LAUROZAMITES, A NEW GENUS AND NEW SPECIES OF BENNETTITALEAN LEAVES FROM THE LATE TRIASSIC OF NORTH AMERICA

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RESUMEN

En la tafoflora cárnica—¿y/o nórica?—de la Formación Santa Clara, de Sonora, México, hay numerosas hojas de Bennettitales; las que se asigna aquí a *Laurozamites* gen. nov. son las más comunes. Con base en mediciones de las dimensiones de las pinas foliares en paleodemos ricos en ejemplares, se describe las especies *L. fragilis* (Newberry) comb. nov., *L. yaqui* sp. nov. y *L. pima* sp. nov. *L. tarahumara* sp. nov.—con dos variedades, *tarahumara* var. nov. y *dubius* var. nov.—se diferencia por la venación menos densa. Tres especies de los Estados Unidos de América también son adscritas al género nuevo, *L. powellii* (Fontaine) comb. nov., *L. macombii* (Newberry) comb. nov. y *L. paraiconicus* sp. nov. Todas las especies previamente conocidas que son incluidas aquí en *Laurozamites,* habían sido asignadas antes a *Pterophyllum, Otozamites* o *Zamites.* Esta práctica expande estos géneros en demasía. El género nuevo tiene el mérito de ser un grupo más natural restringido a América del Norte, al menos durante el Triásico Tardío.

Palabras clave: fósiles, plantas vasculares, Bennettitales, hojas, género nuevo, Triásico Tardío, México, Sonora, EUA.

ABSTRACT

The Carnian—and/or Norian?—Santa Clara taphoflora from Sonora, Mexico, yields a large number of bennettitalean leaves. Most common are those placed here in *Laurozamites* gen. nov. Species are described as *L. fragilis* (Newberry) comb. nov., *L. yaqui* sp.nov., *L. pima* sp. nov. and *L. tarahumara* sp. nov.—with two varieties, *tarahumara* var. nov. and *dubius* var. nov. The first three species are differentiated mainly according to the dimensions of the pinnae measured in specimen-rich palaeodemes, while the fourth, is distinguished by the low venation density. From the Late Triassic of the United States of America, *Laurozamites powellii* (Fontaine) comb. nov., *L. macombii* (Newberry) comb. nov. and *L. paraiconicus* sp. nov. are also assigned to the new genus. All the previously known species assigned here to *Laurozamites* had been placed either in *Pterophyllum, Otozamites* or *Zamites,* but this practice unduly expands these genera. The new genus represents a more natural taxon restricted to North America, at least during the Late Triassic.

Key words: fossils, vascular plants, Bennettitales, leaves, new genus, Late Triassic, Mexico, Sonora, USA.

ZUSAMMENFASSUNG

In der karnischen—und/oder norischen?—Flora der Santa-Clara-Formation von Sonora, Mexiko, treten Bennettiteenblätter sehr zahlreich auf. Die hier zu *Laurozamites* gen. nov. gestellten Formen sind besonders häufig. Sie werden als *L. fragilis* (Newberry) comb. nov., *L. yaqui* sp. nov., *L. pima* sp. nov. und *L. tarahumara* sp. nov.—mit den Varietäten *tarahumara* var. nov. und *dubius* var. nov.—beschrieben. Die ersten drei Arten liessen sich anhand von sehr reichen Paläodemen dank unterschiedlicher Abmessungen der Blattfiedern trennen, während die vierte durch eine geringere Nervaturdichte gekennzeichnet ist. Ausserdem werden die Arten *L. powellii* (Fontaine) comb. nov., *L. macombii* (Newberry) comb. nov. und *L. paraiconicus sp.* nov. aus der oberen Trias der Vereinigten Staaten von Amerika zu der neuen Gattung gestellt. Alle genannten Arten (ausser den neuen) waren früher zu *Pterophyllum, Otozamites* oder *Zamites* gestellt worden. Die neue Gattung ist nötig, da das frühere Verfahren diese Gattungen überdehnt. Ausserdem stellt sie einen (wenigstens in der Spättrias) auf Nordamerika beschränkten natürlicheren Formenkreis dar.

Schlüsselworte: fossil, Gefässpflanzen, Bennettitales, Blätter, neue Gattung, Obere Trias, Mexiko, Sonora, USA.

INTRODUCTION

The Bennettitales (Cycadeoideales) leaves are common plant remains in abundance and diversity, in the Late Triassic Santa Clara taphoflora of Sonora, Mexico (*cf.* Weber, 1985a). Dominant among these are leaves which, on the basis of very scarce and poorly preserved material, were first recorded by

Newberry (1876) as *Otozamites macombii* Newberry—one specimen—and *Pterophyllum fragile* Newberry.

Newberry (1876, pl. 4, figs. 6, 6a) described and illustrated several specimens as *P. fragile,* remarking that they might belong to two species, but added: "I have thought it probable, however, that...there is no tangible difference". Still in conflict with himself, he wrote that "in the future" and under certain conditions it could become necessary to describe an additional species just from the same material. Through time, many morphologically diverse specimens from Sonora were included under the latter species. For example, Silva-Pineda

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(1961), 85 years after Newberry, wrote about her material, identified as *Pterophyllum fragile*: "This species is the most abundant one in the collection which includes some complete fronds and several fragments...that show the already mentioned variability. This variability is so high, that the fronds with short and wide pinnae should not only be placed in another species, but in the genus *Anomozamites*. However, in this collection exists a gradual series linking these forms together, and a clear separation is impossible".

It has become evident during intensive sampling of the Santa Clara taphoflora by the senior author and students, that the variability of this species is not as strong as previously stated, that several taxonomic units are lumped together in the earlier literature under Newberry's (1876) species *P. fragilis* and that additional similar forms never found by the previous collectors are present in the flora. All these were called the "complex of *Zamites fragilis*" or simply *Z. fragilis* by Weber and coworkers (1980a, b) in their first papers on the Santa Clara taphoflora, and represent an assemblage of more or less closely related populations. The study of this assemblage was undertaken both to improve taxonomic precision and to achieve a higher resolution in paleoecological analysis. This paper contains the results of an analysis of this complex at the species and infraspecific level, based on the newly collected Sonoran material. Three species previously described from the United States of America are also considered here in the light of the proposed taxonomic changes. The preservation of the Sonoran material is such that cuticles are not preserved. All the descriptions are therefore based on macroscopic characters alone.

In the foregoing lines, an earlier, non formally proposed change in the generic name of this complex, was mentioned implicitly, which had originally been referred to *Pterophyllum* and *Otozamites* by Newberry (1876), but was placed in *Zamites* by Weber and coworkers (1980a, b) in accordance with the classification scheme for bennettitalean leaves, introduced into the North American literature by Ash (1975). Even though the Sonoran material lacks cuticles, our earlier assignment of the leaves to *Zamites* and therewith to the Bennettitales was taken for granted by accompanying *Williamsonia* and *Weltrichia* (Plate 1, figure 1; Weber *et al.*, 1980a, fig. 4, a-e; see discussion).

Ash's (1975) classification is inspired by the pragmatism and insight of T.M. Harris. It was originally proposed by Halle (1913), then adopted by Harris (1932) and later employed by Wesley (1958) and Harris (1969). Most recently, it was emended by Watson and Sincock (1992), with "no pretense of anything other than complete artificiality" (Watson, personal communication, 1994). However, "complete artificiality" and "naturality" are ideal attributes. "Artificial" classifications—not exactly a synonym of parataxonomic classifications—are welcome in paleobotany only if they represent the best possible approach to natural diversity within a given fossil group—*i. e.*, when they are non-arbitrary—and "natural" ones are the goal

of the never ending synthesis underway in taxonomy. Even the most satisfying classification achieved in practice represents a state of the art.

With the need to choose a generic name for the Sonoran complex under discussion, the authors faced in practice with the problem of generic delimitations in bennettitalean leaves. The classification used by Ash (1975) and by Watson and Sincock (1992), as it stands now, does not provide a clear understanding of natural groups and their relationships, and if it is taken for perfect and definitive, it inhibits the progress towards a more natural system. The present authors agree with Ash (*op. cit.*) and Watson and Sincock (*op. cit.*) in that their classification and generic definitions be used as far as there is no need for change. However, as often as additional and possibly more natural groups are recognizable among bennettitalean leaves, and this is concealed by the use of only those conventional genera adopted in their classification, this classification must be revised.

In contrast with community paleoecologists, who work mostly and best at the species level, students of paleophytogeography must deal with as many natural genera or other supraspecific taxa as possible. Therefore, the revision of the mentioned classification is initiated here. This will entail the revival of some generic concepts of the previous literature, besides the creation of some new ones.

As a first step in this direction, the authors accept Ash's (1975) supposition, discarded by himself, that *Zamites powellii* Fontaine from the Late Triassic of the United States of America might represent a new genus, and *Laurozamites* gen. nov. is erected for the species under discussion.

THE SANTA CLARA FORMATION AND TAPHOFLORA

The Santa Clara Formation (Alencáster, 1961), which outcrops in southeastern central Sonora, was first recognized last century by exploration- and economic geologists (Wilson and Rocha, 1946; former literature quoted here; Alencáster, 1961; Weber *et al.*, 1980a, b; Potter and Cojan, 1985). It belongs to the Barranca Group (Alencáster, *op. cit.*). However, the older stratigraphic ranking—Barranca Formation, instead of Barranca Group, and Middle Member, instead of Santa Clara Formation (King, 1939; Wilson and Rocha, 1946)—is still in use by local geologists.

The abundant fossil plants found in the Santa Clara Formation led earlier writers to assign it to the Triassic—in particular, to the Carnian (-Norian?) (Weber, 1985a)—and to interpret it as an essentially continental sequence deposited in a delta or fluvial flood plain, with only occasional manifestations of marine influx. The preliminary sedimentological work of Potter and Cojan (1985) suggests that the sediments making up the Santa Clara Formation were deposited by small or medium-sized rivers on a low-gradient coastal plain with abundant mud swamps. The Santa Clara Formation has been interpreted as a typical coal-bearing sequence, comparable with that

of the late Paleozoic of the Appalachian Basin (Potter and Cojan, 1985). These authors point out that the rivers were preferentially oriented in a NS-direction. A similar paleoenvironmental model was used in the paleoecological interpretations of the Santa Clara taphoflora by Weber and coworkers (1980a, b) and by Zambrano-García and Weber (1985). In these papers, it was attempted to distinguish recurrent groups of fossil plant species—or other more or less formal taxonomic units—corresponding firstly to the swamp paleohabitats with anoxic soils of the interfluvial areas (peats and muds); and secondly to the sandy deposits of the riversides, where more or less frequently redeposited immature soils offered a variety of paleohabitats. In addition, the existence of transitional paleoenvironments was assumed for a further set of species (Zambrano-García and Weber, 1985).

More recently, Stewart and Roldán-Quintana (1986, 1991) suggest that the Santa Clara Formation, or even the whole Barranca Group, be deposited in a west-east trending rift-graben system, like those extending parallel to the eastern coast of the North American continent in Carnian to Early Jurassic times. Such an interpretation would not alter fundamentally our paleoecological concepts, even though lake deposits and plant communities of lake shores might have played a more prominent role.

The development and current status of paleobotanical knowledge of the Santa Clara Formation was outlined by Weber (1985a). Complete lists of the species found in the flora and of all names previously used for these plants were included (Weber, 1985a, tables 2, 3).

LOCALITIES, MATERIAL AND METHOD

LOCALITIES AND MATERIAL

This study commenced shortly after the senior author started collecting from the Santa Clara taphoflora in 1973 (Weber et al., 1980a, b; Weber, 1985a). From 1978 to 1981, L. Herrera-Gil did research work focussed on statistical analysis of the here proposed new genus *Laurozamites*. The collections of L. Herrera-Gil and students of the Facultad de Ciencias, Universidad Nacional Autónoma de México, gathered between 1979 and 1980, included many specimens of this genus, but his work remained incomplete. Additional materials collected in 1980 and 1981 enabled R. Trejo-Cruz to do new work on the same genus, reported in a draft of a bachelor's thesis (Trejo-Cruz and Weber, 1984). All specimens collected up to 1981 were identified and counted in 1982 by the senior author and his students F. Amozurrutia-Silva, A. Torres-Romo, R. Trejo-Cruz and Á. Zambrano-García. Many of the slabs show more than one leaf fragment of the species here discussed. The number of the leaf fragments used for the measurements—given below and in five figures—does not agree, therefore, with the number of the specimens (slabs) used. After having collected further specimens in 1983 and

1984, the senior author in 1986 invited G. Zamudio-Varela to cooperate with him on the "*Laurozamites*" problem. The method was once again changed allowing for the study of many more specimens. New measurements, replacing those by R. Trejo-Cruz, were made for the present study by the junior author. Consequently, only specimens collected before that year are included in the work reported here. About 90 additional specimens were collected in 1993 by the senior author and his students, A. Hurtado-Cortés and G. Hernández-Castillo; some of them were used for illustrating.

The Sonoran fossils were collected at a large number of localities listed by Weber (1985a, table 1), and the location maps published in the earlier paper are repeated here (Figures 1-5). In the text and in the figure captions, the names of only the more important localities are mentioned. About 1,250 fossiliferous slabs with foliar fragments of *Laurozamites* were obtained from the following sampling areas (Figure 1): Area 1 (San Marcial) with 15 specimens; Area 2 (La Cuesta-Las Peñitas: Figure 2) with 455 specimens, mainly from localities 508 and 1001; Area 3 (San Javier: Figure 3) with about 150 specimens, especially from Section S.J. 3; Area 4 (La Barranca-Santa Clara: Figure 4) with about 420 specimens, mainly from localities 501, 515, 516 and 523; and Area 5 (San Enrique or Los Pilares: Figure 5) with 215 specimens, mostly from localities 517, 519, 535 and 537 of the catalog of paleontological localities of the Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México (CLP-IG-UNAM).
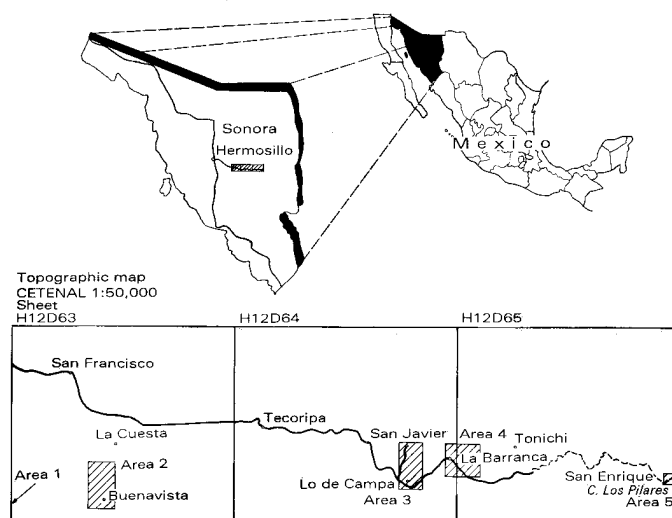

Figure 1.- Location map for the sampling areas 1-5. *1*, San Marcial; *2*, La Cuesta-Buenavista; *3*, San Javier; *4*, La Barranca-Santa Clara; *5*, San Enrique (Los Pilares). Map based on quadrangles CETENAL (1975a, b, c).

