–93.9 Mya) based on the presence of two
62 stratigraphic markers: the ammonites *Graysonites* and *Metengonoceras* (Moreno-Bedmar
63 et al., 2014). The known section of El Chango is 54 m thick and it is composed primarily
64 of marine laminated dolomites with sporadic flint levels (Moreno-Bedmar et al., 2014).
65 The depositional environment has been interpreted as a coastal lagoon with ephemeral
66 freshwater influx (Vega et al., 2006). El Chango and adjacent quarries like “El Espinal” are
67 considered *Konservat Lagerstätten* due to the excellent preservation of their fossils (Díaz-
68 Cruz et al., 2016). In these layers, scientists have found fishes with soft tissue preservation
69 (Díaz-Cruz et al., 2016; Alvarado-Ortega and Than-Marchese, 2012, 2013; Vega et al., 2003)
70 and many different types of fossil plants, including a variety of angiosperms similar to
71 Arecaeae, Bignoniaceae, Combretaceae, Myrtaceae, and seagrasses in Cimodoceaceae and
72 Hydrocharitaceae (Guerrero-Márquez et al., 2013). However, conifers are the most common
73 group of plants present (González-Ramírez et al., 2013).

74 MATERIAL AND METHODS

75 **Specimen collection and curation.** The members of the paleobotany lab of Instituto
76 de Geología, UNAM, and UNICACH (Universidad de ciencias y artes de Chiapas) obtained
77 fossil samples from El Chango in field expeditions from 2010 to 2014. We focused on
78 sampling the 27–30 and 38–41 meter horizons of the stratigraphic column published by
79 [Moreno-Bedmar et al. \(2014\)](#), which are known to contain many plant fossils. We selected
80 three conifer morphotypes based on their abundance and completeness as the subject of this
81 work. We observed and photographed the specimens using a Zeiss Stemi DV4 and Olympus
82 SZH microscope. When cuticles were preserved, we eliminated the rock matrix using HCl
83 and HNO₃ to isolate the cuticles, following the method developed by [Porrás Carrasco \(2012\)](#).
84 The fossil specimens were deposited in the Colección Nacional de Paleontología at the
85 Instituto de Geología, UNAM.

86 **Phylogenetic analysis.** We performed a phylogenetic analysis based on morphological
87 and molecular data from the three fossil morphotypes, 72 extant species of conifers, and
88 one outgroup (*Ginkgo biloba* L.) to investigate the phylogenetic position of the fossils,
89 and to inform our taxonomic treatment (Appendix 1). The 72 extant taxa represent the
90 morphological and phylogenetic diversity of living conifers, with a particularly dense sampling
91 of Cupressaceae and Podocarpaceae because of the morphological similarity of the fossils
92 with members of these families.

93 **Data matrix assembly.** Our molecular data consist of the plastid *matK* and *rbcL* regions,
94 obtained from Genbank (see accession numbers in the Supplemental Material). We aligned
95 the markers using MAFFT v7.409 ([Katoh et al., 2002](#)), and adjusted the alignment manually
96 with AliView v.1.26 ([Larsson, 2014](#)); ambiguous areas of the alignment were excluded from
97 subsequent analyses. For the *matK* alignment, unambiguous indels were recoded manually

98 following the simple gap recoding approach of [Simmons and Ochoterena \(2000\)](#). For fossil
99 terminals, molecular characters were coded as unknown (“?”).

100 Our morphological data consist of fifty-seven categorical characters and nine continuous
101 characters. We defined the categorical characters and their states based on previous works
102 (e.g., [Hart, 1987](#); [Gadek et al., 2000](#); [Little et al., 2004](#); [Farjon, 2005](#)). Nevertheless, because
103 some of these works focused on single conifer families, we redefined some character states
104 to accommodate comparison among families. A complete list of characters and character
105 states used in this study can be found in the Supplemental Material 2. The nine continuous
106 characters were: (1) length of ovulate strobilus; (2) width of ovulate strobilus; (3) seed length;
107 (4) seed width; (5) length of pollen strobilus; (6) width of pollen strobilus; (7) length of mature
108 leaves; (8) width of mature leaves; and (9) number of ovuliferous complexes (i.e., ovuliferous
109 scale + bract taken as a unit). For each continuous character, we obtained 10 measurements
110 from herbarium samples to estimate the mean and variance in that character for each taxon.
111 For the fossils—especially for the cone characters—we often had to rely on one to three
112 measurements. These continuous data were treated following the methodology proposed by
113 [Goloboff et al. \(2006\)](#), assigning ranges of continuous traits (mean \pm sd) to each terminal.
114 We assigned character states for all the extant species based on examination of herbarium
115 specimens from MEXU (National Herbarium of Mexico) and NYBG (Herbarium of the New
116 York Botanical Garden), and a specialized literature search. The final data matrix is available
117 in two repositories: in Github (https://github.com/ixchelgzlzlzr/coniferas_el_chango
118 and Dryad (XXXX)).

