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A NEW SPECIES OF *SCORESBYA* HARRIS AND *SONORAPHYLLUM* GEN. NOV. (PLANTAE *INCERTAE SEDIS*) FROM THE LATE TRIASSIC OF SONORA, MEXICO

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RESUMEN

Se describe a *Scoresbya dentata* Harris, *Scoresbya pinnata* sp. nov. y *Sonoraphyllum mirabile* gen. et sp. nov. de la Formación Santa Clara, Grupo Barranca, Cárnico (¿y/o Nórico?) de Sonora centro-sudoriental, en el noroeste de México. La diagnosis genérica original de *Scoresbya*, basada en *Sc. dentata*, se modificó a consecuencia del descubrimiento de *Sc. integrifolia* Meng Fan-son y *Sc. pinnata*, cuyas hojas tienen segmentos y lóbulos con márgenes enteros o láminas pinadas, respectivamente. Se descarta una asignación provisional previa de *Scoresbya* a las Dipteridaceae. *Sonoraphyllum* es un género de hojas caracterizado por una arquitectura foliar en extremo peculiar. El fragmento disponible, sin importar si se trata de una hoja completa o de un segmento, es profundamente laciniado. Su venación está constituida por una costa media fuerte y por venas secundarias bifurcadas una vez en la base de los lóbulos; las ramas resultantes entran independientemente a lóbulos diferentes, contiguos. Por consiguiente, cada lóbulo tiene dos venas principales subparalelas. Su venación terciaria es reticulada. Se considera que los dos géneros pertezcan probablemente a las pteridospermas, y que formaran parte de las comunidades alejadas de los canales de drenaje, en el marco paleoambiental de planicie de inundación fluvial de la Formación Santa Clara.

Palabras clave: Fósil, plantas vasculares, *incertae sedis*, taxa nuevos, Triásico Tardío, Sonora, México.

ABSTRACT

Scoresbya dentata Harris, *Scoresbya pinnata* sp. nov. and *Sonoraphyllum mirabile* gen. et sp. nov. are described from the Carnian (and/or Norian?) Santa Clara Formation, Barranca Group, southeastern central Sonora, northwestern Mexico. The original generic diagnosis of *Scoresbya*, based on *Sc. dentata*, is modified due to the recent discovery of *Sc. integrifolia* Meng Fan-son and *Sc. pinnata*, whose leaves have entire-margined or pinnate segments and lobes, respectively. An earlier tentative assignment of *Scoresbya* to the Dipteridaceae is discarded. *Sonoraphyllum* is a foliar genus showing an extremely unusual leaf architecture. The only known specimen, regardless of whether it is a whole leaf or a fragment, is deeply laciniate. Its venation is composed of a stout midrib and pinnately arranged secondary veins forking once at the bases of the lobes; the resulting arms enter independently into different neighbouring lobes. Each lobe, consequently, has two subparallel main veins. Its tertiary venation is reticulate. Both genera are probably related to the pteridosperms and formed part of the channel-far communities within the flood-plain paleoenvironment of the Santa Clara Formation.

Key-words: Fossil, vascular plants, *incertae sedis*, new taxa, Late Triassic, Sonora, Mexico.

INTRODUCTION

In the last 20 years, many fossil plants were collected by the present author, together with students, from the Late Triassic Carnian (and/or Norian?) Santa Clara Formation which outcrops in Sonora, northwestern Mexico (Weber, 1985). The bulk of the approximately 70 species belongs to groups that are widespread over Late Triassic floras, such as Equisetales, Marattiales, Matoniaceae, Cycadales, Bennettitales, Ginkgoales and Coniferales. There remains, however, a number of genera and species, which are unexpected from either a stratigraphic or phytogeographic point of view, or puzzling by their unusual morphological features.

Several Late Triassic and Early Jurassic floras from North America and abroad contain leaf genera *incertae sedis* which some authors have taken as more or less attractive candidates as angiosperm precursors. For example, *Marcouia neuropteroides* from the Late Triassic of the southwestern USA (Ash, 1972) is compared by Krassilov (1977) with *Scoresbya* from the earliest Jurassic of Greenland (Harris, 1932), *Imania* from the Late Triassic of Siberia (Krassilov and Schorochova, 1970) and *Sujfunophyllum* from the Late Cretaceous of Siberia (Krassilov, 1967). In addition, *Scoresbya dentata* is compared by Knobloch (1978b) with *Halyserites* from the Cenomanian of Bohemia (Sternberg, 1833). This genus is considered by Knobloch congeneric with *Fontainea* originally described from the Late Cretaceous of New Jersey, USA (Newberry, 1895) which, in turn, seems to be congeneric with *Manihotites* from the Late Cretaceous of Georgia, USA (Berry, 1910). The latter genera are accepted by most paleobotanists as *bona fide* angiosperms.

The plants described in this paper belong to the kind considered in the quoted comparisons. The discovery of new localities bearing material of these plants is considered important because of their potential value for the evolutionary history of the angiosperms. The present taxonomic study of two species of *Scoresbya* improves the systematics of the genus and corroborates its Late Triassic-Early Jurassic range and its cosmopolitan distribution. With *Sonoraphyllum*, a new type of leaf architecture is presented.

The geographical and geological setting of the Santa Clara flora has been outlined previously by Silva-Pineda

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(1961), Weber (1980), Weber and coworkers (1980b) and Weber (1985). Later, important work on the geology of the Santa Clara Formation has been done by Potter and Cojan (1985) and by Stewart and Roldán-Quintana (1991). The present author's latter paper (Weber, 1985) contains the most comprehensive report of the research work done by him and students on this diverse Late Triassic flora and a complete list of the sampled localities, with their numbers in the catalog of paleontological localities of the Instituto de Geología, Universidad Nacional Autónoma de México (CLP-IG-UNAM). The provenience of the material studied here will be mentioned in the descriptive chapters and figure captions. In addition, location maps with locality numbers are published in the paper on *Laurozamites* (Weber and Zamudio-Varela, 1995), elsewhere in this issue.

The plant remains are preserved mostly as impressions in a siltstone or fine-grained sandstone which was heated in a varying degree at different localities by several intrusive events. The organic matter of the large plant remains, if present, is badly damaged, according with the anthracite or graphite rank of the coal beds occurring in the Santa Clara Formation. Fine structural detail is generally not preserved in the fossils, but occasionally some of the larger cells can be observed in the impressions. No palynomorphs have been recovered as yet.

The preparation of the leaves was done with a percussive engraving tool "AIR-Scribe" of Chicago Pneumatic. This tool leaves very visible scars especially on dark sand and siltstone specimens. The scars were not retouched on the photographs. Some of the specimens were photographed under xylene.

All figured specimens are in the type collection of the Paleontological Museum, Instituto de Geología, Universidad Nacional Autónoma de México.

SYSTEMATIC PALEOBOTANY

Genus *Scoresbya* Harris 1932

Emended diagnosis—Only leaves known. Leaf compound, orbiculate to reniform in general shape. Petiole long, dorsally attached to the flat funnel-shaped blade. Blade divided by two or three dichotomies of the petiole at the base of the lamina into four to six palmately diverging, unequal segments. Medium sized and large segments often divided by one or two dichotomies into several lobes, then obtriangular. Basiscopic segments generally not forked and lanceolate to elliptical in shape. Forked segments splitting down to the forking points of the main veins. Lamina not developed from this point to a short distance upwards. Fork of the main veins marginal at this point. Lamina of the segments entire, coarsely dentate or pinnate. Segments provided with slender midrib bifurcated once or twice in the forked segments. Secondary venation delicate, constituted by a loosely reticulate network of essentially parallel, dichotomizing and anastomosing veinlets of only one order. Meshes elongated. Leaves medium sized, probably not exceeding 30 cm in width. Simple segments and terminal lobes of the forked ones not exceeding 5 cm in width.