ANALYSIS OF QUANTITATIVE CHARACTERS

A total of 504 leaf fragments was chosen for the quantitative study to delimit *Laurozamites fragilis*, *L. yaqui* and *L. pima*, excluding the material of *L. tarahumara*, the rather conservative description of which is based on about 85 addi-
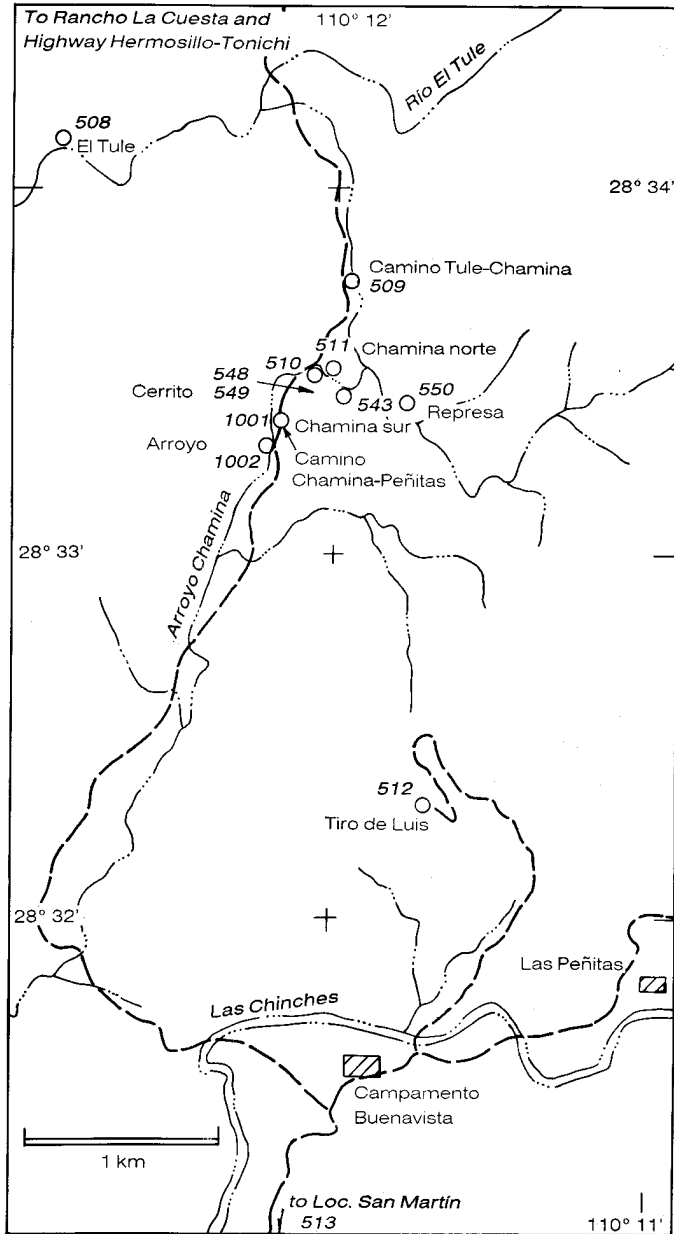
Figure 2.- Fossil plant localities (o) of the La Cuesta-Las Peñitas sampling area. The exact sampling sites for numbers 548 and 549 are not known.

tional leaf fragments. In the first instance, only those fragments that showed either the blade base or apex and with at least 2/3 of the length of the blade were considered for quantitative study. This restricted selection made quite difficult the initial steps of the work, and it was given up for the present paper. The rock at most localities of the Santa Clara Formation easily breaks down into small pieces and, consequently, the larger leaves are destroyed far more often than the smaller ones. The restriction of measurements to more or less complete leaves would hence result in a significant diminution of the dimensional main values.

Instead of discussing all characters of the *Laurozamites* leaves and their potential value for biometrics, only those
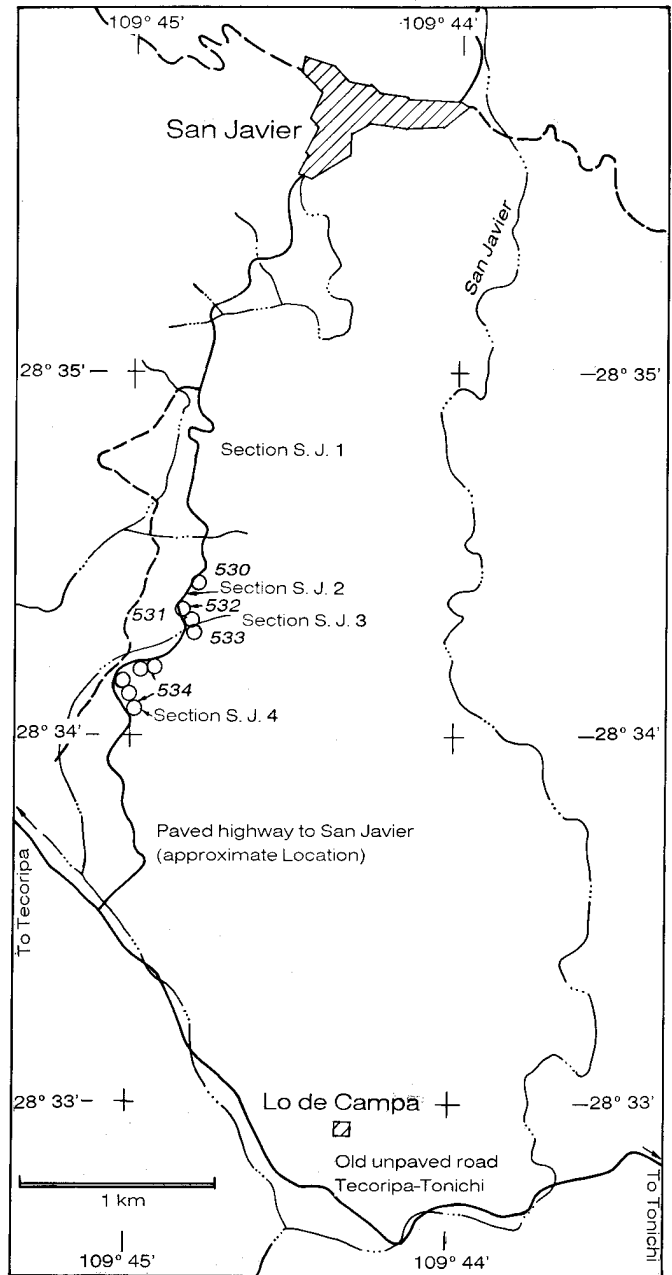

Figure 3.- Fossil plant localities (o) of the San Javier sampling area.

which were actually used will be mentioned. Even in quite incomplete leaf fragments, it is easy to select the largest pinnae. Complete pinnae are very common in our material and the 504 selected leaf fragments allowed the recognition with reasonable certainty of the largest ones. Pinna length and width are, in most of the leaves, unaltered characters, as the pinnae were mostly flat in life. Hence, changes of the dimensions during compaction of the enclosing sediment were rare. Only the dry pinnae of shed leaves of *Laurozamites yaqui* were apparently sometimes not flat. The length was measured between the insertion scar and the apex along the midline of each pinna; the width was measured half way between the insertion
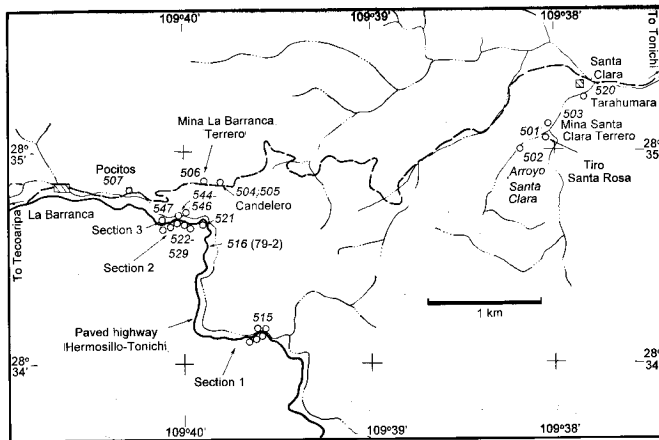
Figure 4.- Fossil plant localities (o) of the La Barranca-Santa Clara sampling area.

Figure 5.- Fossil plant localities (o) of the San Enrique (Las Peñitas) sampling area.

scar and the apex perpendicular to the longitudinal midline. Unfortunately, in many of the fragments used for the measurements, it was not possible to observe venation density readily, normally another unaltered character, since there is no evidence of major shrinkage in the leaves. This character was studied in at least 20 leaf fragments of each presumed species. From the beginning, *Laurozamites tarahumara* was segregated from the other members of the complex under study, due to its very low venation density. The remaining species did not show very distinct ranks in this character. The venation density was established in the apical third of well preserved large pinnae as twice the number of veins crossed by a line 0.5 cm in length and perpendicular to the venation, *i. e.*, venation density is the number of veins/cm of width.

The values of pinna length and width were plotted in a set of graphs which are in part illustrated later. In these graphs, only the values measured in the sample of 504 leaf fragments of *Laurozamites*—except *L. tarahumara* sp.—are plotted. No additional statistical tests were carried out on these data, and the present study is semiquantitative. Consideration of the figures allows to establish very clearly—apart from an uncertain residue—the presence of three sharply distinct leaf types in the sample. The three leaf types are taken here as different species.

TYPE METHOD

It has been deemed useful to typify the described or newly combined species as far as possible with holotypes selected from specimen-rich type palaeodemes (Anderson, 1977; Anderson and Anderson, 1983, 1985, 1989; see discussion) in contrast to the exclusive use of holotypes preferred by the senior author in other papers on fossil plants of the Santa Clara taphoflora (Weber, 1985b, c, 1995) and practiced here in the case of *Laurozamites tarahumara, L. macombii*, and *L. powellii*. In the cases of *L. yaqui, L. pima* and *L. paraiconicus*, holotypes are chosen from the corresponding type palaeode-
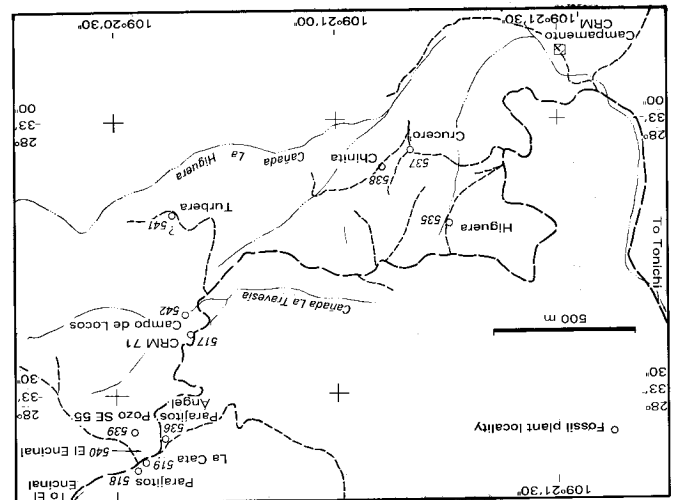
mes. The selection of type palaeodemes offers a number of advantages whenever biometric studies result in the description or redefinition of species with overlapping quantitative characters. The leaves described here sometimes do not permit identification, when only one or very few specimens are available. The specimens constituting a type palaeodeme, with the exception of the holotype, may be considered isotypes. They do not have the same legal status as the holotype, but are the real basis of the diagnosis published here.

For reasons discussed below, in the case of *L. fragilis* (Newberry) it was deemed necessary to chose a protype in addition to the type material figured by Newberry (1876; *cf.* Chaloner, 1993). Furthermore, as for the new species *Laurozamites yaqui* and *L. pima,* a type—protype—palaeodeme of *L. fragilis* is proposed.

COMPARISON WITH MATERIAL FROM OUTSIDE SONORA

The comparison of the species described here with others is based only on the available literature. The gathering of a representative collection of previous publications was greatly hampered by high costs and additional circumstances. A thorough search for *Laurozamites*-like leaves in the worldwide Jurassic floras was, in consequence, not undertaken.

DEPOSITORY

The material described is housed in the Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México. A number of specimens collected in 1979 by L. Herrera-Gil and students belongs to the Museo de Paleontología, Facultad de Ciencias, UNAM. Holotypes and figured specimens are deposited in the special section for type material in the museum.

TAXONOMIC PALEOBOTANY

Genus *Laurozamites* Weber and Zamudio-Varela gen. nov.

Type species—*Laurozamites fragilis* (Newberry) Weber and Zamudio-Varela comb. nov. (see below).

Diagnosis—Leaf pinnate, petiolate; petiole with strongly broadened base, much shorter than the blade; rachis straight, covered with transverse cortical wrinkles on adaxial face; blade lanceolate, elliptical or oblanceolate in general outline; pinnae opposite to alternate, more or less obliquely, latero-adaxially attached, imbricate when overlapping, subrectangular in out-line, pinna base constricted, at both corners with more or less prominent auricles, acroscopic auricle larger, auricles sometimes missing; pinna apex more or less obliquely rounded, truncate or emarginate-truncate. Venation with one order of veins, more or less divergent in the pinna base, subparallel to parallel in the distal parts of the pinna, veins repeatedly dichotomizing, ending free at the lateral and distal margins of the pinnae, never anastomosing; venation density of 20-60 veinlets/cm.