119 **Analyses.** We performed a maximum-parsimony analysis in TNT ([Goloboff et al., 2005](#)).
120 We used 1000 different starting trees and applied “new technology search algorithms” as
121 follows: ratchet (10 repetitions), sectorial search, drift (10 repetitions), and tree fusing
122 (three rounds). We specified all the characters as equally weighted and unordered except for
123 characters 3, 16, 36, and 44, which we treated as ordered because we assume that they evolve

124 in a sequence. We inferred 100 bootstrap trees, also with TNT. We calculated bootstrap
125 support values in R (R Core Team, 2020) using the package phangorn (Schliep et al., 2017).
126 We also edited TNT output in R (Wickham, 2019; Revell, 2012) to obtain a tree in Nexus
127 format, and visualized it in FigTree (Rambaut, 2014). The R script is available in Github
128 (https://github.com/ixchelgzlzlzr/coniferas_el_chango)

129 PHYLOGENETIC RESULTS

130 The *rbcL* and *matK* alignments consisted of 1280 and 1477 positions, respectively. From
131 those, 278 and 713 sites, respectively, were parsimony-informative. We recoded 19 indels, 18
132 of which were parsimony-informative. The total number of parsimony-informative characters
133 in the molecular data set was 1009. The morphological data consisted of 57 discrete and
134 nine continuous characters, all of which were parsimony-informative.

135 When we analyzed the concatenated matrix (molecular + morphological data) for the 75
136 terminals (72 extant species + three fossils) we obtained four equally most-parsimonious trees
137 (MPTs). These trees had a total length of 3962.398 steps, a consistency index (CI) of 44.1%
138 and a retention index (RI) of 78.7% (see Figure 1). The four MPTs differed in the position
139 of *Austrocedurs chilensis* and the position of *Cupressus sempervirens* + *Cupressus funebris*
140 with respect to the *Callitropsis* clade. All four MPTs resolve the currently recognized extant
141 conifer families (i.e., Araucariaceae, Cupressaceae, Pinaceae, Podocarpaceae, Sciadopytiaceae,
142 and Taxaceae) as monophyletic (Figure 1).

143 Despite the ambiguous relationships of some of the extant taxa, the three fossils had
144 the same phylogenetic position in all four MPTs. The bootstrap values of the branches
145 uniting the fossils with their sister groups ranged from 0.30–0.59. These bootstrap values are
146 low for standard molecular phylogenetic inferences, but considering the amount of missing
147 data in the fossils (i.e., the complete lack of molecular information and extensive missing
148 morphological data), we consider the consistent placement of the fossils in the MPTs as