Type species—*Scoresbya dentata* Harris 1932: The fossil flora of Scoresby Sound; Part 2, Seed plants *incertae sedis*. Meddelelser om Groenland 85 (3), p. 38-39, text-fig. 22, pl. II, figs. 7-9, III, fig. 1.

Scoresbya dentata Harris 1932

Previous records

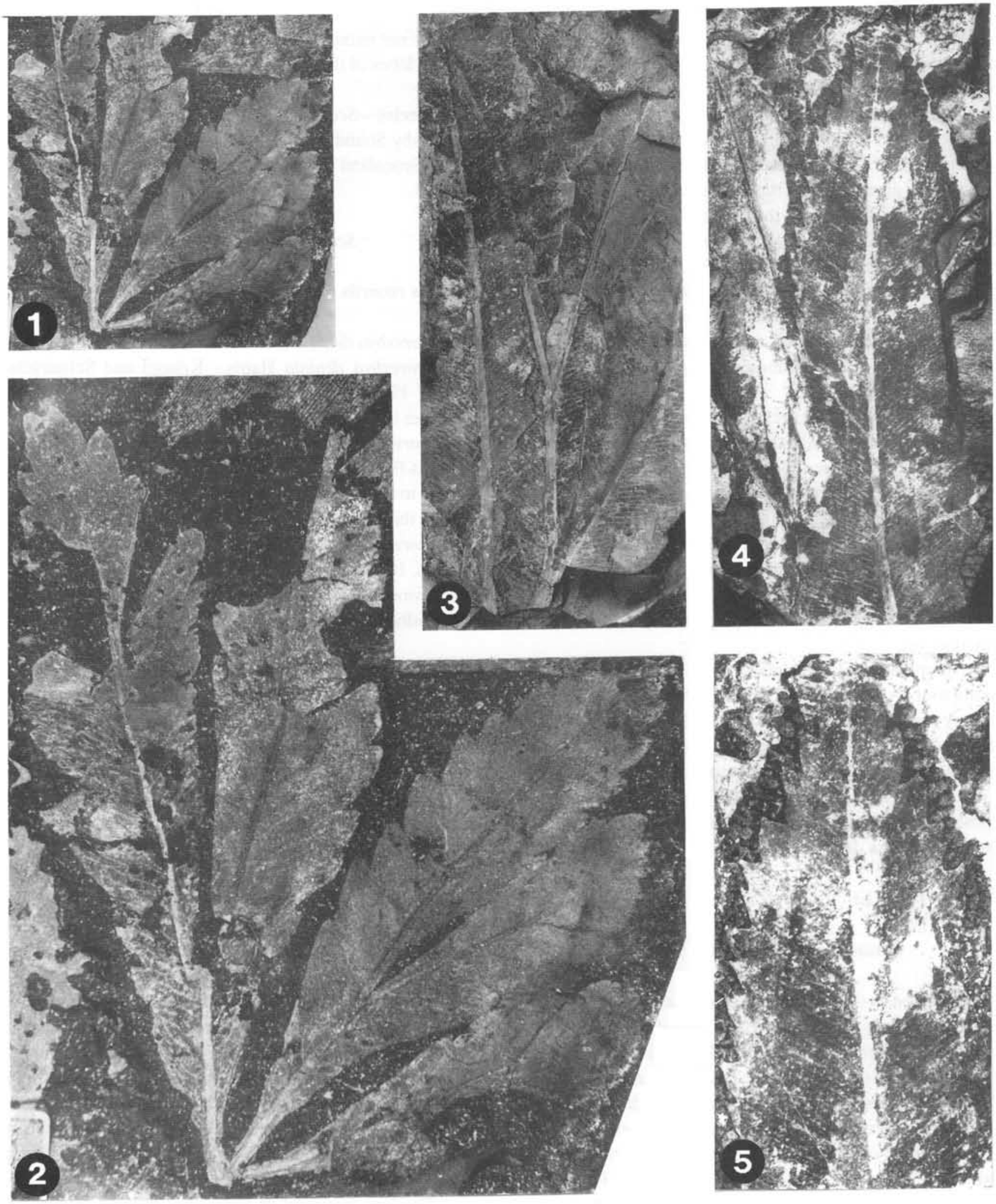
1932 *Scoresbya dentata* Harris.- See above.
1968 *Scoresbya dentata* Harris.- Kräusel and Schaarschmidt, 1968, p. 124-128, text-figs. 1-9, pl. XXVI (in that paper, two references in addition to Harris, 1932, are given).
1982 *Scoresbya dentata* Harris.- Cao Zheng-yao, 1982, p. 344-345, text-fig. 1, pl. I, figs. 1, 2, 2a (two earlier references in addition to those quoted by Kräusel and Schaarschmidt, 1968, are given in this paper).
1983 *Scoresbya dentata* Harris.- Zhou Zhiyan, 1983, p. 20, pl. VII, figs. 10, 11.
1985 *Scoresbya dentata* Harris.- Weber, 1985, p. 120, fig. 6, a (not validly published).

Diagnosis—*Scoresbya* with coarsely dentate leaf segments, lacking submarginal veins (in addition: see Harris, 1932).

Material—Only two specimens of *Scoresbya dentata* were found in the Santa Clara Formation. The first one (Figures 1 and 2) was picked up from a roadside talus near the El Crucero locality, San Enrique area (loc. 537 CLP-IG-UNAM). The slab shows half a leaf and a number of minor fragments which have broken away from the figured part. The second one is preserved as part (Figure 3) and counterpart (Figures 4 and 5). It comes from the outcrop of El Crucero Bed B (loc. 537B CLP-IG-UNAM).

Description—Due to the "fossil" shape and architecture of this leaf type, the traditional angiosperm-centered descriptive terminology is not used here with its rigorous morphological connotations. To facilitate the understanding of the following paragraphs and the diagnosis, the meaning of some terms is shown in Figure 6. The leaves are compound. The reconstructed leaf—of *Scoresbya pinnata*—shows six free segments, which are attached distally to the petiole. Some of them are dichotomized, giving rise to two—or more—lobes.

The first fragment of *Scoresbya dentata* (Figures 1 and 2) probably represents an almost complete half of a comparatively small leaf blade which, symmetrically reconstituted, measures about 7 cm in length and 11 cm—inferred—in total width. The blade is "palmately" dichotomized into an even number of segments. In the present fragment, three unequal segments are preserved, and the author assumes that the largest one, at the left side in the pictures (Figures 1 and 2) which is



Figures 1-5.- *Scoresbya dentata* Harris. Figures 1 and 2, specimen IGM-PB-537-564 (photographed under xylene). Figures 3-5, specimens IGM-PB-537A-691a and -691b. Locality: San Enrique (Los Pilares) sampling area, Loc. El Crucero (537 and 537A CLP-IG-UNAM). Further explanation see text. 1, 3 and 4, x 1; 2 and 5, x 2.

nearly symmetrically divided at a distance of 2 cm from its base, stood next to the longitudinal midline of the leaf. The following segment forks at the same distance but is strongly asymmetrical. The outermost segment is much smaller than the others and does not fork. Each segment has a short, slightly winged stalklet—petiolule—of about 3 to 5 mm in length,