Derivation of name—from Laurentia and *Zamites*.

The genus is distinct from the remaining genera for bennettitalean leaves mainly in that the pinnae in the middle of the leaf are subrectangular in outline, showing frequently auricles at basal corners (Figure 6). Harris (1969) restricted the use of the term "auricles" to pinnae "in which the attachment is nearer the basiscopic margin or ones in which the acroscopic angle is differently shaped from the basiscopic one", apparently in order to restrict the use of the term to *Otozamites*. Accordingly, in his description and discussion of *Laurozamites powellii*, Ash (1975) uses the term auricles only with quotation marks. The present authors see no convincing reason to follow them.

As in many bennettitalean leaves, the basal and distalmost pinnae of the *Laurozamites* species are often different from the middle ones, not only in dimensions but also in shape. While the basal ones are sometimes subtriangular, the most distal ones are commonly spatulate or obcuneate. The distalmost pinnae can be attached laterally or in a pseudoterminal position, continuing the rachis (Plate 1, figures 2, 3; Plate 2, figures 1-3, 5-7, 11, 12; Plate 4, figure 4).

Figure 7 shows the width/length ratios of the largest pinnae in the above mentioned sample of 504 leaf fragments— which includes only the following three species and the material placed in *Laurozamites* ex gr. *fragilis*. It is immediately evident that there are numerous specimens with their largest pinnae between 1 and 2 cm in length and 4 to 7 mm in width. The cloud shows, in addition, two independent prolongations towards much longer or much wider pinnae, respectively, which render it very asymmetrical. It might, on the outset, be concluded that there are at least two, perhaps three, inde-
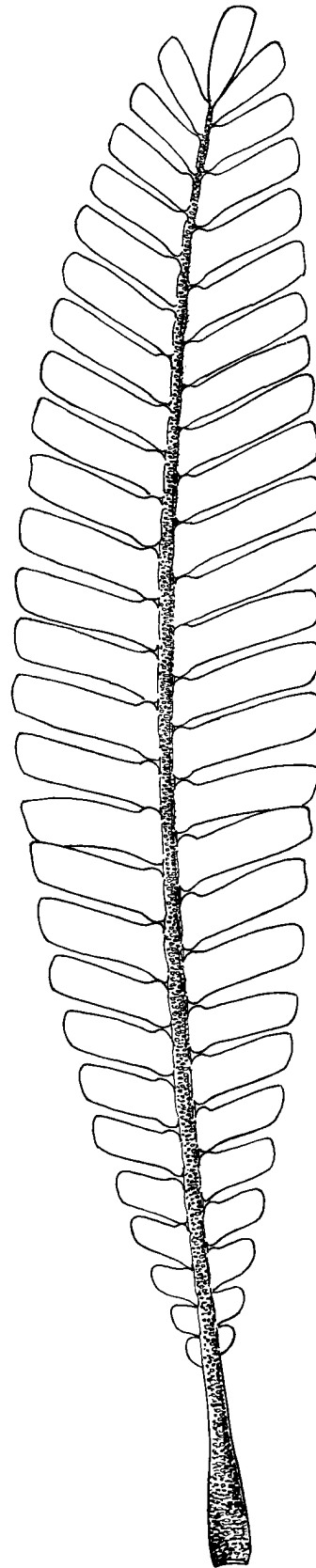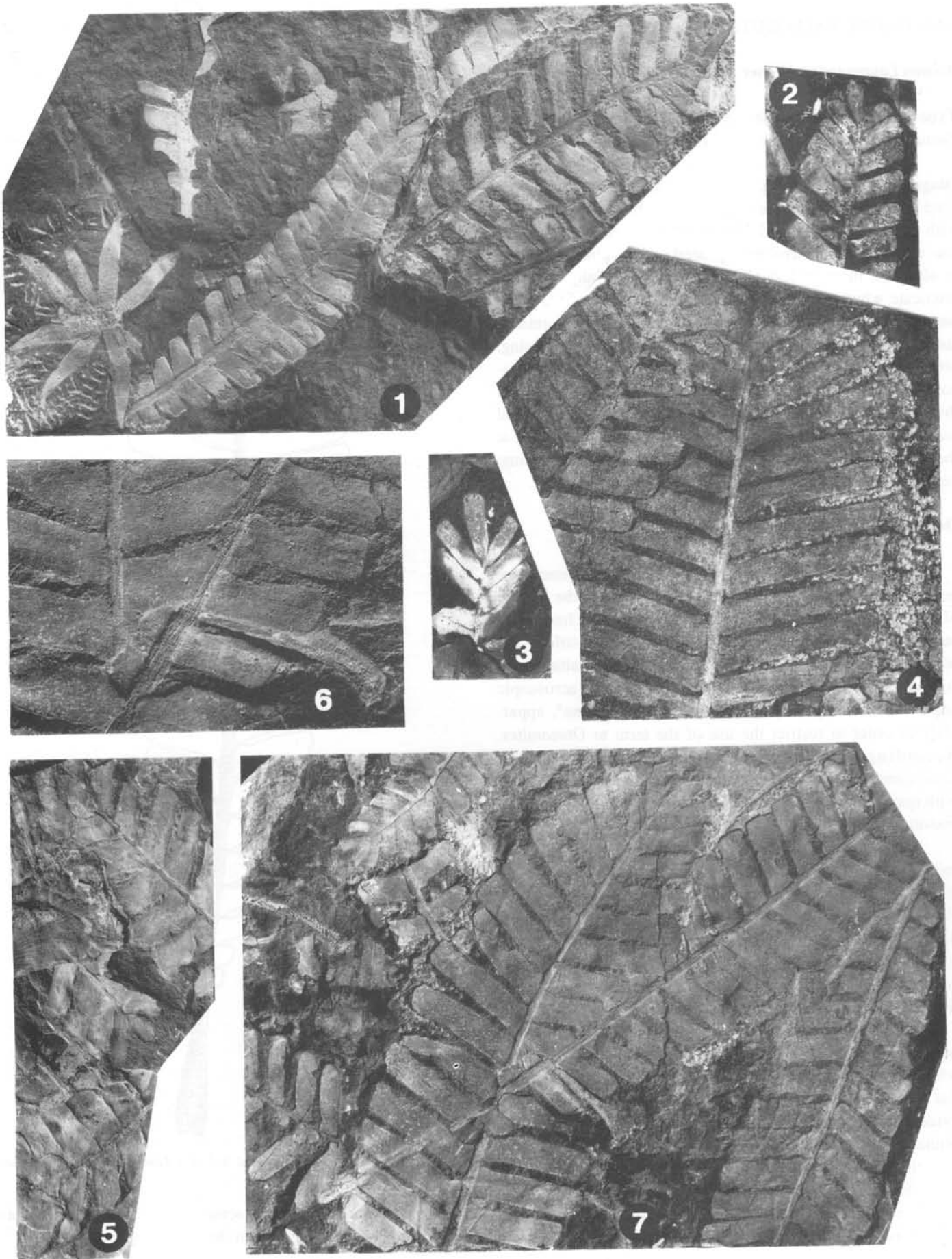

Figure 6.- Reconstruction of typical leaf of a *Laurozamites* species, most similar to *L. fragilis* (x 1.2)

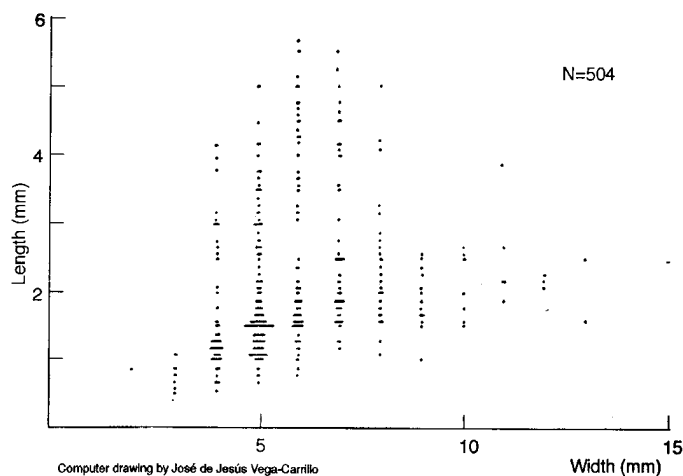pendent "populations" represented within the sample. This first impression is analyzed in the following text.

Figure 7.- Graph showing the length-width ratios for largest pinnae of 504 *Laurozamites* specimens.

DESCRIPTION OF SPECIES FROM SONORA

Laurozamites fragilis (Newberry) Weber and Zamudio-Varela comb. nov.
Figure 8; Plate 1, figures 1-7; Plate 2, figures 1-7

1876 *Pterophyllum fragile* Newberry.- Newberry, 1876, p. 144, pl. 6, fig. 6a; assignment of the specimen Newberry, 1876, pl. 6, fig. 6 uncertain; see *Laurozamites* ex gr. *fragilis*.

1876 *Pterophyllum delicatulum* Newberry.- *Ibidem* (only in explanation of pl. 6, fig. 6, instead of *P. fragile; nomen nudum*).

?1961 *Pterophyllum fragile* Newberry.- Silva-Pineda, 1961, p. 20-21, *pro parte*, pl. 4, fig. 3, 5.

1982 *Zamites fragilis* (Newberry).- Weber and coworkers, 1980a, *pro parte*, fig. 12, g.

Emended diagnosis—Leaf lanceolate in outline, up to 6 cm wide and 15 cm long (or longer?). Petiole basally widened, up to 5 mm wide at base, not longer than 5 cm; rachis with fine cortical wrinkles, 1-2 mm wide near blade base. Pinnae attached at angle of 65-85° (mean 75°) at middle part of blade, opposite to—rarely—alternate, straight or slightly curved; auricles usually present, rounded, limited to basal 5 mm of the pinna; distal margin slightly emarginate or truncate, with rounded corners; pinna 5-33 mm long (mean 15 mm), 2-8 mm wide (mean 5 mm); length/width ratio up to 6.5 (mean 3). Venation very fine, slightly divergent at base of pinna, subparallel or parallel in distal part; venation density 45-50 veins/cm. Venation of auricles not distinct.

Type material—Lectotype: Newberry, 1876, pl. 6, fig. 6, a (see discussion). In support, specimen IGM-PB-1001-659 (Plate 1, figures 6, 7) is chosen as protype.

Type (protype) palaeodeme—All specimens with leaves of *Laurozamites fragilis*, from the type locality—protype locality. Specimens selected from this palaeodeme are figured on Plate 1 (except figure 5) and Plate 2, figures 1-7.

Type (protype) locality—Camino Chamina-Las Peñitas (loc. 1001, CLP-IG-UNAM, Figure 2), about 250 m south of the intersection of the mentioned road and the Chamina Creek, at the roadside; 28°33'15"N/110°12'10"W, Sonora, Mexico.

Type stratum and age—Santa Clara Formation, Barranca Group; Carnian—and/or Norian?—Late Triassic.

Material—The type—protype—palaeodeme was sampled in 1979 by students of the Faculty of Sciences of the UNAM, under the guidance of L.Herrera-Gil, and in 1981 by Á. Zambrano-García. It consists of 215 specimens, all with the number IGM-PB-1001. Only figured specimens have specimen numbers. The uniformity of the leaves is very striking and the presence of more than one population can be excluded. Several additional localities bear specimens identical with the type palaeodeme: Río El Tule (loc. 508; Figure 2); La Barranca, Section 2, Unit 19 "LB 8" with a remarkably uniform palaeodeme (loc. 526 A, B; Figure 4); La Barranca, Section 1, with non uniform material, which was mostly picked up from road-side talus (loc. 515; Figure 4); Santa Clara, Tiro Santa Rosa, generally with rather small leaves (loc. 501; Figure 4) and El Crucero, Bed B (loc. 537 B; Figure 5). The species is very common in the Santa Clara Formation. In some localities, which could not be sampled intensively, the species was apparently as dominant as in the type—protype—locality.

Description—The margins of contiguous pinnae sometimes touch (Plate 1, figure 1), and very rarely become imbricate (Plate 2, figure 1). In curved leaves, the margins of the pinnae can, of course, overlap apparently (Plate 1, figure 5). The space between adjacent pinnae normally does not exceed half their width, except, for example, the leaf figured on Plate 1, figure 1, right. The pinnae of the leaf apex are generally attached at a more acute axillary angle than in the middle of the leaf.

The basal expansions or auricles of the pinnae are generally inconspicuous and are absent in some specimens (Plate 2, figure 5). In only a few leaves do they cover a major part of the adaxial side of the rachis.

The leaves were apparently thin, flexible and shed by abscission but this does not necessarily mean that the plant was deciduous. Detached pinnae are rarely found with very few leaves lacking pinnae, even at localities where the fossils are poorly preserved due to transport. It seems clear that the pinnae were not shed.