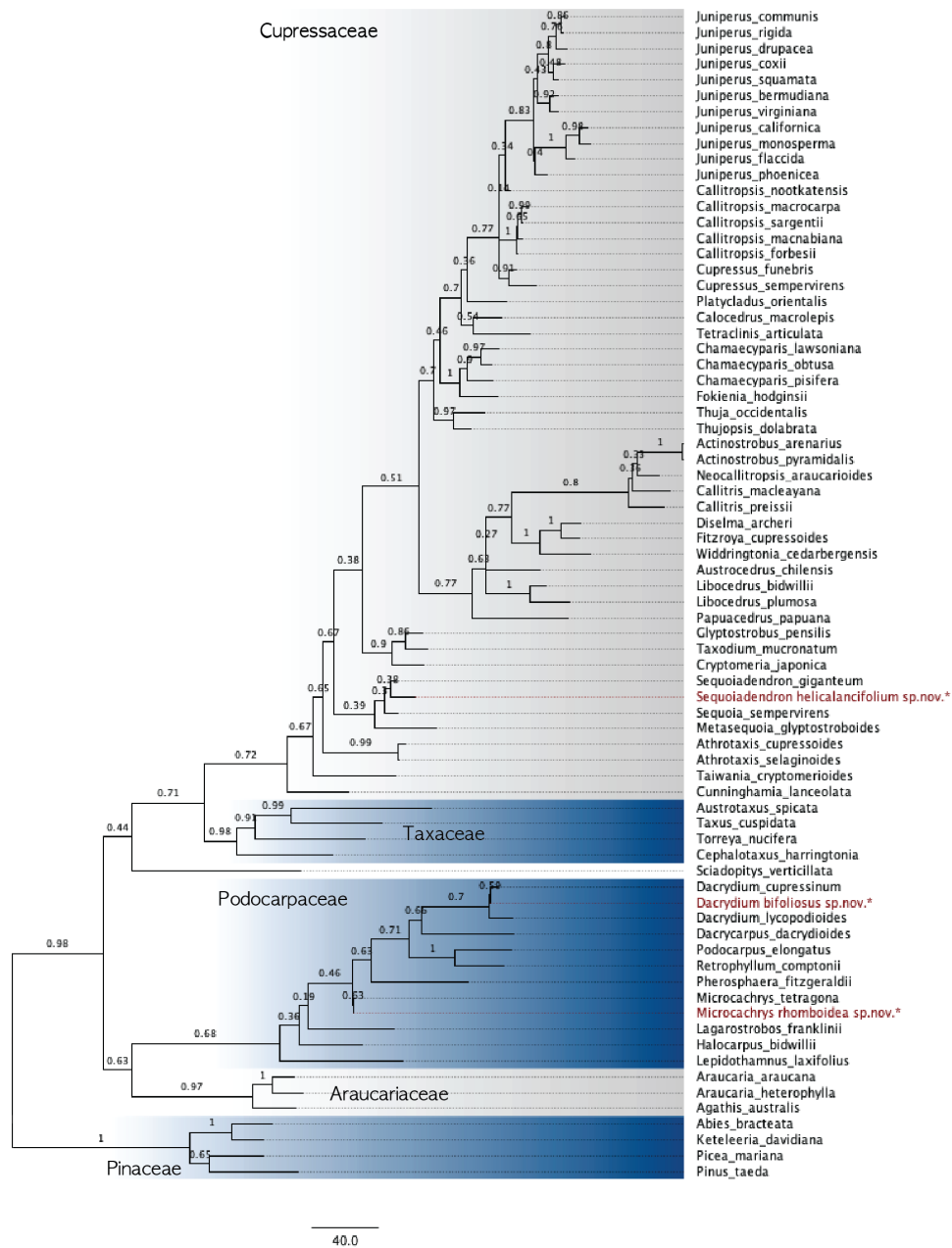


Figure 1: Phylogenetic relationships of 72 extant and three fossil conifers (in red). The relationships were inferred from a parsimony analysis of a combined morphological + molecular dataset. The branch lengths are proportional to the number of steps and the bootstrap values are shown above each branch. The tree was rooted with *Ginkgo biloba*, which was subsequently pruned. The different colors highlight the different families of conifers.

149 strong evidence of their taxonomic affinities, which we describe below.

150 Taxonomic descriptions

151 Kingdom **Plantae** Jussieu (1774)

152 Division **Tracheophyta** Sinnot (1935)

153 Subdivision **Spermatophytina** Cavalier-Smith (1998)

154 Class **Pinopsida** Burnett (1835)

155 Order **Araucariales** Gorozh. (1904)

156 Family **Podocarpaceae** Endl. (1847), nom. cons.

157 Genus *Microcachrys* Hook. f. (1845)

158 Species *Microcachrys rhomboidea* González-Ramírez sp. nov.

159 Holotype: Provisional number M2-007. Figure 2

160 Paratypes: Provisional numbers M2-002, M2-003, M2-006, M2-019, M2-023,

161 **Locality:** México, Chiapas, Municipio de Ocozocuatla, El Chango Quarry (16°34'14"
162 N, 93°16'11" W). Locality number: 3923.

163 **Stratigraphic occurrence and age:** Laminated limestones of the upper section of
164 Cintalapa Formation, Sierra Madre Group (*sensu* [Moreno-Bedmar et al., 2014](#)). Cenomanian,
165 between 100.5 and 97.2 Mya.

166 **Diagnosis:** Scale-like leaves in an opposite criss-crossed arrangement, decurrent and
167 adpressed. Leaves with a distal projection as in *Microcachrys tetragona* (Hook.) Hook. f.
168 Differs from *M. tetragona* in leaves slightly longer and wider. Also, the arrangement and
169 very regular spacing of leaves produce a characteristic pattern (a line of diamonds) on twigs
170 (arrows on figure 2A).

171 **Description:** Ultimate-order branches alternate and regularly spaced along the
172 penultimate-order branches (Figure 2A). Leaves simple, sessile, and in opposite pairs,

173 slightly imbricate and completely appressed to the branches (as opposed to having the leaf
174 fully or partially free). The imbrication and very regular spacing of the leaves produces
175 a rhomboid pattern along the branch that is distinctive of this species (Fig. 2A). Scale-like
176 leaves, as wide as long (~2mm). Leaf apex obtuse with usually a rounded tip. Leaf margins
177 smooth with a continuous distal band—darker than the rest of the fossil—that is interpreted
178 as a cuticle projection (Fig. 2B). This feature is best observed in fully grown leaves, as
179 opposed to the young leaves that occur in the distal part of the branches.

180 Leaves without noticeable variation in shape: no dimorphism between leaves in facial
181 versus lateral position, and no differences in leaves belonging to different branch orders.
182 Resin glands absent. Stomata dispersed and rounded; occlusive cells surrounded by two cycles
183 of irregularly shaped cells, the first cycle of which is usually formed by six cells and the
184 second cycle by nine to 11 cells. Morphology of the stomata is consistent with the cyclocytic
185 type (Porrás Carrasco, 2012). Epidermal cells rectangular, with smooth walls, and arranged
186 in uniform rows. Reproductive structures unknown.

187 **Etymology:** The specific epithet *rhomboidea* refers to the rhomboid pattern that the
188 leaf arrangement produces.