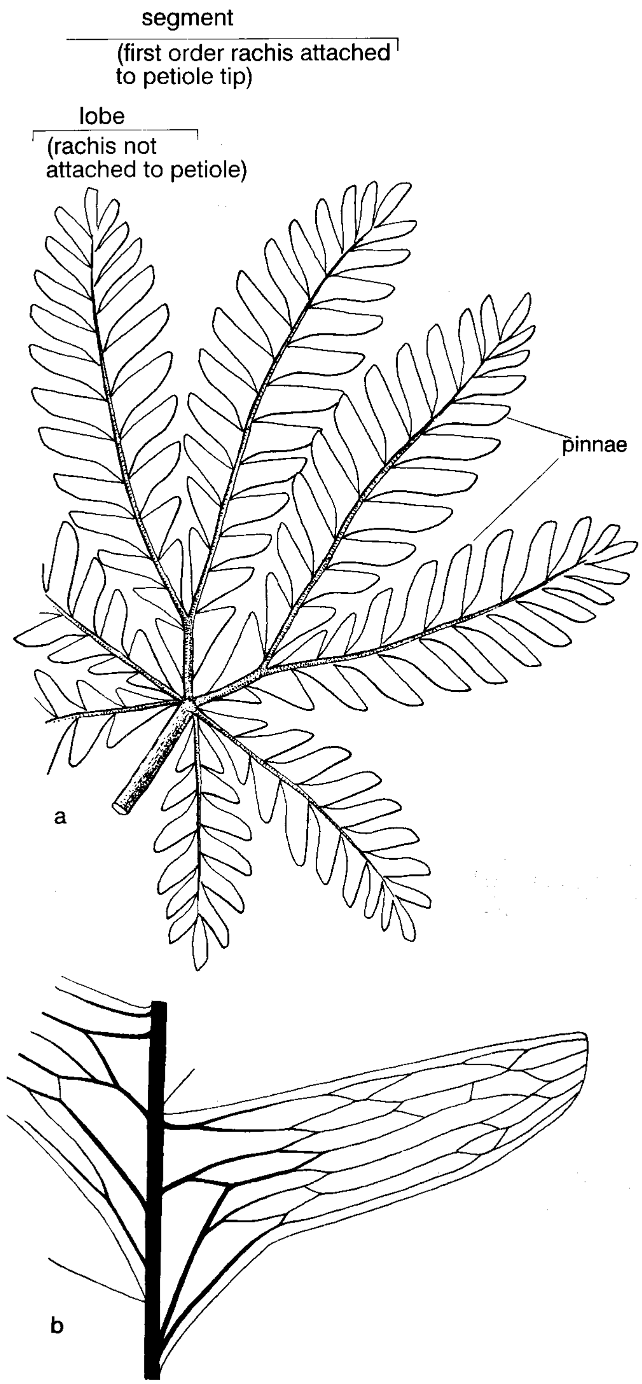


Figure 6.- *Scoresbya pinnata* sp. nov. *a*, Reconstruction of leaf shown in Figures 7-9, with explanation of the terms segment, lobe and pinna, as used in this paper; *b*, detail of venation (compare Figures 12 and 13).

which grades into the cuneate base of the segment blade. The blade of the undivided segment is oblanceolate, the lower margin being concealed. In the forked segments, which are narrowly obtriangular in shape, the blade is divided into two more or less unequal lobes, which are very asymmetrical at their base. Distal to the dichotomies, the lobes of the segments are strongly asymmetrical and separate down to the bifurcation points of the main veins. The two lobes tend to touch or overlap in their middle part, and leave a space near the bifurcation point. The blade margin is entire near the bases of the segments and in the proximal part of the terminal notch, if present. The remaining margins are coarsely toothed. The primary teeth are rounded to acute and may occasionally show very small secondary teeth or crenulation.

The main venation of the whole blade follows the pattern of repetitive dichotomies described for the segments. All the midribs of the segments are considered here as first order venation. In the segment bases, the midribs reach about 0.7 mm in width. This measurement remains constant in the forked segments up to the midrib bifurcation. No midrib is preserved in the most distal parts of the segments. The secondary venation is not differentiated into more than one veinlet order. No submarginal vein can be observed in the available specimens.

The second leaf (Figures 3-5) is badly fragmented. Figure 3 shows two segments, probably belonging to one leaf, although the connection of the segments at the blade base is not preserved. The right hand segment shows two dichotomies, the left one none. In the counterpart (Figures 4 and 5), the lobe margin of the unforked segment was prepared. It is coarsely serrate. The teeth are very clearly visible in Figure 5 (x 2). The notches between the teeth are sometimes rounded, but more commonly acute. The basiscopic margin of the teeth is normally curved and the tip is acute to rounded acuminate.

Comparison—The described leaf fragments resemble very closely the type material reported by Harris (1932), and cannot be considered specifically different.

Scoresbya pinnata Weber sp.

Previous record

1985 *Scoresbya pinnata* n. sp.- Weber, 1985, p. 120, fig. 6, b (not validly published).

Diagnosis—*Scoresbya* with pinnate segments and lobes.

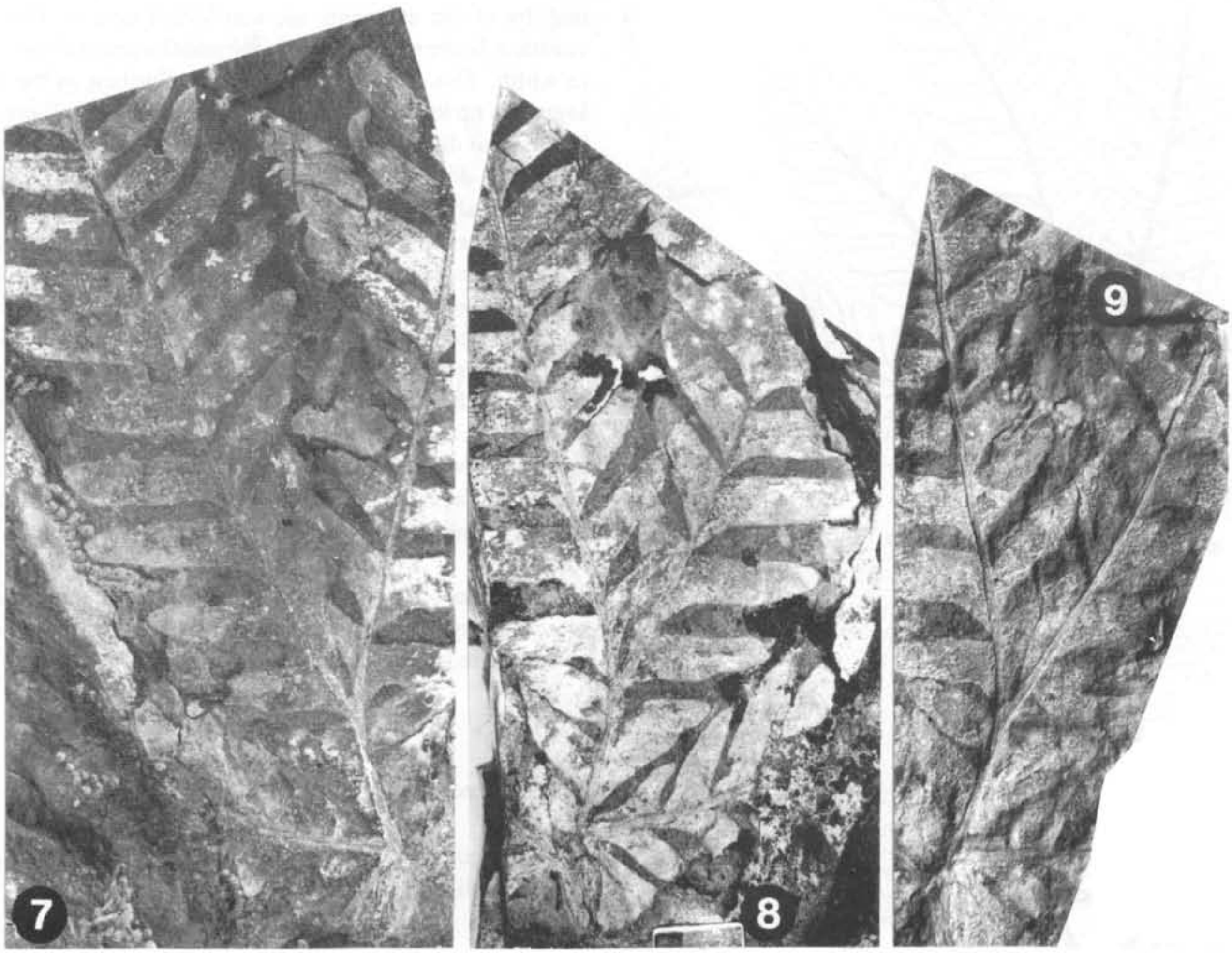
Holotype—Specimen IGM-PB-537B-565 a, b (Figure 7, part, and Figures 8 and 9, counterpart).