The length/width ratio is shown in Figure 8 for the largest pinnae of 193 leaves selected from the type palaeodeme. Com-

PLATE 1.- *Laurozamites fragilis* (Newberry) emend. (all except figure 5 from protype palaeodeme, locality 1001, La Cuesta-Buenavista sampling area; all x 1, except figure 6). Figure 1—Several leaves, one almost complete, and specimen of *Williamsonia* (x 1); specimen IGM-PB-1001-509a. Figures 2 and 3—Leaf apices with uppermost pinna in different orientations; specimens IGM-PB-1001-659 and 660. Figure 4—Broadest leaf of the protype palaeodeme; specimen IGM-PB-1001-661a. Figure 5—Assemblage of leaves from locality 501, La Barranca-Santa Clara sampling area. Figures 6 and 7—Slab with several leaves of medium size; protype specimen IGM-PB-1001-663; figure 6 enlarged x 2, to show venation.
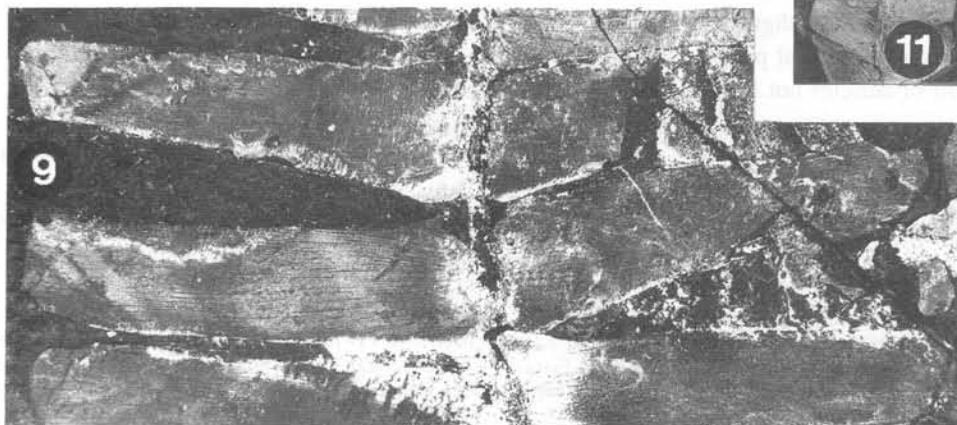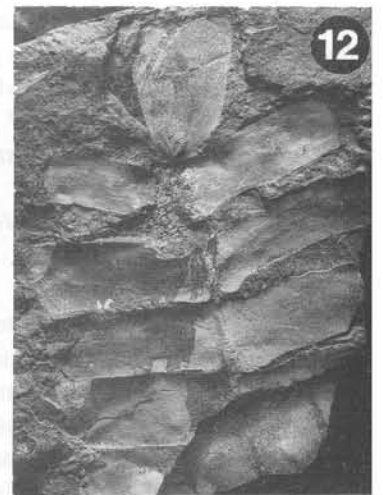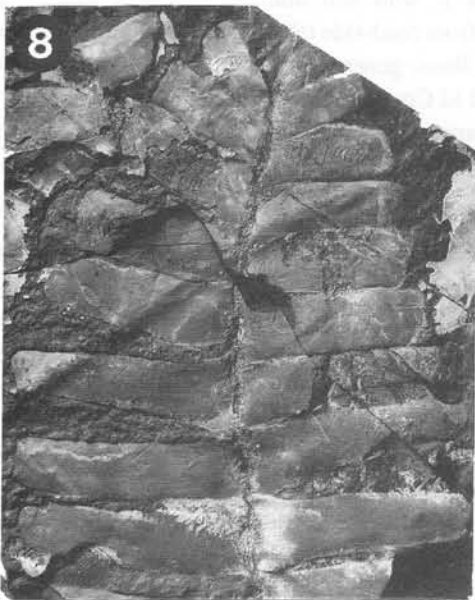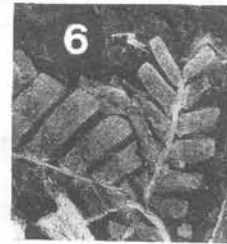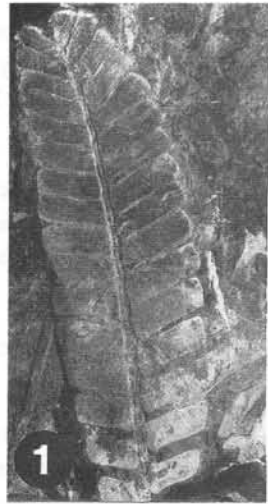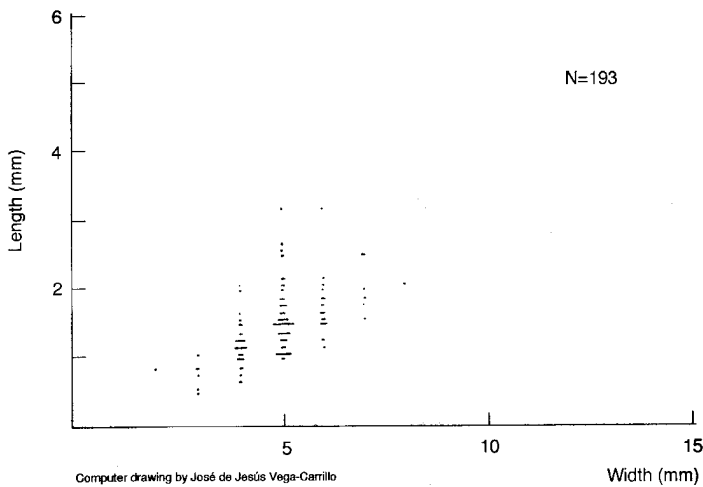
Figure 8.- Graph showing the length-width ratios for largest pinnae of 193 leaves of *Laurozamites fragilis*, belonging to the type palaeodeme from locality 1001 (sampling area 4).

parison with Figures 7 and 11 shows that the values for the type palaeodeme coincide with a great majority of the leaves from the remaining localities, except localities 515—material of *Laurozamites yaqui*—516 and 523—material of *L. pima*.

Comparison—Only *Laurozamites powellii* (Fontaine) comb. nov. is closely similar to *L. fragilis*. The first species was described and well illustrated mainly by Daugherty (1941) as *Otozamites powellii* and by Ash (1975) as *Zamites powellii*. The materials of these authors—and additional ones quoted by Ash, 1975—were collected from numerous localities across six of the states from the United States of America. They clearly embrace a much less uniform complex than *Laurozamites fragilis*. *L. fragilis* differs from *L. powellii* above all in its longer leaves—lanceolate instead of elliptical, according to Ash (1975)—and to the higher number of pinnae—although the specimen illustrated here on Plate 1, figure 2 resembles those figured by Ash *(op. cit.,* pl. 2, figs. 1, 2) in this respect. In *L. powellii* there is a stronger tendency towards rounded pinnae bases and cuneiform pinnae. In the type—protype—palaeodeme of *L. fragilis,* the length/width ratio reaches 6.2, whereas in the specimens of Ash (1975, pl. 1, fig. 3 and pl. 2, figs. 3 and 5) the ratio is 7.5, 12.5 and 8.7, respectively, and the specimens figured by Daugherty (1941, pl. 17) reach ratios of over 15. Even bearing in mind that the material of *L. powellii* seems to be heterogeneous, the two species are not identical.

Typification of *Laurozamites fragilis* (Newberry) Weber and Zamudio-Varela comb. nov.—The basionym was based on two poor specimens from Los Bronces near San Javier (Figure 3), by

Newberry (1876), who did not propose a holotype. The original material of Newberry *(op. cit.),* formerly in the paleobotanical collections of the New York Botanical Garden, Bronx, is now housed in the Peabody Museum, New Haven, USA. The specimen on which Newberry's description is mainly based (Newberry, 1876, p. 144, pl. 6, fig. 6), according to Tiffney (1985, personal communication) is available and could serve as a lectotype. This specimen, however, cannot be assigned faithfully to *Laurozamites fragilis* in its new delimitation, but only to *L.* ex gr. *fragilis.* On the contrary, the specimen figured by Newberry *(op. cit.,* pl. 6, fig 6, a) which fits the new delimitation, could not be found in the Peabody Museum. Newberry thought it might represent a different species (see introduction). However, according to the International Code of Botanical Nomenclature (Greuter *et al.,* 1988), the original figure of Newberry (1876, pl. 6, fig. 6, a) must be chosen as lectotype in this case. A third specimen (Newberry, 1876, pl. 6, fig. 5) identified as *Otozamites macombii* may belong to *Laurozamites fragilis,* but is also not suitable. In any case, the old original material of Newberry (1876) is "demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name" *Laurozamites fragilis.* In addition, the exact topographic and stratigraphic position of Newberry's (1876) Los Bronces type locality is not known and additional material from this site cannot be collected. Therefore, the present authors decided to nominate a protype *(cf.* Chaloner, 1993).

Laurozamites yaqui Weber and Zamudio-Varela sp. nov.
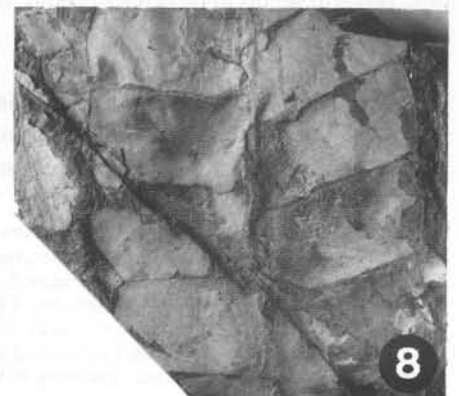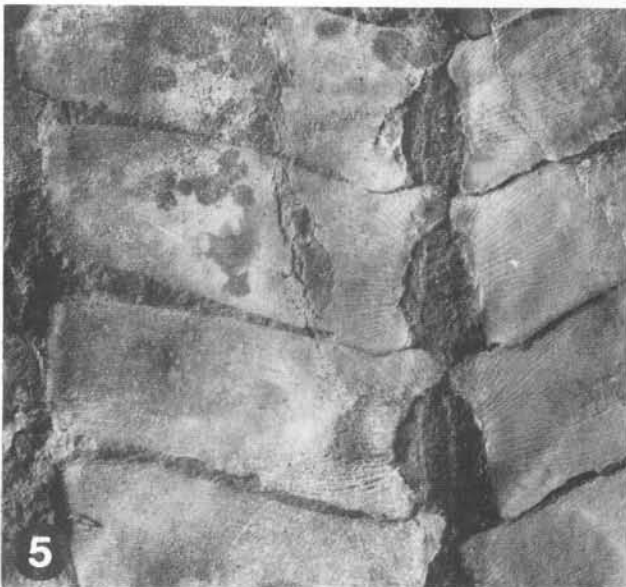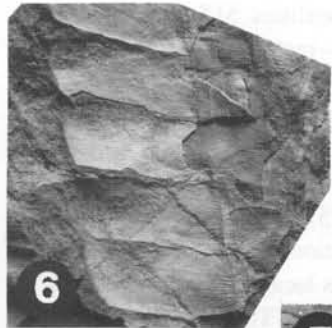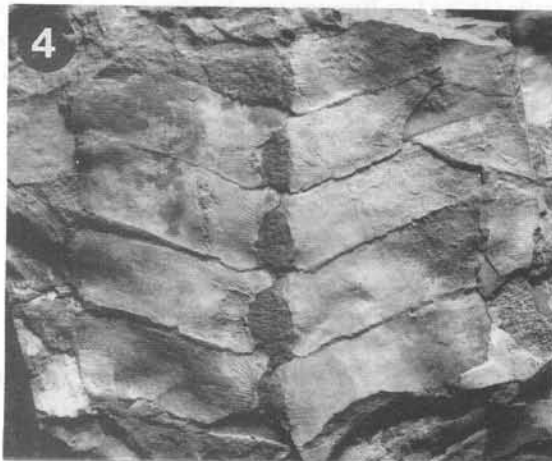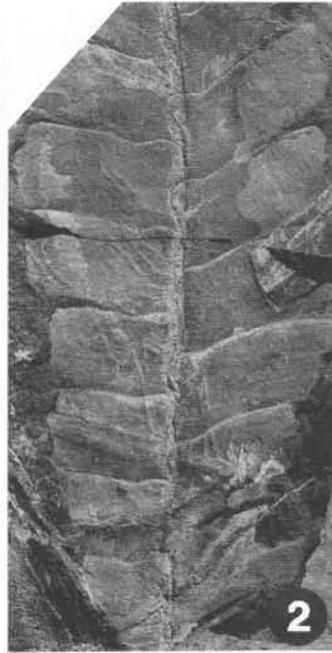Figure 9; Plate 2, figures 8-13; Plate 3, figures 1-9; Plate 5, figure 1

1961 *Pterophyllum fragile* Newberry.- Silva-Pineda, 1961, p. 20-21 *(pro parte),* pl. 4, fig. 6; pl. 5, fig. 2.
1982 *Zamites fragilis* (Newberry).- Weber and coworkers, 1980a, p. 150 *(pro parte),* fig. 12, b, c, d?, e.
1985 *Zamites* aff. *macombii* (Newberry).- Weber, 1985a, p. 120, tab. 3 *(nomen nudum).*

Diagnosis—Leaf up to 7 cm wide. Petiole basally curved, narrow, up to 2.5 cm in length, with strongly thickened basal portion up to 7 mm wide. Rachis narrow, straight, like the petiole provided with thick and very conspicuous cortical wrinkles, up to 2.5 mm wide at lamina base, adaxial face of rachis sometimes completely covered by the pinna bases. Pinnae opposite, subopposite or subalternate, attached at angles of 60-90° (mean 75°), attachment scar slightly curved, pinna base contracted, frequently with very conspicuous auricles, especially at acroscopic margin; pinna often weakly tapering towards the apex, straight or somewhat

curved, apex more or less obliquely and rounded truncate, occasionally emarginate. Pinnae 1-4 cm long (mean 2 cm), 5-13 mm wide (mean 9 mm); length/width ratio up to 4 (mean 2). Venation often strongly divergent at pinna base, with numerous dichotomies, parallel in distal half of the pinna; venation density distally 40-60 veins/cm. Venation of auricle sometimes with a submarginal vein slightly curved back towards or subparallel to rachis.

Holotype—Specimen IGM-PB-515-533a, b (Plate 3, figures 2, 3).

Type palaeodeme—All specimens from the type locality with leaves of *Laurozamites yaqui*. Specimens selected from the type palaeodeme are illustrated on Plate 2, figures 8-13 and Plate 3, figures 1-8.

Type locality—Highway Hermosillo-Tónichi, La Barranca Section 1 (measured by Potter *et al.*, 1980), Units 1-7 (loc. 515, CLP-IG-UNAM, Figure 4). The specimens were collected from roadside talus. The bed bearing this material could not be located in the outcrop; 28°34'08''N/109°39'35''W, Sonora, Mexico.

Type stratum and age—Santa Clara Formation, Barranca Group, Carnian—and/or Norian?—Late Triassic.

Derivation of name—*Yaqui*, from the name of an indian tribe, the Yaqui, that settles in the southern part of Sonora, Mexico.

Material—The type palaeodeme has been sampled on several occasions between 1979 and 1983 by the first author and students of the Facultad de Ciencias, UNAM. Some 30 specimens, all with number IGM-PB-515 were collected, but there are more leaf fragments. Although the bed bearing these specimens could not be located at the outcrop, at the time of collecting, the first author has since found a stratum with numerous specimens of the species in the type section. However, the quantitative work of this study was finished earlier, and the new material is not included here. The following observations are based on the type palaeodeme. All specimens seem to belong to one stratum of fine grained shale, which is organic-rich, almost black and crossed by fossil roots. At the same locality, good specimens of *Laurozamites fragilis* and *L. tarahumara* var. *dubius* were also found, but they stem from different strata and are easily distinguished in the field. The type palaeodeme of *L. yaqui* is doubtless homogeneous.