189 **Notes:** We resolve this species as the sister group of *Microcachrys tetragona* (Figure 1,
190 Bootstrap support = 0.53). Furthermore, the characters of the fossils are consistent with the
191 circumscription of the genus *Microcachrys* (Eckenwalder, 2009). However, the reproductive
192 structures of this fossil morphotype are unknown and its placement in *Microcachrys* should
193 be re-evaluated with the discovery of more fossils.

194 Genus *Dacrydium* Lamb. (1807)

195 Species *Dacrydium bifoliosus* González-Ramírez sp. nov.

196 Holotype: Provisional number M1-003. Fig. 3A

197 Paratypes: Provisional numbers M1-001 (Fig. 3B), M1-002 (Fig. 3E), M1-004, M1-005

198 **Locality:** México, Chiapas, Municipio de Ocozocuatla, El Chango Quarry (16°34'14"



Figure 2: *Microcachrys rhomboidea* Provisional number M2-007. A. Branch with leaves. The arrows point to the typical rhomboid like pattern formed by leaf phyllotaxy. B. Magnification of the specimen showed in A (scale bar = 1mm). Arrows point to the cuticle projections on the tip of the leaves that show as darker bands in the fossils. C(20X) and D (40X) show a segment of isolated cuticle. The epidermal cells are rectangular, and the stomata are rounded with two cycles of cells. E. Sample illustrating the regularly spaced branching. The rulers are in millimeters.

199 N, 93°16'11"O). Locality number: 3923.

200 **Stratigraphic occurrence and age:** Laminated limestones of the upper section of the
201 Cintalapa Formation, Sierra Madre Group (*sensu* [Moreno-Bedmar et al., 2014](#)). Cenomanian,
202 between 100.5 and 97.2 Mya.

203 **Specific diagnosis:** Ultimate and penultimate branches similar to *Dacrydium lycopodi-*
204 *oides* Brongn. & Gris. Differs from that species in that leaves of penultimate branches are
205 incurved. Ultimate branches flattened with shorter distal branches, thus creating an arrow-
206 shaped outline to the branching system. Ultimate branches flattened and very regularly
207 spaced.

208 **Description:** Branches and leaves dimorphic. In penultimate and higher order branches,
209 the branching pattern is irregular and occurs in different planes. The leaves of these branches
210 are simple, sessile, awl-like, falcate, usually more than 8mm long, helically attached to the
211 branch (forming an acute angle between the leaf axis and the branch), not imbricate, and
212 slightly adpressed. The base of these leaves is approximately twice as wide as the distal
213 portion; the apex is acute and usually pointy, but sometimes rounded. These leaves have a
214 single central vein, smooth margin, and there is no evidence of resin glands.

215 In ultimate and sometimes penultimate branch orders the branching pattern is almost
216 opposite, regularly spaced, and occurring in a plane. The leaves of these branches are simple,
217 sessile, opposite, regularly spread in a single plane, and slightly adpressed to the branch,
218 forming an acute angle. These leaves are awl-like, non-falcate, usually less than 5 mm long
219 and similar width at the distal and the proximal ends; the apex acute and pointy. These
220 leaves have a single mid-vein, smooth margin, and no evidence of resin glands.

221 Stomata dispersed and ovate. Occlusive cells surrounded by one or two cycles of elongated
222 cells, with typically four cells in the first cycle and between six and eight cells in the second
223 cycle. The morphology of the stomata is consistent with a cyclocytic type. The epidermal
224 cells are rectangular with smooth walls and arranged in regular rows.

225 The reproductive structures of this species are unknown.

226 **Notes:** This fossil species' circumscription was challenging. During the first two years of
227 fieldwork, we collected only fragmented specimens, and from this material we distinguished
228 two forms (Figure 3B and E). The two forms were most clearly distinct in their branch
229 arrangement (in one plane and shortening towards the tip, forming an arrow versus irregular
230 and three-dimensionally branching) and leaf shape (linear versus falcate). In subsequent
231 years it became clear that this original distinction was blurry as we found fossils with
232 intermediate traits, and ultimately we discovered individual fossils (Figure 3) that showed
233 both types of branches. The last piece of evidence that the two forms represented the same
234 species came from the cuticles: both types of branches have the same cuticular traits (Figure
235 3C and D). The phenomenon of leaf- and branch-dimorphism is common in conifers and is
236 associated with the age, season, and reproductive status of the branches (Hernandez, 2006;
237 Farjon, 2010; Eckenwalder, 2009). The placement of this fossil in the Podocarpaceae is based
238 on the phylogenetic analysis (Figure 1), where this fossil was resolved within *Dacrydium*
239 based on the the uniform length of the branching pattern (character 6) and the epidermal
240 cell arrangement (character 24) and as the sister group of *Dacrydium cupressinum* Sol. ex G.
241 Forst. based on leaf shape (character 10). Furthermore, the known traits of this morphotype
242 are consistent with the traits of the members of *Dacrydium*, and the extant species of
243 this genus present leaf and branch differentiation similar to that observed in the fossils
244 (Eckenwalder, 2009). While we resolve this species within Podocarpaceae, it is important to
245 recognize that it is also similar to species in Cupressaceae, such as *Cryptomeria japonica*
246 (Thunb. ex L. f.) D. Don and *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch. Once
247 again, it is important to continue fieldwork in this locality, as finding reproductive structures
248 associated with this morphotype would provide decisive evidence to support or reject its
249 current placement.