Type locality—El Crucero locality, Bed B, San Enrique area (loc. number 537B: CLP-IG-UNAM).

Type stratum and age—Santa Clara Formation, Barranca Group, Carnian (and/or Norian?), Sonora, Mexico.

Derivation of name—*Pinnatus* (lat.): pinnate.

Material—About 10 identifiable and some doubtful specimens of this species were found at four localities of the Santa Clara Formation. One single specimen (Figure 10), unsuitable for identification, was first uncovered in a roadside talus of the type section of the formation, La Barranca locality, La Barranca-Santa

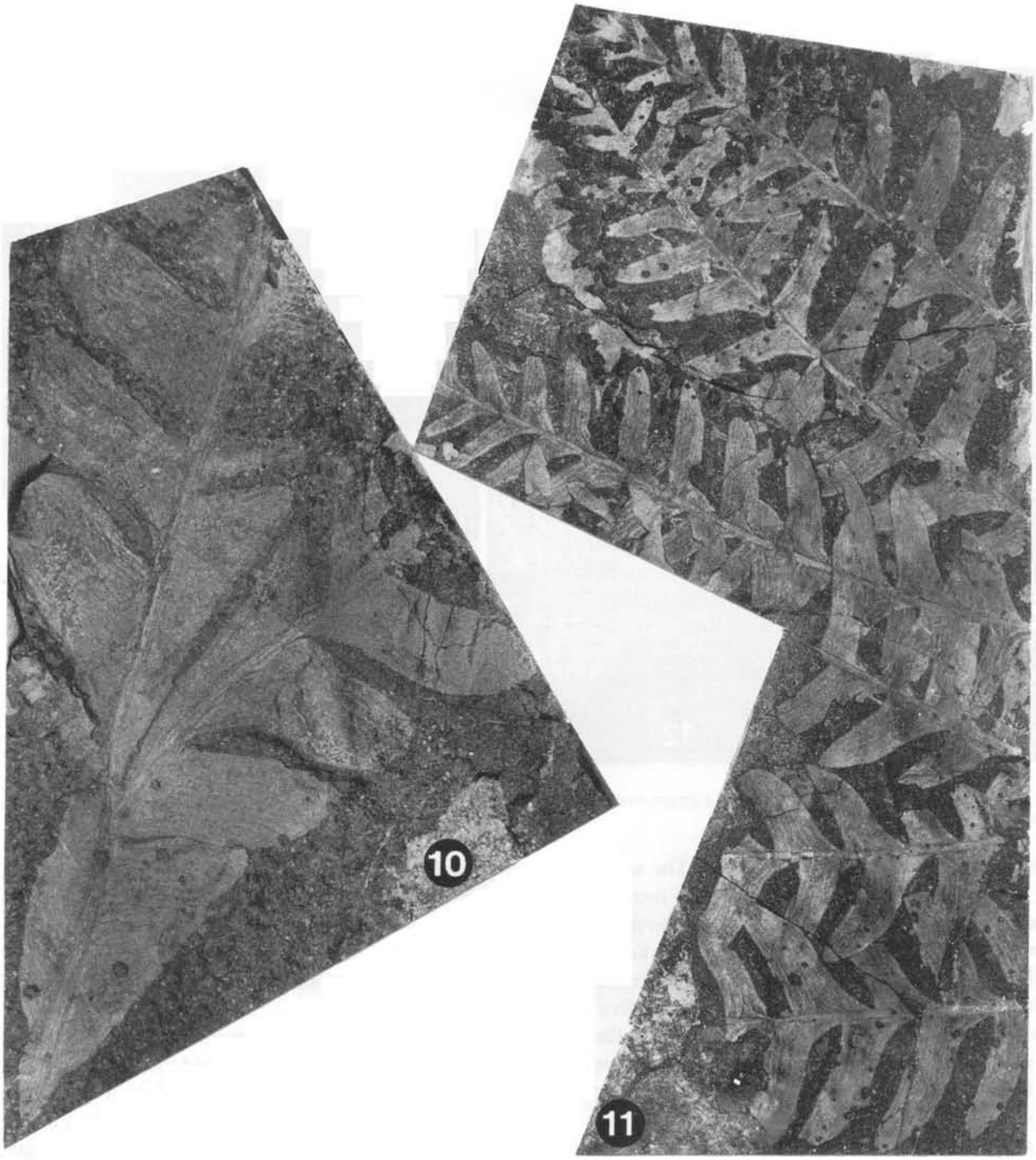


Figures 7-9.- *Scoresbya pinnata* sp. nov. Type specimen, part and counterpart. IGM-PB-537B-565a, b (8 photographed under xylene). Locality: San Enrique (Los Pilares) sampling area, Loc. El Crucero Bed B (537B CLP-IG-UNAM). Further explanation see text.

Clara area (locality number 515 CLP-IG-UNAM). The species was later collected and identified at the Parajitos and El Crucero localities, San Enrique area (localities 518A and 537B CLP-IG-UNAM). Recently, an additional fragment was found at the Mayo locality, San Javier area (locality 533 CLP-IG-UNAM). The best remains were collected at the El Crucero locality (Figures 7-9, 11-13).

Description—The principal diagnostic characters of the genus can be observed in the type specimen (Figures 7-9). Only a short length of about 12 mm of the petiole is preserved. It is 2.8 mm in width. It forks thrice distally at very small intervals, giving rise to the midribs of six segments, which are mostly broken near the blade base—one of them is poorly preserved due to slickensiding along the bedding plane at this point. Only one of the resulting segments, the most central one of the right half of the leaf, is reasonably complete. It is once forked at 2 cm from its base. The tips of the resulting terminal lobes are broken away, and all others are much more damaged. Nothing can be said about the overall outline and dimensions of this leaf. Certainly, however, the blade reached a length of over 12 cm, measured from the base, and a width of more than 15 cm. The segments resemble in outline those of *Scoresbya dentata* and the terminal lobes reach a maximum width of about 4 cm.