The species is not common in the Santa Clara Formation. The specimens figured by Weber and coworkers (1980b, fig. 11, b, c, h) have been given new catalog numbers, and are figured again here (Plate 3, figures 2, 3, 7). The new numbers

are given in the caption to Plate 3. Those figured by Weber and coworkers (1980a, figs. 11, i, j; 12, d) have been given the numbers IGM-PB-515-531 and IGM-PB-515-435, respectively.

Description—The material of the type palaeodeme is generally fragmented or damaged by root action. No complete leaves were found and their form can only be tentatively reconstructed. The qualitative leaf features are not very constant in this species. This is especially true regarding the auricles which are most prominent in the proposed holotype (Plate 3, figures 2, 3) and in the specimen of Plate 3, figures 4, 5. The latter leaf has subopposite pinnae detached form the rachis due to stress at the time of burial or splitting during collecting. In one of the auricles, a submarginal vein that curves back to the rachis can be observed. The remaining veinlets of the auricle spread out from this vein. The holotype, figured on Plate 3, figures 2, 3, which has alternate pinnae, shows an *Otozamites*-like arrangement of the acroscopic pinnae auricles, which cover the rachis almost completely. The coarse cortical wrinkles of the rachis, which are a distinguishing feature of this species, are especially well preserved in the specimens of Plate 3, figures 1, 7 (x 2).

No value for the length of the leaves is given in the diagnosis. All specimens known to date are too badly fragmented to enable generalizations. The specimen shown on Plate 5, figure 1, which does not belong to the type palaeodeme, is part of a large leaf which probably was about 25 cm long (19 cm preserved).

The length/width ratios of the largest pinnae of 51 leaf fragments from the type palaeodeme are shown in Figure 9. The resulting cloud is simple and appears as a well recogniz-

Figure 9.- Graph showing the length-width ratios for largest pinnae of 51 leaves of *Laurozamites yaqui*, belonging to the type palaeodeme from locality 515 (sampling area 4).

PLATE 3.- *Laurozamites yaqui* sp. nov. (all except figure 9 from type palaeodeme, locality 515, La Barranca-Santa Clara sampling area, figures 2, 4, 6, 8 and 9, x 1). Figure 1—Central portion of leaf, enlarged to show venation of pinna bases and cortical wrinkles of rachis; specimen IGM-PB-515-674, x 2. Figures 2 and 3—Leaf of medium size, with well developed auricles; holotype specimen IGM-PB-515-533a; figure 3, x 3. Figures 4 and 5—Middle portion of large leaf; acroscopic auricles very well developed, covering the rachis, which is not preserved; specimen IGM-PB-515675; figure 5, x 2. Figure 6—Specimen IGM-PB-515-676. Figure 7—Small leaf fragment enlarged to show venation and cortical wrinkles of rachis; specimen IGM-PB-515-535, x 2. Figure 8—Specimen IGM-PB-515-677. Figure 9—Small leaf with very conspicuous petiole; locality 537B, San Enrique (Los Pilares sampling area), specimen IGM-PB-678a; the identity of this specimen with *L. yaqui* is not proven statistically.
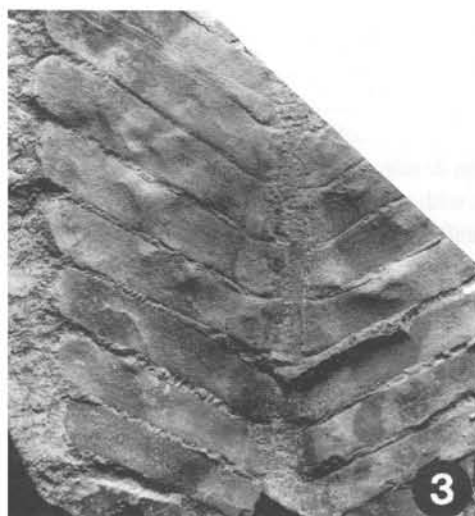
able component of the cloud seen in Figure 7. This observation becomes even more striking when Figure 11 is compared.

Comparison—The previously described species *L. macombii* (Newberry) Weber and Zamudio-Varela comb. nov. resembles *Laurozamites yaqui* rather closely. This was described by Newberry (1876, pl. 4, pl. 5, fig. 3) from the Late Triassic of Copper Mines near Abiquiu, New Mexico. He also referred one specimen from the Santa Clara Formation to this species (Newberry, *op. cit.*, pl. 6, fig. 5), but the authors have assigned it to *L.* ex gr. *fragilis* (Newberry) Weber and Zamudio-Varela. *L. yaqui* and *L. macombii* are doubtless closely related species, and taking into account that the original drawings of Newberry (1876) are possibly a bit unexact, it is not easy to defend the segregation of the new species. To do that, it is necessary to use features which might be unstable in both species.

    Laurozamites macombii has short petioles of hardly 1 cm in length (Newberry, 1876, pl. 4, fig. 1), whereas *L. yaqui* shows longer ones (Plate 3, figure 7). *L. macombii,* according to all illustrations of Newberry, lacks the cortical wrinkles which are so marked in *L. yaqui* (preservation damage?), but shows longitudinal striae. *L. macombii* does not possess prominent auricles at the pinna bases, the rachis is not covered by them, and the pinnae are more symmetrical than in *L. yaqui,* where they reach a maximum width of 13 mm. In *L. macombii* this width is attained by the pinnae of three or four leaves figured by Newberry and in one of them (pl. 5, fig. 3), the pinnae become almost 2 cm wide. In *L. macombii* the veins diverge along most of the length of the pinnae (Newberry, 1876, pl. 4, figs 1, 2), whereas in *L. yaqui,* the veins are parallel or subparallel in the distal half of the pinnae. In addition, Ash (1975) mentions that in *L. macombii,* the venation density of the middle portion of the pinnae is only 20 veins/cm, whereas in *L. yaqui* it lies between 40 and 60 veins/cm.

    Accordingly, despite no modern study of *L. macombii* is available, the authors decided to erect *L. yaqui* as a separate species.

Laurozamites pima Weber and Zamudio-Varela sp. nov.
Figure 10; Plate 4, figures 1-7

Previous records from Sonora

1982 *Zamites* aff. *powellii* Fontaine.- Weber and coworkers, 1980b, p. 130, figs. 3, d, e.
1985 *Zamites* aff. *powellii* Fontaine.- Weber, 1985a, p. 119, tab. 2 (name only).

Diagnosis—Leaf lanceolate or oblong-elliptical in outline, largest leaves over 10 cm wide. Petiole up to 5 cm long or slightly longer, with broadened base up to 1 cm or more in width. Rachis up to 7 mm wide near blade base, with conspicuous cortical wrinkles up to 0.5 mm broad. Pinnae attached at the upper side of the rachis at an angle of 45-85° (mean 70°) in the middle part of the blade, opposite or rarely perfectly alternate, imbricate in a small degree, with touching or slightly distant margins, straight or slightly curved; auricles often conspicuous, sometimes lacking, the acroscopic ones larger, limited to the basal 3 mm of the lateral margins; distal margin obliquely truncate, sometimes slightly emarginate or rounded; largest pinnae of the leaves 2-6 cm long (mean 4 cm), 4-8 mm wide (mean 5.5); length/width ratio 10 (mean 7). Venation very fine, only slightly divergent at the pinna base; venation density 40-60 veins/cm. Venation of the auricles not distinct.

    Holotype—Specimen IGM-PB-516-506 (Plate 4, figure 7).

    Type palaeodeme—All specimens with leaves of *Laurozamites pima* from the type locality. Specimens selected from the type palaeodeme are figured on Plate 4, figures 1-5, 7.

    Type locality—Hermosillo-Tónichi highway, Km 153, near La Barranca (loc. 516, CLP-IG-UNAM, Figure 4), road cut, southern side of road; 28°34'35"N/109°39'50"W, Sonora, Mexico.

    Type stratum and age—Santa Clara Formation, Barranca Group, Carnian—and/or Norian?—Late Triassic.

    Derivation of Name—*Pima,* from the name of an indian tribe, the Pima, who settled in central Sonora, east of Hermosillo, and have now been assimilated into the population of Sonora.

    Material—The type palaeodeme was sampled in 1979 by students of the Facultad de Ciencias, UNAM, under the guidance of L.A. Herrera-Gil, and in 1981 by R. Trejo-Cruz. The material includes 175 specimens with the number IGM-PB-516. All the *Laurozamites* leaves collected from the site doubtless belong to the palaeodeme described here. Several additional localities yielded material identical to the type palaeodeme. Particularly important among them is Unit 28 (LB 5) of La Barranca Section 2, measured in 1980 by Potter and coworkers (Loc. 523; Figure 4), with 100 specimens. This material was used together with the type palaeodeme to prepare Figure 10. The species is not very consistent in occurrence in the Santa Clara Formation, but locally, above all in the La Barranca area, it becomes very abundant.

PLATE 4.- *Laurozamites pima* sp. nov. (all except figure 6, from type palaeodeme, locality 516, La Barranca-Santa Clara sampling area; all x 1, except figure 2). Figures 1 and 2—Central part of medium size leaf, enlarged in figure 2 to show venation and cortical wrinkles; specimen IGM-PB-516-679 (after the photograph was made, the left part of the specimen was lost); figure 2, x 2. Figure 3—Medium size leaf; specimen IGM-PB-516-505a. Figure 4—Distal part of relatively small leaf, with apex preserved; specimen IGM-PB-516-680. Figure 5—Fragment of very small leaf; specimen IGM-PB-516-681. Figure 6—Basal part of medium sized leaf with petiole preserved; cortical wrinkles; specimen IGM-PB-523A-682a from locality 523A, La Barranca-Santa Clara sampling area. Figure 7—Fragment of large and medium sized leaves; holotype specimen IGM-PB-516-506.
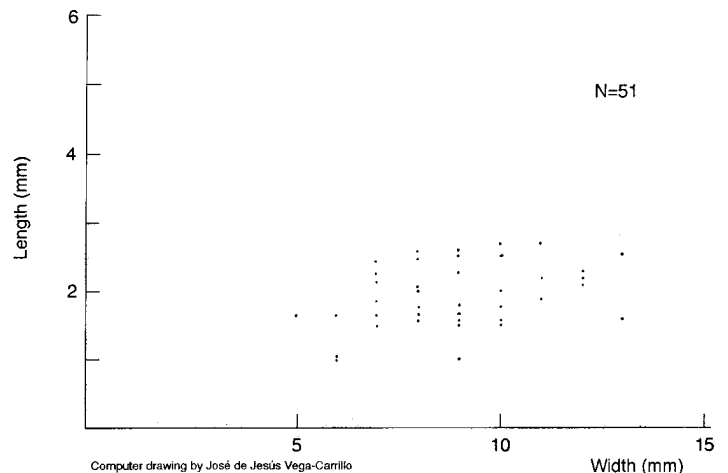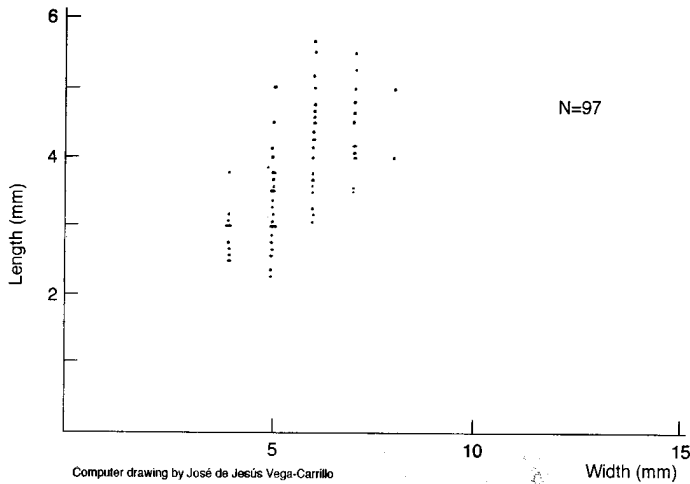
Figure 10.- Graph showing the length-width ratios for largest pinnae of 97 leaves of *Laurozamites pima*, belonging to the type palaeodeme from locality 516 and an additional palaeodeme from locality 523 (sampling area 4).

Description—Little remains to be added to the qualitative characters given in the diagnosis. The leaves are variable, most notably in that the pinnae are sometimes lacking the auricles. Though this may sometimes be due to preservation, such leaves look quite similar to those of *Pterophyllum*. The largest leaves probably reached a length of about 30 cm or more. The material is generally badly fragmented and includes very few specimens with preserved petioles or apices. The data regarding the petiole given in the diagnosis are based on one specimen of the type palaeodeme. The last pinnae of the blade are frequently inserted at an angle of less than 45° and show a tendency to cuneiform outline. The last pinna appears to be a continuation of the rachis (Plate 4, figure 4).

The larger leaves, especially, appear to have been coriaceous and not flexible in life. The leaves rarely lack pinnae, which were persistent, in contrast with the whole leaves which were shed by abscission.

The length/width ratios of the largest pinnae of 97 foliar fragments selected from the type palaeodeme and from locality 523, are shown in Figure 10. The cloud representing these values in the graph is very uniform and clearly stands apart from that in Figure 7. It is even more easily recognized as representing an independent species when Figures 10 and 11 are compared.

Comparison—Aguilera and Ordóñez (1893) recorded *Zamites occidentalis* Newberry from the Santa Clara Formation, but they published neither description nor illustrations. An obsolete unpublished manuscript by Aguilera (1938) handed out to the senior author by G. Alencáster, however, shows a very poorly preserved specimen (pl. 3, fig. 10) which indeed resembles *Zamites occidentalis* Newberry 1876 from the Copper Mines near Abiquiu, New Mexico. Aguilera (1938, pl. 3, fig. 12) illustrated an additional specimen identical to *Laurozamites pima* under the name *Ctenophyllum latifolium* (non valid ms. name). The precise localities of these specimens are not given in the manuscript, although it is reasonable to suppose that they were collected by

Aguilera himself in the area of Los Bronces, near San Javier (*cf.* Aguilera and Ordóñez, 1897).