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Order **Cupressales** Link (1829)

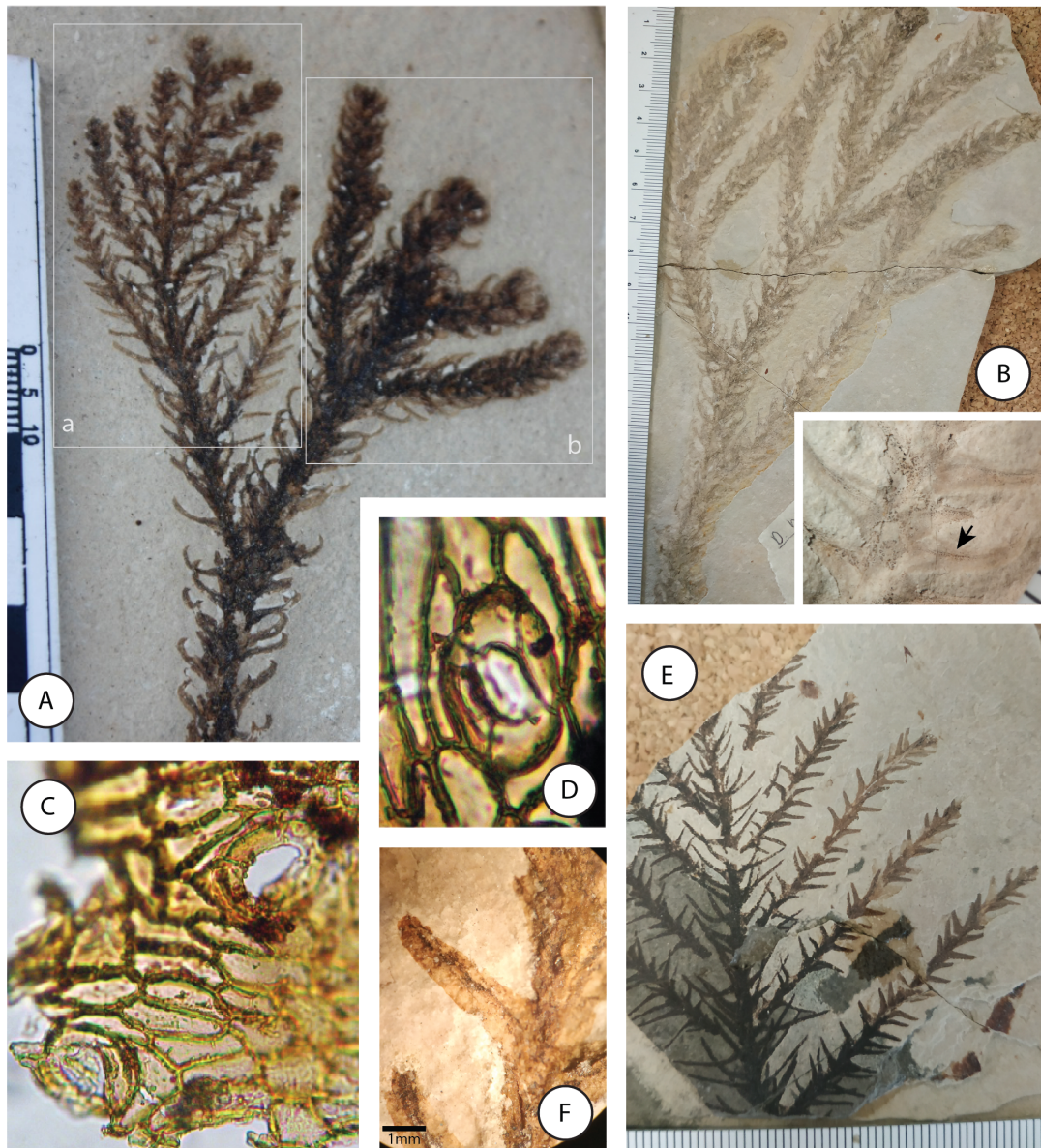


Figure 3: *Dacrydium bifoliosus*. A. Provisional number: M1-003. Fossil showing the two different branch morphologies (a and b) in organic connection. B. Provisional number: M1-001. Shoot morphology “b”, the most common among the fossils of this locality, with a zoom image where the mid-vein can be observed (arrow). C and D illustrate the cuticles of this morphotype at 20X and 40X respectively. E and F (provisional number: M1-002) show the shoot morphology “a” where branches are regularly arranged in a single axis and leaves are straight.

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Family **Cupressaceae** Gray (1822)

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Genus **Sequoiadendron** J. T. Buchholz, nom. cons. (1939)

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Species ***Sequoiadendron helicalancifolium*** González-Ramírez sp. nov.