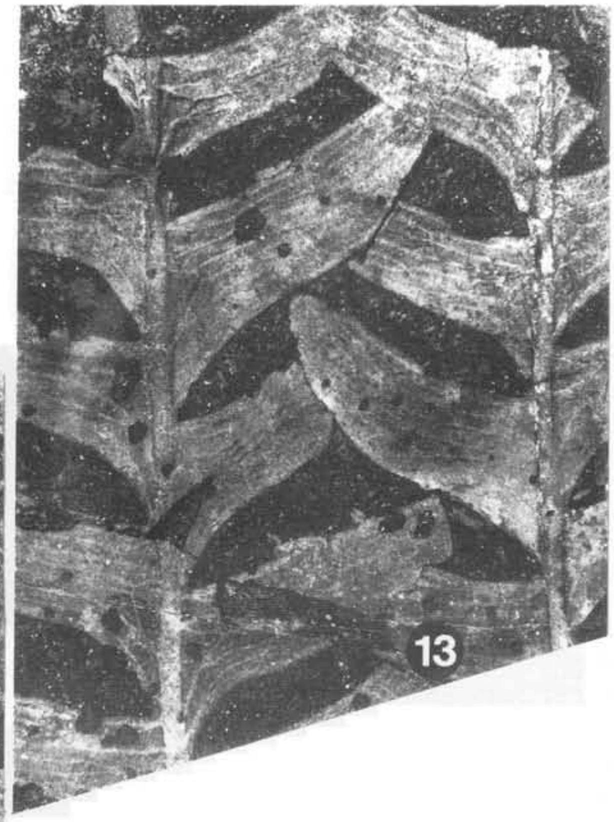
All segments—and their lobes rising from dichotomies—are perfectly pinnate. The pinnae are inserted at inter-



Figures 10 and 11.- *Scoresbya pinnata* sp. nov. Figure 10, Base of segment; combined photograph: part and counterpart specimen IGM-PB-515-693a, b, x 2. Locality: La Barranca-Santa Clara sampling area, La Barranca, Section 1 (515 CLP-IG-UNAM), x 2. Figure 11, Fragment of large leaf with well preserved reticulate venation. Photograph taken under xylene. Enlarged illustrations: 12 and 13. Specimen IGM-PB 692. Locality: San Enrique (Los Pilares) sampling area, loc. El Crucero Bed B (537B CLP-IG-UNAM), x 1.

vals of about 1 cm and an axillary angle of 50-70°. Their bases are not constricted and they are more or less decurrent. The pinnae of the segment bases are asymmetrically triangular and more distally, they have subparallel sides. The basiscopic margin is sigmoid; the acroscopic margin is straight or nearly so. The apex is rounded, or rounded acuminate, asymmetrical. The pinnae are sometimes falcate, but more commonly straight. Neighboring pinnae are separate, 5-7 mm in width—measured in the middle portion of the pinna—and up to 2.3 cm in length—measured along the midline.

The venation is not easily observed in the holotype, although it is visible in Figure 7, mainly so in the largest segment. It is much better preserved in a second, rather large specimen (Figure 11, at x 1 magnification; Figures 12 and 13,



Figures 12 and 13.- *Scoresbya pinnata* sp. nov. Two enlarged details of slab shown in Figure 11. At the bases of the pinnae, large triangular meshes are easily observable in the reticulate venation, x 2.

at x 2 magnification; see also Figure 6, b). The slab shows several segments, which probably belonged to one leaf. The secondary venation, which is rather well preserved in this specimen, is loosely reticulate. All veinlets belong to one order and follow a subparallel course to the tip, where they are difficult to observe. At the pinna bases, two to five main veinlets enter into the blade, generally fork very near the base, where one—or seldom two—large triangular or subtriangular-polygonal meshes are formed. N- and H-anastomosis are common, but X-veinlet crossings and λ-junctions are also sometimes present. The mean veinlet density is about 10/cm—measured perpendicular to the pinna in its middle part—and it increases distally. The length of the meshes decreases considerably towards the pinna apex. The available material does not reveal whether the reticulum is open or closed at the pinna tips. Nothing reasonably comparable to a pseudo- or submarginal vein is present in the species.

Discussion of *Scoresbya* Harris—All but two of the above described leaf fragments of *Scoresbya* come from the San Enrique sampling area. The two distinguished species were found together in a single bed at the locality El Crucero. Consequently, all specimens could belong to one highly variable species. The leaves assigned to *Sc. dentata* might represent young plants, whereas those of *Sc. pinnata* could belong to older ones, or vice versa; *i. e.,* the full set of material might illustrate a case of extreme leaf dimorphism. However, such speculations are rejected here, since specimens with transitional features have been found neither in Sonora nor elsewhere.

It is worthwhile to mention, on the other hand, that several colleagues even questioned the assignment of *Scoresbya pinnata* to the genus *Scoresbya*. Schaarschmidt (personal communication, 1982) wrote: "The pinnate leaf has certainly nothing to do with the other one [*Sc. dentata*], at least it does not belong to the same species". Dobruskina (personal communication, 1983) asked: "Are you sure, that these... leaves belong to the same genus? May it be that [*Sc. pinnata*] represents another genus...?".

The two species, however, share two important morphologically relevant features, the overall leaf segmentation and the primitive reticulate venation. Actually, they differ only in the deepness of dissection of the segment blades. The apparently striking difference between *Scoresbya dentata* and *Sc. pinnata* is thus a state difference in only one character, which is insufficient to justify generic segregation.

The genus *Scoresbya* was first erected by Harris (1932) on the basis of leaves collected from Neill Cliffs, Liverwort Bed, Kap Stewart Formation, Scoresby Sound, eastern Greenland, that according to Harris (1932, 1937) corresponds to the "*Thaumatopteris*-Zone", *i. e.,* lowermost Jurassic. Especially after the discovery of *Dictyophyllum (Thaumatopteris) variabilis* (Stanislavskiy) in the Late Triassic Protopivskaya Series (Stanislavskiy, 1976), *Thaumatopteris*, which is considered a subgenus of *Dictyophyllum* in agreement with Herbst (1992), can no longer be considered a genus providing good Early Jurassic time markers. Nevertheless, Pedersen and Lund (1980) recently corroborated Harris's (1937) assignment of his Greenland "*Thaumatopteris*-Zone" to the Hettangian, *i. e.,* earliest Jurassic.

Scoresbya dentata Harris was later found forming part of several widely scattered Early Jurassic floras of central Asia, China and Germany. These reports were summarized by Kräusel and Schaarschmidt (1968) in their paper on *Scoresbya*, which at that time was considered a monotypic, Liassic genus restricted geographically to Laurasia.

Shortly before and after the publication of Kräusel and Schaarschmidt's (*op. cit.*) paper, several new species were added to the record of *Scoresbya*. *Sc. szeiana* Li Peijuan from the Hsuchiao Series of northern Sichuan (Li Peijuan, 1964, pl. 19, fig. 12) and *Sc. entegra* Chen and Duan from the Late Triassic Qinghe flora of Sichuan (Chen *et al.,* 1985, pl. 2, figs. 1 and 2, 1987, pl. 42, figs. 9 and 10) however, most probably do not belong to this genus, because a central rachis and a terminal segment seem to be present in both species. Unfortunately, the present author could not read the original description of *S.? speciosa* mentioned in another Chinese paper (*cf.* Cao Zheng-yao, 1982). Herbst (1974) reassigned *Phlebopteris? dichotoma* Shirley 1898 from the Blackstone Formation, Ipswich Coal Measures, Queensland, Australia, to *Scoresbya*. The same species *S. dichotoma* (Shirley) Herbst was reported once again from the Late Triassic of Livingston Island, South Shetlands, Antarctica, by Banerji and Lemoigne (1987). The above species, as far as the present author knows, shares the dentate segment margin with *Scoresbya dentata* Harris. *S. integrifolia* Meng Fan-son (1986) from the Late Triassic Jingliang Formation, western Hubei, China, however, shows segments and lobes with entire margins. Meng Fan-son's report, together with the present description of *Scoresbya pinnata*, rendered a new generic diagnosis necessary.