Zamites occidentalis Newberry most closely resembles *Laurozamites pima* in the North American Triassic. The original description of the former is very poor and the illustrations (Newberry, 1876, pl. 5) may be misleading, although the lithographed drawings of the Sonoran material, published in the same paper, are quite good. In contrast to *Laurozamites pima*, the pinnae of *Zamites occidentalis* attain a maximum width of only 5 mm half way between the base and apex, they are lanceolate in outline with subacute to rounded apex and are never truncate. The auricles seem to be poorly developed, but this may perhaps be related to the quality of the drawings rather than to the material. The drawings, furthermore, do not enable to judge whether *Zamites occidentalis* Newberry can be assigned to *Laurozamites*.

Other material resembling *Laurozamites pima* was described by Hope and Patterson (1969, pl. 10) as *Otozamites hespera* Wieland. It is redescribed here as *Laurozamites paraiconicus* comb. nov. As far as it is possible to judge from the illustrations given by Hope and Patterson (*op. cit.*) and Delevoryas and Hope (1976, pl. 1, 2), the leaves of this species are smaller in all dimensions than those of *Laurozamites pima*.

Laurozamites tarahumara Weber and Zamudio-Varela sp. nov.

Plate 5, figure 2; Plate 6, figures 1-5, 7-8

Previous records from Sonora

1982 *Zamites* aff. *fragilis* (Newberry).- Weber and coworkers, 1980 (1982)b, tab. 2 (name only).
1985 *Zamites* Brongniart, sp. A var. A and var. B.- Weber, 1985a, tab. 3 (name only).

Diagnosis—Leaf lanceolate, oblong-elliptical or oblanceolate in outline, petiolate. Rachis straight, with scarce cortical wrinkles on adaxial face. Pinnae attached at an angle of 65 to 80°, straight or slightly curved, subrectangular in outline; basal corners with or without auricles, distal corners rounded. Veins well marked, relatively thick; venation density between 20 and 40 veins/cm. Acroscopic auricles sometimes with sigmoid submarginal vein curved back towards the rachis.

Holotype—See under the var. *tarahumara* and *dubius*.

Type locality—The El Crucero locality, Stratum A (loc. 537 A, CLP-IG-UNAM, Figure 5), road-cut, 28°33'02"N/ 109°21'10"W, Sonora, Mexico.

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

Derivation of name—*Tarahumara*, from the name of an indian tribe, the Tarahumara, that settles in eastern Sonora and Chihuahua.
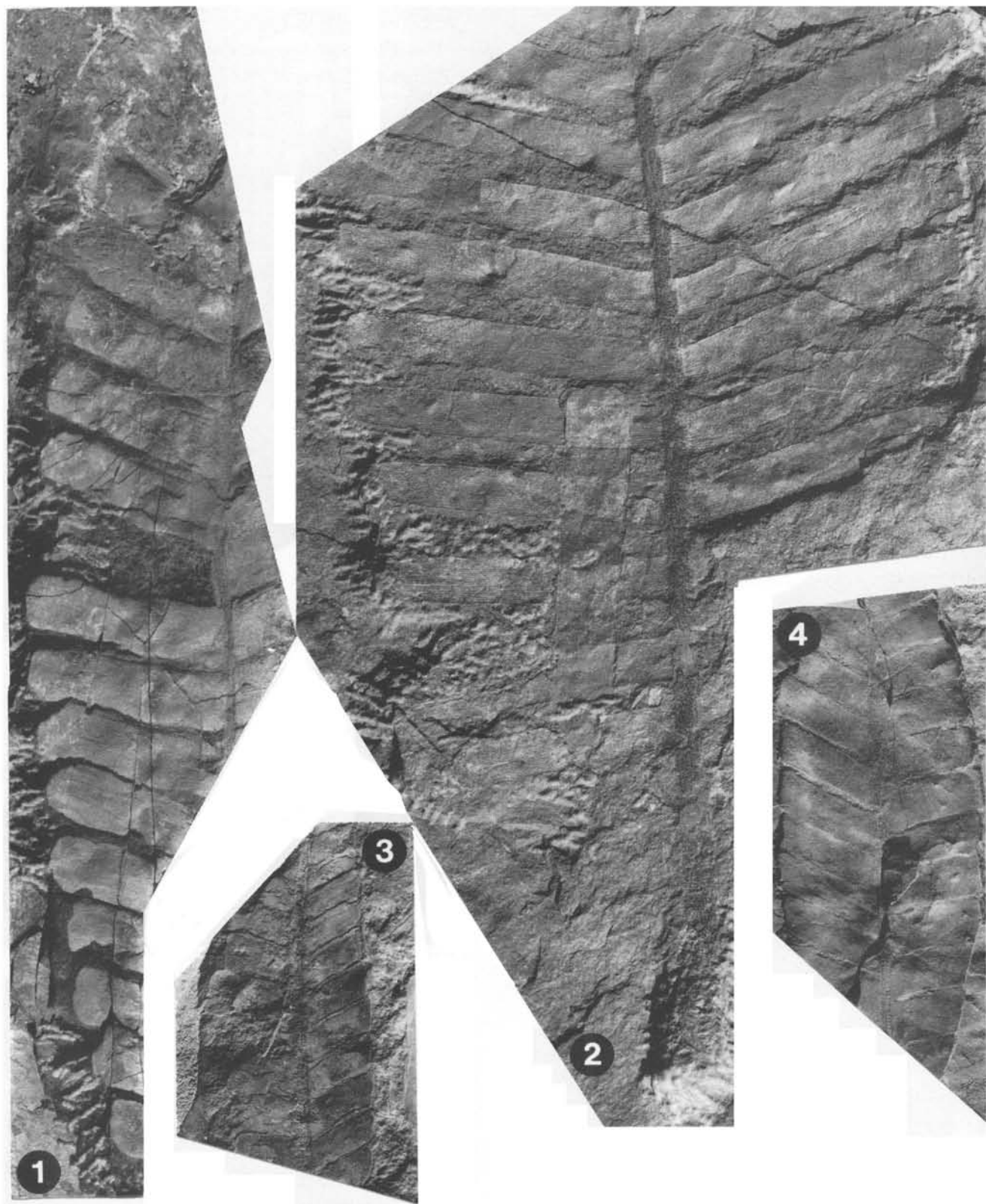
PLATE 5.- Figure 1—*Laurozamites yaqui* sp. nov.; large leaf fragment; locality 537B, El Encinal (Los Pilares) sampling area; specimen IGM-PB-527B-683, x 1.
Figure 2—*Laurozamites tarahumara* sp. nov. var. *tarahumara*; type specimen IGM-PB-527A-684a; locality 537A, El Encinal (Los Pilares) sampling area, x 1.
Figures 3 and 4—*Laurozamites* ex gr. *fragilis* (Newberry); fragments of two leaves; note the very straight delimitation of the leaf margin; locality 509, La Cuesta-Buenavista sampling area; specimens IGM-PB-509-536a and 685, x 1.
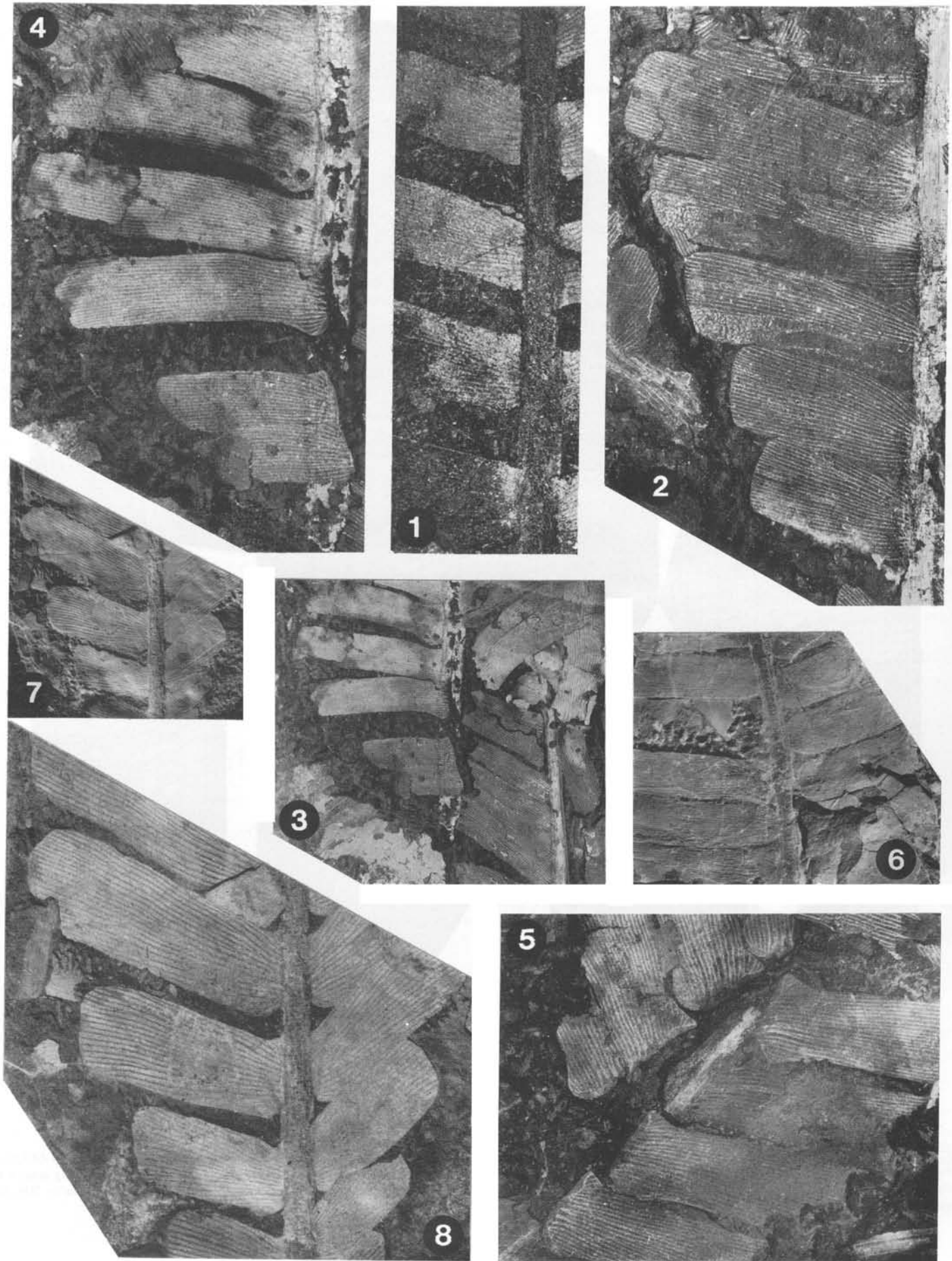
Material—About 85 slabs with leaf fragments of this species were collected. The most outstanding localities are mentioned under the varieties. Except one belonging to the var. *dubius*, the specimens belong to the typical variety. The material assigned to *Laurozamites tarahumara* is relatively poor and mostly not well preserved. It was not possible to find a palaeodeme as homogeneous and rich as those of the previously described species. The type variety was found mainly in the San Enrique—or Los Pilares—area (area 5, Figure 5); and var. *dubius* was collected from the type section of the Santa Clara Formation, near La Barranca (area 4, Figure 4).

Plate 6, figure 6 shows a specimen from a palaeodeme of about 50 specimens (loc. 532A, sampling area San Javier) which closely resembles *L. tarahumara*. It was originally described in this paper as a variety of this species. However, no doubtless auricles were observed in the assemblage.

Laurozamites tarahumara var. *tarahumara* Weber and Zamudio-Varela var. nov.
Plate 5, figure 2; Plate 6, figures 1-5

Previous records from Sonora

1982 *Zamites* aff. *fragilis* (Newberry).- Weber and coworkers, 1980b, tab. 2 (name only).
1985 *Zamites* Brongniart, sp. A var. A.- Weber 1985a, tab. 3 (name only).

Diagnosis—Leaf to more than 25 cm in length and up to 12 cm wide. Petiole widened at base, tapering towards blade base, 1 cm of basal width. Rachis straight, up to 7 mm wide near blade base. Pinnae attached at adaxial sides of rachis, leaving a free adaxial longitudinal zone at least 1 mm in width. Pinnae often imbricate, at least basally, or separate by spaces up to 5 mm wide, pinnae up to 7 cm long (mean 4.5 cm) and 12 mm wide (mean 7.5 mm); length/width ratio of largest pinnae up to 10.5 (mean 6). Venation density in middle part of pinnae 25-35 veins/cm. Auricles normally present, sometimes with sigmoid submarginal vein curved back towards rachis.

Holotype—Specimen IGM-PB-537A-684a, b (Plate 4, figure 2; Plate 5, figure 3).

Type locality, stratum and age—The same as for the species.

Derivation of name—See under the species.

Material—The variety was collected in 1980 and 1981 by A. Torres-Romo, R. Trejo-Cruz and Á. Zambrano-García. It consists of about 85 specimens from the type locality and from loc. Consejo de Recursos Minerales (CRM), Borehole 71 (loc. 517, CLP-IG-UNAM, Figure 5). Only one specimen was found outside the San Enrique area, at the Río El Tule locality (loc. 508, CLP-IG-UNAM, Figure 2).

Description—The holotype (Plate 5, figure 2; Plate 6, figure 1) shows the basal part of a large leaf—20 cm in preserved length—which must have reached over 25 cm. This species, therefore, falls within the length range of *Laurozamites pima*. Most of the leaves, however, are smaller. Of particular interest are the specimens figured in Plate 6, figures 2-5, from the Borehole 71 locality, which are preserved in a rather fine grained claystone extremely rich in dispersed organic matter and almost black in colour. The fossils collected from this type of rock show well preserved venation details. A submarginal vein curved back to the rachis is present in the almost triangular acroscopic auricles (Plate 6, figure 5). Such a vein is also present in the less prominent basiscopic auricle, but it is neither curved back nor sinuous. This vein, however, does not compare with the curved venation of the acroscopic auricle in *Otozamites*.