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Holotype: Provisional number M3-001 Fig. 4D and Fig. 4E

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Paratypes: Provisional numbers M3-002 (Fig. 4A), M3-003 (Fig. 4B), M3-004 (Fig. 4C),

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Locality: México, Chiapas, Municipio de Ocozocuatla, El Chango Quarry (16°34'14" N, 93°16'11" O). Locality number: 3923.

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Stratigraphic occurrence and age: Laminated limestones of the upper section of the Cintalapa Formation, Sierra Madre Group (*sensu* [Moreno-Bedmar et al. \(2014\)](#)). Cenomanian, between 100.5 and 97.2 Mya.

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Description: The phyllotaxy and dichotomous branch arrangement is similar across the different branch orders (i.e., no branch dimorphism was observed). Leaves simple and sessile, with helicoidal arrangement. Leaves imbricate (covering up to a half of the supra-adjacent leaves), and adpressed approximately half the length of the leaf, but with free tips. Leaves awl-like, longer (mean = 8.2 mm) than wide (mean = 1.6 mm). The apex of the leaves is acute and angular. Leaf margin entire. Resin glands absent. Cuticle-associated traits unknown. Ovulate cone terminal in a lateral branch, globose, dehiscent, 16.9 mm long and 14.5 mm wide (cone measurements from one specimen). No clear differentiation between bract and scale, thus each appendage is referred to as ovulate complex. Ovulate complex

277 peltate, 16–19 in number, helically arranged on a central axis; the axis of each ovulate
278 complex widens towards the distal part.

279 **Etymology** The specific epithet describes the shape of the leaves—awl-like and helically
280 arranged—which is one of the most characteristic traits of this species.

281 **Notes.** The leaves of this fossil have a shape, arrangement, and position similar to
282 *Sequoiadendron giganteum* and they differ in that the fossil leaves are slightly longer and
283 more imbricate. The ovulate cone of *S. helicalancifolium* is similar to the ovulate cone of
284 extant Cupressaceae species in that it has peltate ovuliferous complexes. In particular, it is
285 similar to the extant *Athrotaxis*, *Fokienia*, *Sequoia*, and *Sequoiadendron*. The distal shield
286 of the ovuliferous complex of the fossil is square to rectangular, consistent with *Sequoia*
287 and *Sequoiadendron*. The phylogenetic analysis supports a relationship between the fossil
288 and the sequoioid conifer clade, placing it as the sister group of *Sequoiadendron giganteum*.
289 Given this phylogenetic evidence and the morphological congruence, we name this fossil as a
290 new species of the genus *Sequoiadendron*.

291 DISCUSSION

292 **Implications of the fossil affinities.** The three fossils described in this paper closely
293 resemble extant groups of conifers, supporting our current understanding that the traits that
294 distinguish the modern conifers—as opposed to the Paleozoic Voltzian conifers—evolved
295 early in the Mesozoic ([Taylor et al., 2009](#)). Furthermore, our findings support the current
296 classification of conifers in two orders: Voltziales—including the Paleozoic conifers—and
297 Coniferales—including the Mesozoic and Cenozoic species ([Taylor et al., 2009](#)). Similarly,
298 the fact that the three fossil conifers included in this analysis are sister groups of different
299 extant clades demonstrates that at least some modern genera were clearly differentiated by
300 the Cenomanian. Indeed, other authors (e.g., [Leslie et al., 2012](#)) have suggested that the
301 evolution of conifer genera was driven by the break up of Pangaea that occurred ca. 60My