No compelling evidence regarding the natural relationships of *Scoresbya* is yet available, and following Harris (1932), the author prefers to avoid a suprageneric assignment. It is clear, however, that the genus could belong to the ferns, to some group of gymnosperms, or even to some precursor group of the angiosperms—see introduction. Whereas Harris (op. cit.) through his comparisons suggested a linkage between *Scoresbya* and the Caytoniales, Kräusel and Schaarschmidt (1968) rather inclined themselves to consider it a dipteridaceous fern. As soon as reproductive organs are discovered for *Scoresbya,* they probably will serve to elucidate the natural relationships.

Conversely, their absence in the fossil record might be used as an argument against any attempt to make a taxonomic assignment. At the time of the discovery of this genus (Harris, 1932), this was indeed the only possible decision. At present, however, a number of species and specimens has been recorded from several localities. The total absence of fertile *Scoresbya* leaves supporting fern sporangia can now more reasonably be used to argue against the fern nature of this plant, and particularly against its interpretation as a dipteridaceous fern. The fossil floras with such ferns commonly bear fertile fronds which are easily recognized. Hence, it becomes now less and less probable that *Scoresbya* belongs to any fern family. Furthermore, the new segmentation type seen in *Sc. pinnata*, as well as the primitive undifferentiated net venation characterizing the genus, render its assignment to the Dipteridaceae even more unlikely (Herbst, 1992).

The Dipteridaceae consistently possess a very elaborate net venation with veinlets of several orders, very similar to the venation of many angiosperm leaves. In agreement with the new classification of the Dipteridaceae proposed recently by Herbst (1992), *Dictyophyllum* Lindley and Hutton, subgenus *Clathropteroides* Herbst, has the venation of the highest rank, speaking in terms of angiosperm leaf architecture (Hickey and Wolfe, 1975). *Dictyophyllum,* subgenus *Dictyophyllum* (*sensu* Herbst, 1992) has a less orderly reticulum with several orders of veinlets and meshes, and *Hausmannia* Dunker shows approximately the same rank. Although not fundamentally different, the pattern in *Dictyophyllum,* subgenus *Thaumatopteris* (*sensu* Herbst, 1992) is somewhat simpler, a feature correlated with the generally less developed surface of the blade.

Quite on the contrary, the secondary venation of *Scoresbya* never shows veinlets of more than one order, the veinlets are essentially parallel and dichotomize with a frequency that varies from species to species. Anastomoses, veinlet crossings and junctions are not very common and are frankly rare in *Scoresbya integrifolia.* In conclusion, the author considers untenable the preliminary and tentative assignment of *Scoresbya* to the Dipteridaceae, proposed by Kräusel and Schaarschmidt (1968).

Unfortunately, a more convincing assignment to another suprageneric group of ferns or seed plants cannot be proposed at present. In a personal communication of 1982, Harris wrote: "My specimens [of *Scoresbya dentata*] were few, and the bed had been heated by a basalt dyke and cuticles were badly damaged, but I had the strong impression that the leaves originally had thin cuticles. This suggests a gymnosperm rather than a fern". In addition, the venation pattern of *Scoresbya* also suggests gymnosperm affinities. Although reticula such as in this genus can be found in a good number of ferns, their pinnules normally show midveins. To sum up, *Scoresbya* is not a fern, but probably a gymnosperm, and perhaps a pteridosperm. The cuticular structure, which could serve to strengthen this conclusion, remains unknown.

The biostratigraphic range of *Scoresbya* now clearly extends from the Late Triassic Carnian—and /or Norian?—to the Liassic (*cf.* Herbst, 1974). Geographically, the genus is now known from most continents, except from Africa and South America—if the Southern Shetlands are accepted as forming part of continental Antarctica. Modern geography, however, is not that important in this context, and *Scoresbya* was in its lifetime distributed both in Laurasia and Gondwanaland, *i. e.,* "cosmopolitan".

The Laurasian record, however, seems to be slightly younger—earliestmost Jurassic—except one finding in the Late Triassic of China (Meng Fan-son, 1986) and the Sonoran material. The occurrences in Gondwana are Late Triassic in age, and the Sonoran material, although belonging to Laurasia, might be considered a borderland occurrence because of the proximity of northwestern South America and Mexico in Late Triassic time (Howarth, 1981, fig. 13.1). This contention, however, becomes questionable when a major NS-move of the western part of Sonora along the Mojave-Sonora Megashear (Anderson and Silver, 1979) in Jurassic time is taken as a fact. The paleophytogeographical interpretation of *Scoresbya* with its scarce record cannot be satisfactory at the present time. However, it is tempting to propose that the genus evolved during the Late Triassic in Gondwanaland or near the paleo-equator in Pangaea, and later became distributed northwards throughout Laurasia.

Genus *Sonoraphyllum* Weber gen. nov.

Sonoraphyllum mirabile Weber sp. nov.

Previous report

1985 *Sonoraphyllum mirabile* n. sp.- Weber, 1985, p. 120, fig. 6, c (not validly published).

Diagnosis—Only leaf (or segment) known. General outline not known. Blade with basal portion like a winged petiole about 2 cm in length and 1 cm in width, main portion of the blade deeply pinnatisect, leaving undissected the median part of the blade about 2 cm in width. Lobes inserted at distances of 1 - 2 cm, at an angle of 60 - 80°. Lobes over 6 cm in length in middle part of blade, maximum width of lobes 9 mm—at 2 cm from base—lobes straight, linear, slightly tapering towards rounded apex. Lobe margin entire. Midrib straight, stout, about 5 mm in width near base, tapering towards apex. Secondary venation pinnate, each secondary vein forking once dichotomously; each lobe with two main veins originating from neighboring dichotomies. Each lobe with two main veins occupying positions half way between center and margins. Tertiary venation reticulate with veinlets of at least two orders. Total length of the leaf over 20 cm—inferred—maximum width over 15 cm.

Holotype—Specimen IGM-PB-515-566a, b (Figures 14-16).

Type locality—La Barranca locality, La Barranca-Santa Clara collecting area (loc. number 515 CLP-IG-UNAM).