Comparison—Some specimens—not figured here—from the El Crucero locality are tentatively referred here to *Laurozamites tarahumara* var. *tarahumara*. They show relatively long and wide pinnae more or less cuneiform in shape and lack auricles. They resemble certain specimens of *Zamites* cf. *truncatus* Zeiller, which will be described and discussed elsewhere. In general terms, no other species resembling closely *L. tarahumara* var. *tarahumara* is described in the North-American literature. The only similar specimen is the leaf of *L. powellii* figured by Ash (1975, pl. 1, fig. 6). Its auricles are rudimentary, if not absent, and it has lower venation density than the bulk of *L. powellii*; hence, it may not belong to that species.

Laurozamites tarahumara var. *dubius* Weber and Zamudio-Varela var. nov.
Plate 6, figures 7 and 8

Diagnosis—Leaf with subopposite pinnae; pinnae attached at angle of 70-80°, with small, subtriangular auricles and rounded truncate distal margin. Venation divergent within basal half of pinna, parallel in distal half. Veins rather thick; venation density in middle portion of the pinnae 20 veins/cm.

PLATE 6.- *Laurozamites tarahumara* sp. nov. Figures 1-5—*Laurozamites tarahumara* var. *tarahumara* var. nov. Figure 1—Detail of type specimen shown on Plate 5, figure 2, enlarged to show pinna bases and venation, x 2. Figures 2-5—Specimens from locality 517, El Encinal (Los Pilares) sampling area; all x 2, except figure 3. Figure 2—Pinnae of basal part of leaf, enlarged to show venation; specimen IGM-PB-517-686. Figures 3 and 4—Fragments of badly fragmented leaves showing good details of venation and shape of pinna bases; specimen IGM-PB-517-687; figure 3, x 1. Figure 5—Note venation in the acroscopic auricles of pinnae; a submarginal vein curved back towards the rachis is present in several pinnae; specimen IGM-PB-517-688a. Figure 6—*Laurozamites tarahumara* sp. nov. (?); leaf fragment with pinnae lacking auricles; possibly a variety of this species; specimen IGM-PB-532A-689. Figures 7 and 8—*Laurozamites tarahumara* var. *dubius* var. nov.; note thick veins and very low venation density; holotype specimen IGM-PB-515-690A; locality 515, La Barranca-Santa Clara sampling area; figure 7, x 1, figure 8, x 2.

Holotype—Specimen IGM-PB-515-690a, b (Plate 6, figures 7, 8).

Type locality—Hermosillo-Tónichi highway near La Barranca. Type section of the Santa Clara Formation (measured by Potter *et al.*, 1980) Units 1-7 (loc. 515, CLP-IG-UNAM, Figure 4). Roadside talus. The bed with this plant could not be determined in the outcrop, 28°34'08"N/109°39'35"W, Sonora, Mexico.

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

Derivation of name—*Dubius* (lat.), doubtful.

Observation—The variety differs from the above described materials of *Laurozamites tarahumara*, mainly in the thickness of the veins and the extremely low venation density. The holotype slab, in addition to the foliar fragment illustrated on Plate 6 (figures 7, 8) shows two pinna fragments on its back side, which show the same diagnostic features. Hence, there are remains of two very similar leaves, which offer a sufficient basis for the description of a separate variety.

Laurozamites ex gr. *fragilis* (Newberry) Weber and Zamudio-Varela
Plate 5, figures 3 and 4

A number of more or less superficially sampled localities bear leaf remains of *Laurozamites* gen. nov., which cannot be identified with the species recognized here, either because they fall in the part of the generic cloud (Figure 7) where these species overlap, or due to subtle peculiarities in qualitative characters. No description and further analysis of these materials is attempted here.

When carrying out their study on the complex of *L. fragilis* already mentioned above, Trejo-Cruz and Weber (1984) worked only with the type palaeodemes of *L. fragilis*, *L. yaqui* and *L. pima*. In order to obtain less subjective results, the work reported here deals with specimens from as many localities as possible, with preservation—largest pinnae of the leaves preserved—being the only selection criterion. Figure 11 shows the length/width ratios for the largest pinnae of those specimens remaining after removing from the full sample of 504 leaf fragments (Figure 7), the specimens collected at localities 1101 (type palaeodeme of *L. fragilis*), 515 (those belonging to the type palaeodeme of *L. yaqui*), 516 (type palaeodeme of *L. pima*) and 526 (additional palaeodeme of *L. pima*); the locality numbers are those of the CLP-IG-UNAM. The figure thus shows values only of a residual sample of 163 leaves still including a number of *L. fragilis*, some *L. pima* and very few *L. yaqui* as described above.

Even when the leaf fragments corresponding to these latter two species are not considered, the residual cloud still does not coincide with that of the type palaeodeme of *L. fragilis* (Figure 8), but shows a trend to slightly higher length
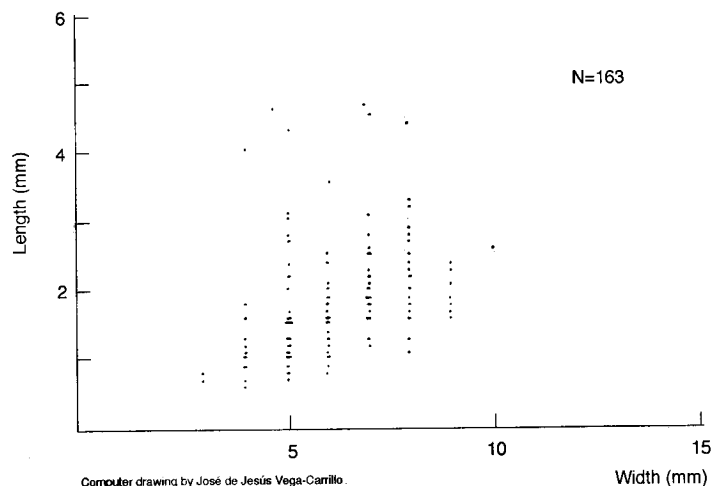

Figure 11.- Graph showing the length-width ratios for largest pinnae of 163 leaves of *Laurozamites*, after removing from the whole sample of 504 leaves (Figure 7) those used for the graphs in Figures 8-10.

and width values. Although *L. fragilis* is the most constant and abundant species of the genus in the Santa Clara taphoflora, a considerable number of specimens of the residue cannot be referred to this species in its new definition. If the afore-designated type palaeodeme is taken as a standard, the presence of one or more undescribed taxonomic units, species or otherwise, within the residue must be assumed at least hypothetically.

During the field work and the preliminary identification of the present materials, it was already noted by the senior author that most of the specimens from localities Camino El Tule/Chamina (loc. 509, CLP-IG-UNAM; Figure 2), Mina Tiro de Luis (loc. 512, CLP-IG-UNAM; Figure 2) and San Javier, Section 2, Units 5 or 6 (loc. 530, CLP-IG-UNAM; Figure 3) taken together may represent such an additional species or variety. These specimens are distinguished by their smaller pinna width from *L. yaqui* and in their generally somewhat larger dimensions from *L. fragilis*. They are more distinct, above all, in certain qualitative features (Plate 5, figures 3, 4). These leaves seem to have been quite stiff in life, the pinnae are often more or less imbricate or contiguous, and their apices are often abruptly and evenly truncate as if they had been jointly cut with plate-shears. To this material also belong the specimens figured by Weber and coworkers (1980a, fig. 12, a, d, f).

It was decided not to describe a new formal taxonomic unit on the basis of this material, because no reliable diagnostic features could be found and no palaeodeme granting a clear quantitative definition has been uncovered so far.

ASSIGNMENT OF SPECIES FROM THE UNITED STATES OF AMERICA TO LAUROZAMITES

Laurozamites macombii (Newberry) Weber and Zamudio-Varela comb. nov.

Previous records

1876 *Otozamites macombii* Newberry.- Description of fossils, Newberry, 1876, p. 141-142, pro parte, pl. 4, fig. 1, 2; pl. 5, fig. 3 (from Abiquiu, New Mexico; refigured by Ash, 1974, fig. 3, 1, 2; fig. 4, 3).

1916 *Otozamites macombii* Newberry (?).- Humphreys, 1916, p. 77 (not figured; "exceedingly provisional identification" of material from Sonora).

Diagnosis—See Newberry, 1876, p. 141.

Holotype—Newberry, 1876, pl. 4, fig. 2.

Type locality—Copper Mines, Cañón del Cobre, near Abiquiu, New Mexico, USA (see Ash, 1974).

Type stratum and age—Agua Zarca Sandstone Member, Chinle Formation; Carnian, Late Triassic.

Derivation of name—*Macombii*, in honour of Captain Macomb, leader of the exploring expedition from Santa Fe, New Mexico, to the junction of the Grand and Green Rivers...in 1859.

Comment—The species is compared with *Laurozamites yaqui* (see above).

Laurozamites powellii (Fontaine) Weber and Zamudio comb. nov.

Previous records

1890 *Zamites powelli* Fontaine.- Fontaine, *in* Fontaine and Knowlton, 1890, p. 284, fig. 5-7 (poor illustrations).
1975 *Zamites powelli* Fontaine.- Ash, 1975, p, 145-151, text-fig. 1, 3, 4; pl. 1, 2.
Further records: see Ash, 1975.

Diagnosis—See Ash, 1975, p. 145.

Type material—USNM 175704-6.

Type locality—Copper Mines, Arroyo del Cobre near Abiquiu, New Mexico, USA.

Type stratum and age—Chinle Formation, Carnian, Late Triassic.

Derivation of name—*Powellii*, in honour of Major Powell, collector of the type material.

Comment—The species, as delimited by Ash (1975), seems to embrace a number of minor, perhaps infraspecific taxonomic units. The addition of an i to the specific epithet is an orthographic modification required by the International Code of Botanical Nomenclature (Greuter *et al.*, 1988), which was already used by Ash after his 1975 paper.

Laurozamites paraiconicus Weber and Zamudio-Varela sp. nov.

Previous records

1969 *Otozamites hespera* Wieland.- Hope and Patterson, 1969, p. 9-10, pl. 10, fig. 1-4 (erroneous identification).
1976 *Ischnophyton iconicum* Delevoryas and Hope.- Delevoryas and Hope, 1976, p. 95-99, pro parte, pl. 2.

Holotype—Specimen BP 154 (Hope and Patterson, 1969, pl. 10, fig. 1).

Type palaeodeme—All specimens with detached leaves of *Laurozamites paraiconicus* from the type locality. Several leaves from the type palaeodeme were figured by Hope and Patterson (1969, pl. 10).

Type locality—Boren Clay Products Company quarry 1 mile north of Gulf, North Carolina, USA (Hope and Patterson, 1969, p. 2).

Type stratum and age—Pekin Formation, Late Triassic.

Derivation of name—*Paraeikonikos* (gr.), joint to the species *Ischnophyton iconicum.*

Comment—The species is erected here to embrace detached leaves of *Ischnophyton iconicum* Delevoryas and Hope 1976. The species is compared with *Laurozamites pima*. Even though, in the figures published by Hope and Patterson (1969) the auricles at the pinnae bases are not easily distinguished, Delevoryas and Hope (1976) mentioned that "there is a tendency for auricles to occur at the base, and these are occasionally asymmetrical". This observation corroborates the generic assignment proposed here.

DISCUSSION

ASSIGNMENT OF LAUROZAMITES TO THE BENNETTITALES

Association of Laurozamites *with* Williamsonia *and* Weltrichia

The assignment of the Sonoran *Laurozamites* leaves to the Bennettitales might be questioned, because cuticles are missing. *L. fragilis* comb. nov., however, was found together with a good number of specimens of one kind of *Williamsonia* (Plate 1, figure 1) and one specimen of *Weltrichia* at the type—protype—locality, where no other *Laurozamites* occurs (Weber *et al.*, 1980b, fig. 4, b-d). At the El Tule locality—loc. 508 CLP-IG-UNAM—*L. fragilis* was found in association with a *Weltrichia* identical to the above mentioned specimen (Weber *et al.*, 1980b, fig. 4, a). Both reproductive structures

belong most likely to the *L. fragilis* plant. Similar specimens of *Williamsonia* are associated with *Laurozamites* leaves at several localities, and recently—1993—a slab with another *Weltrichia* and *L. pima* was collected from roadside talus near locality La Barranca, Section 2, Unit 28 (loc. 523; Figure 4). At this locality, *L. pima* is one of the most abundant species. This *Weltrichia* is close to the one of the *L. fragilis* localities in shape, but it is considerably larger. No such reproductive organs are known to belong to *Macrotaeniopteris* sp. A or *Zamites* cf. *truncatus* which are also reasonably abundant at the type—protype—locality of *L. fragilis*. The recurrent association in the Santa Clara Formation of *Laurozamites* leaves with a certain type of bennettitalean reproductive structures corroborates the authors placement of the type species in the Bennettitales.

Zamites *and* Laurozamites

    The genera *Zamites* Brongniart 1823 (or Z. Braun 1842; Ash, 1975) and *Pterophyllum* Brongniart (to both of which the present material of *Laurozamites* has been previously referred) belong, according to Andrews (1970), to those form genera which due to their very early definition, the great fluctuations in their definition or "to innumerable name changes in the cycadophyte leaf genera..." have rather little systematic meaning. They cannot really be considered "good" genera. This situation was not substantially improved through the above mentioned classification scheme introduced into the North American literature by Ash (1975). In the most modern version of this scheme, proposed by Watson and Sincock (1992), characters of pinna shape, proportions, margin, and venation—and even cuticular characters in one case—are used to distinguish a number of form genera among bennettitalean leaves. Among these, *Pseudocycas, Eoginkgoites, Sphenozamites* and *Neozamites* seemingly are rather "natural" taxa. However, the highly "artificial" genera *Ptilophyllum, Otozamites, Zamites* (and *Pterophyllum/Anomozamites*) are differentiated only on the basis of pinna insertion. Strictly speaking, *Pterophyllum* and *Anomozamites* are distinguished (*i. e.,* additionally defined) on the basis of pinna proportions. Hence, the bulk of the bennettitalean leaves is placed in form genera which are distinct only in one set of mutually excluding characters of attachment. The practical difficulties arising from this are evident in Watson and Sincock's (1992) generic identifications of *Zamites dowellii* (*op. cit.,* fig. 34, D), *Ptilophyllum ashleyi* (*op. cit.,* fig. 68, B) and *Pterophyllum fontarianum* (*op. cit.,* pl. 13). The merit of the Watson and Sincock's (*op. cit.*) classification lies in allowing, *cum grano salis,* to place each bennettitalean leaf in its genus, but it is not suitable to distinguishing reasonably natural groups within the *Otozamites, Zamites, Pterophyllum* (with *Anomozamites*) and *Ptilophyllum* complex.