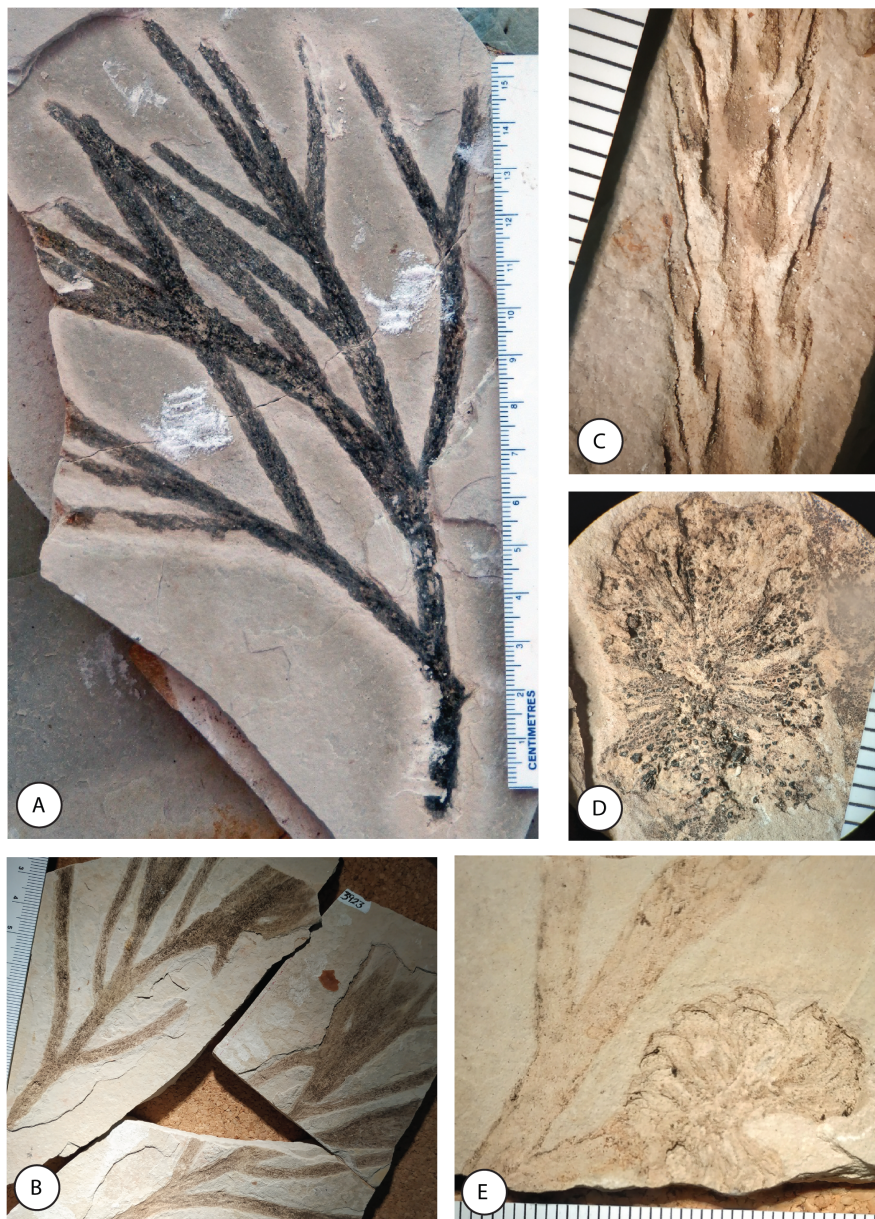


Figure 4: *Sequoiadendron helicalancifolium*. A (provisional number M3-002) and B (provisional number M3-003). Foliage with dichotomous branching. C. Close-up to the awl-like leaves (provisional number M3-004). D. Ovuliferous cone where the peltate ovuliferous complexes can be observed (provisional number M3-001). E. Ovuliferous cones in organic connection with the foliage (provisional number M3-001).

302 before the Cenomanian, in the Jurassic.

303 The co-occurrence of the three lineages of conifers we describe for El Chango might seem
304 surprising at a first glance, given that extant members of *Microcachrys* and *Dacrydium*
305 occur mainly on islands like New Caledonia, New Zealand, Borneo, and Tasmania, while
306 *Sequoiadendron* is restricted to the Sierra Nevada range in California. Nevertheless, there
307 is substantial evidence that both sequoioid and podocarpoid conifers were much more
308 widespread in the past. In particular, our discovery of *M. rhomboidea* constitutes the oldest
309 macrofossil of *Microcachrys* and fills a gap on the macrofossil record of a lineage that has an
310 broad pollen record that extends geographically to the Cenozoic of Alaska ([Reinink-Smith
311 and Leopold, 2005](#)) and temporally to the Jurassic ([Truswell and Macphail, 2009](#)), but for
312 which the oldest previously reported macrofossil was from the Cenozoic ([Carpenter et al.,
313 2011](#)). Our results are also congruent with divergence-time estimates that place the origin
314 of *Microcachrys* in the Mesozoic ([Turner and Cernusak, 2011](#)).

315 **El Chango flora in a global context.** Our current understanding is that the late
316 Cretaceous (Cenomanian to Masstrichtian) was the period of Earth history when angiosperms
317 became the dominant group of terrestrial vegetation. Therefore, it is particularly important
318 to study Cenomanian floras to understand the tempo, mode, and specific drivers of this
319 global transition. One outstanding pattern of the fossil assemblage found in El Chango is
320 that conifers outnumber angiosperms by approximately five-to-one. Determining whether
321 this pattern is the result of taphonomic bias would require a detailed taphonomic study,
322 but it seems safe to conclude that conifers were an important—if not dominant—element
323 of the canopies of El Chango. This abundance of conifers contrasts with other reported
324 Cenomanian floras—for example in Argentina ([Iglesias et al., 2007](#)), Utah ([Rushforth, 1971](#)),
325 and Russia [Moiseeva \(2010\)](#)—where angiosperms were the dominant group.

326 Nevertheless, our findings are consistent with the idea that the “rise” of angiosperms
327 was geographically structured, a pattern that [Coiffard et al. \(2006, 2012\)](#) observed in mid-

328 Cretaceous European fossil assemblages where gymnosperms dominated coastal environments
329 while angiosperms were prominent in freshwater environments. Our interpretation of
330 El Chango as a conifer-dominated coastal forest with potentially swampy species like
331 *Microcachrys rhomboidea* supports the idea of conifers remaining dominant in coastal
332 ecosystems during the Cenomanian.