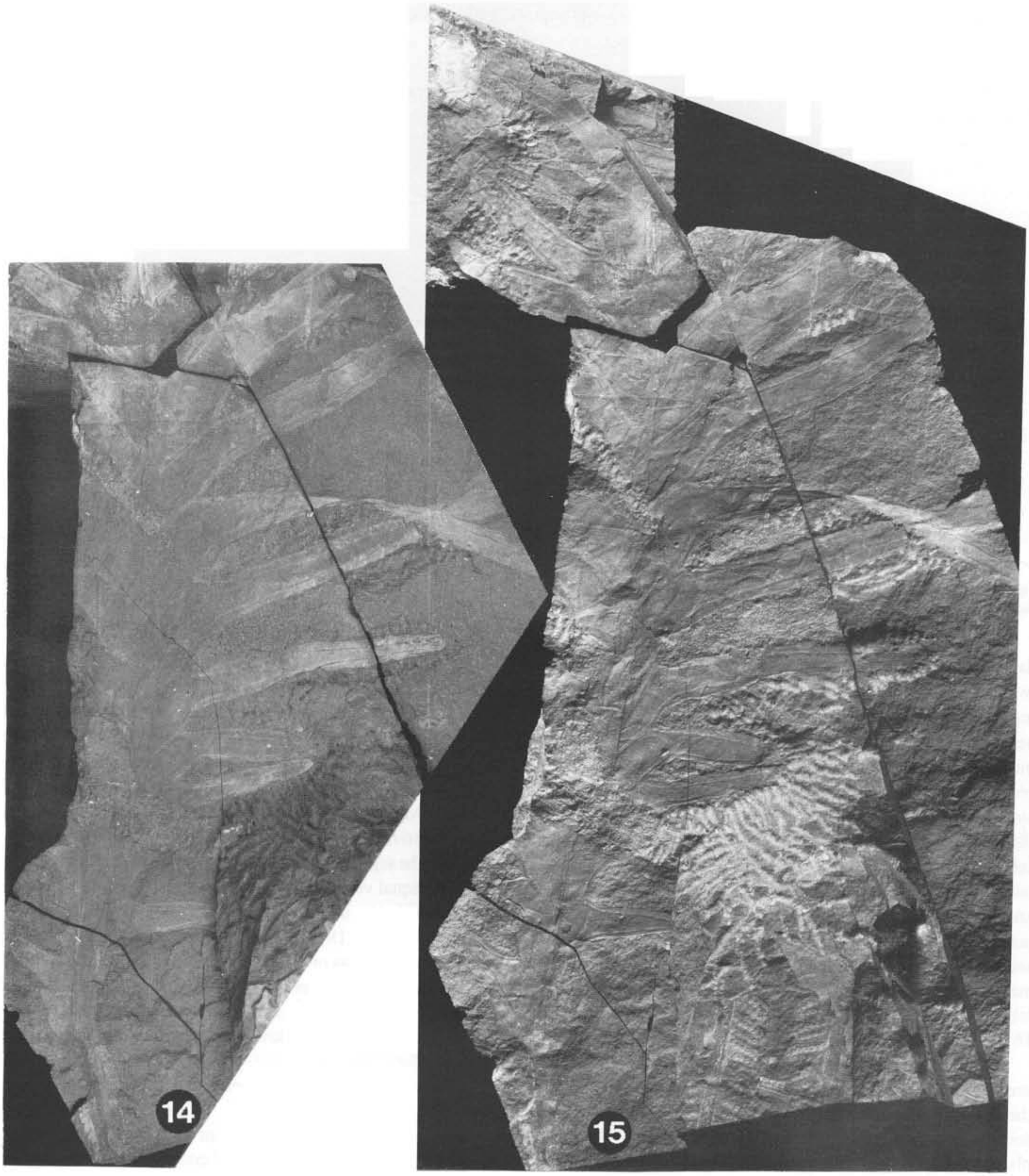
Type stratum and age—Santa Clara Formation, Barranca Group, Carnian (and/or Norian?), Sonora, Mexico.

Derivation of name—After the State of Sonora, Mexico; *phyllon* (gr.): leaf; *mirabilis* (lat.): amazing.

Material—Only the type specimen has been found within a slab originally collected by Ricardo Trejo-Cruz, because *Asterotheca santaclarae* was exposed. In the field, a good fragment of *Pseudoctenis* appeared on splitting. At Mexico City, Ángel Zambrano-García noticed at the edge of the slab a small part of the leaf described here. Later, it was prepared by the present author. The counterpart was destroyed, except for a small chip showing the basal part of the leaf.

Description—The above-mentioned plant fragments are well preserved in a block of dark grey, fine-grained siltstone. The texture of the leaf fragment of *Sonoraphyllum* (Figures 14-16) can be inferred through comparison with the other leaf remains. The reproduction of the venation relief is good to excellent both in the *Asterotheca* and *Pseudoctenis*, and the synangia of the former are also very well molded. Both the fern and the cycad appear rather rigid and stiff, whereas the *Sonoraphyllum* leaf does not. Its tertiary venation is almost completely obscured and can only be observed in some small portions of the lamina, especially due to slight differences in color. The rachis of the fern and the cycad are strongly marked by secondary minerals injected into the bedding plane. This means they were thick and probably rich in conductive tissue and sclerenchyma in lifetime. *Sonoraphyllum* does not show such secondary material and, consequently, was a thin, neither strongly cutinized nor sclerenchyma-rich leaf. Certainly, it was neither leathery nor rigid.

A good number of features of this plant was already mentioned in the diagnosis. Although the petiole-like basal part of the blade is somewhat crushed, a broad, flat midrib with a central strand of conductive tissue, about 1 mm in breadth, flanked by laminar wings, is easily observable in the above mentioned chip of the counterpart. Save at its very base, the fragment looks symmetrical, and hence, it seems possible that this is not a segment of a compound leaf but a whole simple leaf. This is additionally reinforced by the straightness of the midrib. The most striking feature of the leaf is the very peculiar secondary venation and its relationship to the lobes of the blade (Figures 14, 15 and 17, a). The secondary veins arise at distances of 10 to 15 mm and at an axillary angle of about 35 to 50°, forming a pinnate pattern. The individual secondaries follow a rather straight course of about 5 to almost 20 mm from their bases. Then they fork, with only one exception, the first secondary vein at the left side of the blade; this vein is much weaker than the other secondaries, and is transitional between these and the tertiary veins. The secondaries reach a maximum width somewhat over 1 mm, which is much



Figures 14 and 15.- *Sonoraphyllum mirabile* gen. nov., sp. nov. Two different photographs of type specimen (IGM-PB-515-566a). *14*, Taken under xylene. Enlarged detail shown in Figure 16. *15*, Taken under oblique illumination, to show secondary venation. (Preparation scars in lower half of the photograph). Locality: La Barranca-Santa Clara samplig area, La Barranca Section 1 (loc. 515 CLP-IG-UNAM). Further explanation see text, x 1.

reduced after the bifurcation. The two arms of each secondary vein—produced by dichotomy—are considered here to belong to the secondary venation too. The forks in the lower half of the leaf—or segment?—are rather asymmetrical regarding the course of the resulting arms, but towards the apex of the leaf they become progressively more symmetrical.

Figure 16.- *Sonoraphyllum mirabile* gen. nov., sp. nov. Enlarged detail from specimen shown in Figures 14 and 15. The lobe in the lower half of the photograph shows clearly the pair of main veins of the lobe and, especially in the lobe tip, the reticulate tertiary venation. Photograph taken under xylene, x 2.

Contrary to usual types of leaf architecture, each secondary vein, below its fork, is directed toward the notch between two lobes of the lamina. The basiscopic arm of each fork runs regularly into the acroscopic marginal zone of the basally neighboring lobe of the blade, whereas the acroscopic arm runs into the basiscopic side of the lobe following distally. As a result, each lobe has two subparallel main veins. All of the sinus between the lobes extend down to the forking points of the secondary veins (Figures 14, 15 and 17, b), whose arms are submarginal for a short distance at the lobe bases. More distally, they occupy positions half way between the lobe margin and its center and reach a distance of 1 to 1.5 mm from the margin in the distal part of the lobes. The distance between the secondary veins of a lobe at 1 cm from the forking point, measures 4 to 6 mm, and decreases toward the apex. At the lobe tip the main veins merge with the tertiary venation (Figure 16).

The tertiary and higher order venation is shown in Figures 14 and 17, b. It is easily distinguishable only at the tip of the lobe in the lower part of the photograph. Between the secondary veins and the margins of the lobes—at some places—long arches of tertiary veins can be observed, but no continuous marginal veinlet is formed by these arches. Communications between these and the secondaries are occasionally visible. At the tip of the lobe shown in the lower right part of Figure 16, a reticulum of elongated polygonal tertiary meshes is present and, within them, higher order veinlets appear at some points. The leaf has a highly organized venation of true reticulate type.