333 **A glimpse of the Cenomanian forests of El Chango.** Although we will never have
334 a full picture of the El Chango ecosystem, our studies provide some insights about the
335 organisms that lived there and the environmental conditions they likely experienced (Fig. 5
336 is a reconstruction of the terrestrial landscape associated with the El Chango deposits). First,
337 the co-occurrence of marine and terrestrial fossils is strong evidence that the fossil community
338 of El Chango constitutes a death assemblage, a “tanatocenosis” (i.e., at least some of the
339 organisms were transported before deposition and fossilization). The type of sediments is
340 consistent with a coastal lagoon environment ([Alvarado-Ortega and Than-Marchese, 2013,](#)
341 [2012; Alvarado-Ortega et al., 2009](#)) and the degree of completeness and the abundance of
342 the plant fossils suggest that the plant remains were transported from a nearby location by
343 moderately calm waters. So, the plants that we find in El Chango probably lived near their
344 deposition site in a coastal forest.

345 We know, based on estimates from oxygen isotopes, that the surface-temperature of the
346 ocean adjacent to Chiapas during the Cenomanian was warmer than today—around 31 to
347 36°C ([Clarke and Jenkyns, 1999; Laugié et al., 2020](#)), likely because this region was in the
348 path of warm water currents incoming from the Equatorial Atlantic Ocean ([Laugié et al.,](#)
349 [2020](#))—so the El Chango forest probably grew in an environment with mild temperatures.
350 The living relatives of the fossils—e.g., *Sequoia sempervirens*, *Sequoiadendron giganteum*,
351 *Dacrydium dacrydioides*, and *Microcachrys tetragona*—are tolerant of a wide range of
352 temperatures but dependent on moist environments. Therefore, the physical environment of
353 this coastal forest was likely mild and humid, perhaps even swampy.



Figure 5: Reconstruction of El Chango site in the Cenomanian. *Sequoiadendron helicocalanctifolium* sp. nov. (top left) is represented as a tall tree similar to extant redwoods and sequoias. A close-up of its foliage can be seen in the fallen branch on the bottom left. *Dacrydium bifoliosus* sp. nov. appears as a shorter tree (middle right). And *Microcachrys rhomboidea* sp. nov. is illustrated as a small shrub (central part of the image) and a close-up of its branches is on the bottom right. The plants live in a coastal environment associated with a lagoon. Drawing by Aldo Dominguez.

354 The specific community where the fossils found in El Chango quarry lived was probably
355 a mixed forest where *Sequoiadendron helicalancifolium* dominated the highest canopy strata,
356 in the same way *Sequoiadendron giganteum* and *Sequoia sempervirens* do today in California.
357 We can visualize *Microcachrys rhomboidea* as a shorter plant—perhaps even a shrub similar
358 to the extant *Microcachrys tetragona*—associated with swampy areas, in the same way
359 *Microcachrys novae-zelandiae* R.J.Carp., G.J.Jord., Mildenh. & D.E.Lee did in the Oligo-
360 Miocene (Carpenter et al., 2011). *Dacrydium bifoliosus* probably occupied an intermediate
361 stratum in the forest, and all three conifers coexisted with angiosperms, likely in the form of
362 shrubs.

363 CONCLUSIONS

364 Every study of new fossil assemblages offers a unique opportunity to visit the past. The
365 co-occurrence of *Sequoiadendron helicalancifolium*, *Dacrydium bifoliosus*, and *Microcachrys*
366 *rhomboidea* during the Cretaceous in the area that today is Chiapas, Mexico is a valuable
367 insight from the southernmost North American Cretaceous ecosystems. The discovery
368 of these fossils in El Chango adds to the fossil record of podocarpaceous and sequoioid
369 conifers. In particular, *Microcachrys rhomboidea* is the oldest macrofossil of *Microcachrys*,
370 filling in the expectation of finding this lineage in the Mesozoic based on the pollen-record.
371 Finally, according to our interpretation, El Chango was a humid coastal conifer-dominated
372 forest, supporting the hypothesis of a geographically and ecologically structured “rise of
373 angiosperms” at the end of the Cretaceous, with conifers remaining dominant in coastal
374 environments while angiosperms became dominant in freshwater-associated ecosystems. El
375 Chango has proven to be a quarry with outstanding preservation quality. Given the relevance
376 of the geographic and temporal location of this quarry, more paleontological and geological
377 work here—in particular the study of the angiosperm assemblage, taphonomic studies, and
378 fine-scale geology—will have a great impact in our understanding of the evolution of plant

379 lineages and terrestrial ecosystems.

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398 **Author Contributions**

399 IGR curated the fossils, assembled the data matrices, conducted the phylogenetic analyses
400 and wrote the first draft of the manuscript. SRSCF conceived the project, supported the
401 fieldwork through his research grant, and reviewed the manuscript. CJR contributed to

402 manuscript writing.

403 **Data availability statement**

404 All the data and supplemental materials associated with this research are available in the

405 GitHub repository: https://github.com/ixchelgzlzlzr/coniferas_el_chango And the

406 Dryad repository **XXXXXX** (It will be updated once the manuscript is accepted).

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