Comparison and discussion of *Sonoraphyllum*—The present author has never before seen a leaf with such venation features, neither living nor fossil. Sketches of the leaf were sent years ago to a number of colleagues, but nobody knew about previous findings of leaves with a comparable architecture. The very advanced organization of the tertiary venation is suggestive of dipteridaceous ferns or of angiosperms, or of the extant genus *Gnetum*. All known Dipteridaceae, however, and especially the genus *Dipteris*, very constantly possess only one midvein or midrib in the segments or lobes of the frond. There are never lobes with two equal veins. This is also the normal case in the angiosperms and in *Gnetum*.

Whereas the Dipteridaceae are well known from the Late Triassic fossil floras onwards, *bona fide* angiosperms have not yet been discovered in rocks of this age. There is no basis for the assignment of *Sonoraphyllum* to any presently known fossil or modern group below the taxonomic level of vascular plants.

However, the author thinks that it might be a pteridosperm. During Permian and Triassic times, the pteridosperms developed a number of highly innovative leaf features. There were processes of compaction of highly dissected compound leaves independently in the Gigantopteridales and the Peltaspermales (*cf.* Asama, 1974; Dobruskina, 1975) associated with incipient reticulum development in the venation of the same groups. There occurred the origin of the digitate Caytoniales leaves of *Sagenopteris*—and perhaps also *Scoresbya* and other genera mentioned in the introduction. But so far, no pteridosperm leaf resembles that of *Sonoraphyllum*.

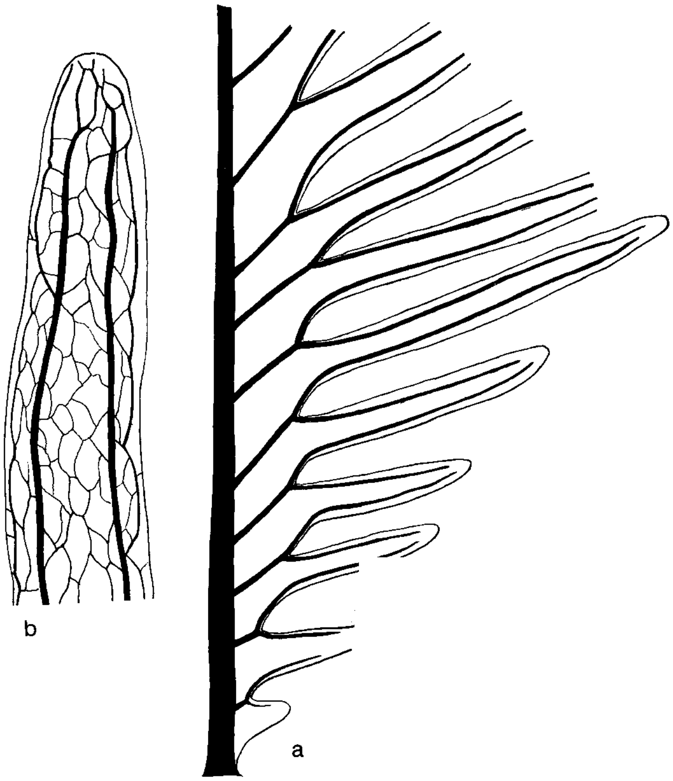


Figure 17.- *Sonoraphyllum mirabile* gen. nov. sp. nov. *a*, First and second order venation of part of the leaf. Approx. x 1; *b*, Reconstruction of fine venation of part of a lobe. Approx. x 3.

Dichotomous forking is not a rare feature in the fronds of pteridosperms, and generally it is combined with pinnate dissection of the leaf, which normally is of higher and even last order. In *Sonoraphyllum,* this sequence is inverted; pinnate dissection of the leaf is of the first order—if the fragment is a whole leaf—and the subsequent bifurcation of the last order. At first glance, the forking is expressed only in the venation pattern and not reflected in the blade outline.

There are, however, two characters suggesting a farther going interpretation. Firstly, there is the unusual dissection of the blade in between the arms resulting from dichotomy of the secondary veins and down to their forking points. And secondly, there is the highly exceptional presence of two subparallel secondary veins in each lobe. It is a common case in leaves with forking petiole, first order rachis or suceeding veins, that no lamina is developed for some length along the inner side of the resulting arms. This is quite clearly illustrated by *Scoresbya*. Hence, the notches of the *Sonoraphyllum* blade can be understood as a primitive feature which testifies to a more complex leaf architecture in the unknown ancestors of this genus. This earlier construction can be visualized if the lobes of *Sonoraphyllum* are considered to be a result of lateral connation of originally free and once forked lobes. Even so, the hypothetical predecessor of *Sonoraphyllum* would remain unusual, but it could, with the help of additional assumptions, be linked with the more common types of forked pteridospermous leaves (*cf.* Daber, 1980).

GENERAL DISCUSSION

This report has a lengthy history. At first, the author recorded *Manihotites* from the Late Cretaceous Olmos Formation of Coahuila, Mexico (Weber, 1972). In a later paper, he described the same material and compared it with *Scoresbya,* which was not known from Mexico at that time (Weber, 1978). This paper had earlier been read in 1977, at the International Meeting of Angiosperm Paleobotanists at Liblice, where Knobloch in his lecture stressed the similarity between *Scoresbya* and *Halyserites* assuming a phyletic affinity. At the same meeting, the present author rejected this suggestion because of the paucity of evidence and preferred to consider it a case of convergence (Weber, 1978). At present, however, the interpretation by Knobloch (1978a, b) seems again more attractive. After the discovery of *Scoresbya* in Sonora, Weber and Lorea-Hernández (1986) presented orally the plants described here, as well as *Manihotites,* emphasizing the fact that rachis bifurcation is a very old feature shared by many pteridosperms and some early angiosperms. This could indeed be one, although weak, argument favouring phyletic relationships between certain Mesozoic pteridosperms—including *Sagenopteris* Presl in Sternberg, and perhaps also *Scoresbya* and *Sonoraphyllum*—and early angiosperms like *Halyserites, Manihotites* and *Liriophyllum* Lesquereux (*cf.* Dilcher and Crane, 1984). These ideas have not been published, because the data are still regarded as incomplete, and because the suggestions regarding phyletic relationships between the plants described here and the angiosperms are still tentative. Finding of reproductive material belonging to the leaf genera *Scoresbya* and *Sonoraphyllum* will shed more light on the true systematic position of the plants considered here.

PALEOECOLOGICAL COMMENTS

The localities bearing the most important materials of *Scoresbya* and the specimen of *Sonoraphyllum* have been taken into account in previously published paleoecological studies (Weber *et al.*, 1980a; Zambrano and Weber, 1985). The Santa Clara Formation, which had not been studied before from a sedimentological point of view, following Potter and Cojan (1985), shows all the features of a continental sequence deposited on a coastal plain by meandering rivers of small or medium size, comparable to what is found in the Appalachian Basin. Coal-bearing intervals with dominant dark, relatively fine-grained sediments, alternate with coarse-grained sandstones from near the channels. The Barranca locality (Figure 2, loc. 515), besides of river sandstones, clearly embraces strata deposited far from a channel, and the paleo-communities of both localities under consideration are similar. *Asterotheca santaclareae* is dominant in both, followed by various species of *Laurozamites*. In addition, there are *Pterophyllum* spp. and *Ctenophyllum braunianum* at both sites. All these species belong to the paleoenvironments characterized by frequent flooding, stagnant water and poor oxigenation of soils, although not necessarily swampy. Coal seams are locally present in these rocks. The paleocommunities of these strata are very diverse in species, especially in the case of the La Barranca locality. *Scoresbya pinnata* was recently collected also from the San Javier area—loc. 533, CLP-IG-UNAM; San Javier Highway, near Section 3—where it belongs to a community showing no relationship with interfluvial coal-swamps. *Scoresbya* and *Sonoraphyllum* are rare species. Neither serves as meaningful paleoecological index species.

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