    Andrews (1970) selected the Jurassic species *Zamites gigas* (Lindley and Hutton) Morris 1843, from Yorkshire, England, as the type species of *Zamites.* This species belongs

to the same kind of *Zamites* leaves represented in the Middle Jurassic of Mexico by species such as *Z. oaxacensis* (Wieland) Person & Delevoryas 1982, characterized by leaves with lanceolate pinnae which are widest near the base, lack lateral expansions or auricles at the base and are acute tipped. If the selection of the type species by Andrews was correct—the authors have no reason to doubt—the genus *Zamites* should in the future include only leaves of this kind.

    In contrast, the species of the Santa Clara taphoflora which at one time or another were referred to *Zamites* in agreement with the implicit diagnosis of Ash (1975), are quite different from those related to *Z. gigas.* A first group of species from Sonora, which is taxonomically difficult, includes *Zamites* cf. *truncatus* Zeiller, and is clearly distinguished from *Z. gigas* by its leaves with relatively large pinnae which are commonly opposite or subopposite—not a very stable character—have flabellate or spatulate shape, lack basal auricles and often show rounded dots—resin bodies?—between the veinlets. The pinnae are, in addition, often detached from the rachis—or, conversely, leaves that do not lack pinnae are seldom encountered. This kind of *Zamites* is closely related to *Glandulozamites* Bock (based on the former *Sphenozamites rogersianus* Fontaine) from the Late Triassic of Virginia, *Macropterygium bronnii* (Schenk) Schimper from the Late Triassic of Austria and other more or less coeval similar species. The second group of species from Sonora, placed previously in *Zamites,* is the one here referred to the new genus *Laurozamites.* It is distinguished from the former by its commonly alternate or subalternate, more or less rectangular pinnae with basal auricles and often truncate apices.

    In his paper on *Zamites powellii,* Ash (1975) discussed the generic assignment. He avoided erecting a new genus from this species, although he observed that it did not exactly fit into his own concept of *Zamites.* This was to avoid new problems of delimitation created through elimination of others. Such a decision, from the point of view of mere morphological and descriptive practice, seems to be reasonable, but it cannot be easily accepted in phytogeography, where natural and operative supraspecific taxa other than the form genera like *Zamites* are needed.

    In fact, the proposed new genus *Laurozamites,* including the species discussed by Ash (1975), seems to be restricted to North America—except one Jurassic record from Sudan, *"Pterophyllum" nubiense* Lejal-Nicol 1984. Besides its morphological and descriptive delimitation, the genus has a limited geographic distribution which corroborates its segregation.

    Decisions such as the present proposal of the new genus *Laurozamites* were probably meant by Harris (1969) in his following remarks: "It is tempting to avoid taxonomic difficulty in a particular flora by creating new genera, and several have been made though they are not used widely...". Doubtless, Ash (1975) had this comment in mind when he decided not to create a new genus for *Zamites powellii.* However, this decision was too cautious, because this and other species assigned

here to *Laurozamites* do not agree with the generic diagnosis written for *Zamites* Brongniart by Harris (1969): "Leaf simply pinnate, pinnae attached to upper side of the rachis; pinnae lanceolate, base of pinna symmetrically contracted and attached by a small area in middle of basal margin; apex of pinna acute; veins diverging from pinna base, dichotomizing but not anastomosing; ending in pinna margins or apex. Cuticle..." *Laurozamites* clearly does not have lanceolate pinnae and the pinnae do not have acute apices. Recently, Watson and Sincock (1992) emended Harris's (1969) diagnosis of *Zamites* as follows: "Leaf once pinnate, pinnae attached to upper surface of rachis. Base of pinna symmetrical, usually contracted to narrow region of attachment in middle of basal margin; rarely proximal portion of pinna narrowing to wide attachment area with basal angles little contracted. Veins parallel or diverging from pinna base...". After this diagnosis, *Zamites* includes *Laurozamites* and the leaves with cuneate-truncate pinnae of *Zamites* cf. *truncatus* and related species mentioned above. The present authors consider this diagnosis too wide, even though it is said to suffice in the English Wealden (Watson and Sincock, 1992).

Generic diagnosis and type species of Laurozamites *gen. nov.*

Cuticular characters were not taken into account in the generic diagnosis, since within the genus they are known only in *Laurozamites powellii and L. paraiconicus.* The first species is known in great detail, but it is not proposed here as the type species of the new genus, because it was described by Fontaine (1890) later than *L. fragilis* (Newberry, 1876). In addition, *L. powellii* seems to embrace a heterogeneous assemblage of species or subspecific taxa which should be defined after new extensive collecting at many of the widely scattered localities listed by Ash (1975). Preference was given to *L. fragilis* (Newberry) emend. as generitype, because it was segregated with the same quantitative—or semiquantitative—method as *L. yaqui* and *L. pima.*

Laurozamites powellii might be regarded more suitable as generitype, because it allows to place *Laurozamites* in the Bennettitales with the help of cuticular characters. However, the simple assignment of *L. powellii* to this genus offers the same factual basis and logical background for the assignment of the genus to the Bennettitales as its selection as type species.

According to Harris (1969) and Watson and Sincock (1992), it becomes increasingly clear that cuticular characters are of no diagnostic value in the leaf genera of the Bennettitales. It is, therefore, irrelevant whether or not the generic diagnosis of *Laurozamites* does include them. Like other bennettitalean leaf genera, *Laurozamites* can include species based on material with or without cuticles. By the way, it would be unwise to define one set of genera with cuticles and a parallel set of genera without cuticles. Consequently, the species placed in each genus must be classified also in the future according to the preservation of the different materials.

The palaeodeme concept and type palaeodemes

The term palaeodeme has been introduced into the palaeobotanical literature by Anderson (1977, p. 13) and Anderson and Anderson (1983, p. 68). It has been controversial since that time. We adopt it as a term replacing "fossil population" and consider it useful as long as it is defined as "a non limited number of fossil remains (organs, organically connected organ combinations or whole-plant or animal fossils) collected from one only lithosome at one locality, and assignable beyond reasonable doubt to one single fossil species or infraspecific taxon". This definition is modified after the quoted publications by Anderson and Anderson. The main difference between the original definition and our modified version is due to a shift from the term "population" to "species or infraspecific taxon", not implying a major shift in biological meaning, but highlighting, perhaps too much, the trivial fact that actual mating and interfertility amongst fossil individuals cannot be observed. In addition, the present authors excluded from the Anderson and Anderson definition that the characters of the individuals in a given palaeodeme must show normal distributions—rarely this is shown in practice by Anderson and Anderson—a condition which renders meaningless the contention of those authors, that a palaeodeme can have only one specimen; and last not least, the authors of this paper do not agree that different non-connected organs can be placed in one palaeodeme. The palaeodeme concept is designed to offer natural basic units for taxonomy, and contamination of palaeodemes by potentially erroneous reconstructions must be excluded. It is also clear that the term palaeodeme does not imply collecting on only one occasion by solely one person or team.

Type palaeodemes have a similar legal status as type localities, and must not be taken as type specimens all together, even though the specimens belonging to them can be isotypes.

The present authors second the Anderson and Anderson (1983, 1985, 1989) proposal to use type palaeodemes—from which holotypes must be selected—whenever new, specimen-rich palaeodemes are found, but only if violation of the rules of botanical nomenclature is avoided. In practice, no difficulties will arise, when new species are described. Conversely, they will be encountered in many cases of taxa described and typified previously in accordance with the ICBN (Greuter *et al.,* 1988). Strictly speaking, a type palaeodeme for a previously described and typified species or infraspecific taxon can be proposed only when both the previous holotype—or type material or figures—and the new type palaeodeme correspond with certainty to the same locality and lithosome bed. However, here are given two examples of other situations in which new type palaeodemes might support old types. Firstly, old typification becomes meaningless in species recorded in the literature only once and typified with lost materials that are poorly illustrated in the original publications. Secondly, a holotype or other type material coming from a locality—type lithosome—not recorded in the literature or no longer suitable

for sampling, can become useless, when it can no longer be placed in its species after fundamental change in the diagnosis—for example shift from qualitative to statistical diagnostic characters. Instead of detailed theoretical discussion of these points, a practical example in the case of *Laurozamites fragilis* (Newberry) is given. The new protype concept, recently adopted at the 15th International Botanical Congress in Japan, offers much help in such cases (*cf.* Chaloner, 1993).

Laurozamites *gen. nov. and* Ischnophyton *Delevoryas and Hope*

At this point, it is convenient to discuss a specially interesting genus in the literature on Late Triassic floras of North America, *Ischnophyton* Delevoryas and Hope 1976. It was described just one year after Ash (1975) published his work on *Zamites powellii,* on the basis of detached leaves and a slender axis with a number of leaves attached; the leaves originally had been identified as *Otozamites hespera* Wieland, a Middle Jurassic species from the Mixteca Alta, Oaxaca, Mexico. *Ischnophyton iconicum* stems from the Late Triassic Pekin Formation, North Carolina, USA, and its leaves fall within the range of what it is included in *Laurozamites.* Nevertheless, *Ischnophyton* is not adopted in place of *Laurozamites* for our newly described genus, and *Laurozamites* is not considered a junior synonym of *Ischnophyton,* for the following reasons. Like Ash (1975), Delevoryas and Hope felt they were dealing with a new leaf genus, and they wrote "Leaves of *Ischnophyton* bear some resemblance to those of *Otozamites,* on one hand, as well as to *Zamites* on the other... Thus, these leaves cannot be placed with certainty in either genus...". Whereas Ash (1975) faced with the same difficulty and obliged to deal with the taxonomic complexity of form genera for dispersed leaves, decided to include *Zamites powellii* in *Zamites,* thus expanding the definition of the genus. Delevoryas and Hope (1976) took the reverse option; they wrote: "Because the material presents some insight as to the habit of a whole plant, it is deemed advisable to place this plant into a new genus, rather than to place it in an existing form genus for Mesozoic cycadophyte leaves".

Ischnophyton is a genus conceived strictly for slender axes with leaves, to which species based only on detached leaves cannot be assigned, because a diagnostic character is missing. Moving from the level of character availability corresponding to taxa for detached leaves, and creating a new genus at the higher level of taxa for stems with attached leaves, Delevoryas and Hope (1976) tried to approach the ideal of taxa for whole plants. At once, they avoided facing the difficulties of generic delimitation among bennettitalean leaves, but yet saved the new genus which Ash (1975) had sacrified. There is, as a result, a new bennettitalean genus with an extremely limited record, non-operative in paleo-phytogeographic work, and in which *Zamites powellii* and the here described species cannot be placed due to the lack of axes in the materials.

The detached leaves associated with *Ischnophyton iconicum*—and belonging to this species after Delevoryas and Hope (1976)—are placed here in *Laurozamites paraiconicus* sp. nov.

PALEOBIOLOGY AND SYSTEMATICS

In the foregoing chapter, the following comment of Harris (1969) was quoted: "It is tempting to avoid taxonomic difficulties in a particular flora by creating new genera...". It is opportune, nevertheless, to recognize that one can also evade taxonomic difficulties in a particular flora by replacing the description and fundamentation of previously unknown taxa for uncritical and forced identifications. Instead of debating these points, which are full of subjective elements, and falling into apologies regarding the classical attitudes of lumping and splitting, it is preferred to ask: Are the taxa here differentiated objectively distinct and operative? or are they only phenotypically different? Yet they might be only manifestations of one—or a very low number of—species due to intrinsic physiological or ecophysiological polymorphism—*i. e.,* plants with different leaves in juvenile and adult individuals; different leaves in primary shoots, twigs or adventicious sprouts, different sun and shadow leaves, etc.—or extrinsically determined ecotypes.

The leaves of different ecotypes should show a tendency to be rarely associated in one fossiliferous stratum or at one locality—this would also be the case for genetically distinct vicarious species. Conversely, plants with leaf polymorphism or anisomorphism, produce their different leaf forms wherever they live. Hence, in the case of fossil floras, the different leaf forms of polymorphic species would show a trend to be associated frequently within the same strata or localities.

Such a trend has not been observed during our sampling program. Its absence is also evident from the correlation indexes calculated according to the formula of Pearson for the species described here—varieties excluded—on the basis of material collected from 37 strata by Zambrano-García and Weber (1985; Figura 12). The highest—negative—index was

Laurozamites fragilis

0.09	*L. pima*		
0.19	-0.05	*L. yaqui*	
0.12	-0.22	0.02	*L. tarahumara*

Computer drawing by José de Jesús Vega-Carrillo

Figure 12.- Pearsonian correlation indexes based on presence and absence of four species of *Laurozamites* from Sonora, based on work by Zambrano-García, 1983.

calculated for *Laurozamites pima* against *L. tarahumara* var. *tarahumara*. It amounts to -0.22 and is of little significance. Even so, it reflects the fact that *L. tarahumara* var. *tarahumara* is almost completely restricted to the San Enrique—Los Pilares—sampling area (area 5, Figure 5), whereas *L. pima* was found mainly in the La Barranca-Santa Clara area (area 4, Figure 4). This geographical separation excludes the possibility to understand these populations, which are in fact distinct, as simply manifestations of hetero- or anisomorphism. All other correlation indexes have lower values, but according to the above reasoning, much higher values should be expected in the case of polymorphism. In conclusion, there is no evidence strengthening the above assumptions. The hypothesized existence of ecotypes, on the other hand, cannot be verified due to the limitations inherent in paleobotanical studies—interfertility cannot be proven.

Another kind of observational fallacy might have led to erroneous description of species and varieties. In some cycadophyte leaf species, a non-linear increase of values of certain quantitative characters has been previously reported. Weber (1968), for instance, described material of *Nilssonia minima* Gothan from the earliestmost Liassic of Franconia, Germany, in which the number of veins per pinna and the pinna width increased by duplication. There are pinnae with two, four and eight veins. Such discontinuities should normally be observable in materials collected from one stratum or locality, and transitional leaves should be available. No such case has been observed in the *Laurozamites fragilis*-complex of the Santa Clara Formation.

Hence, it is concluded that the distinguished taxonomic units were most probably genetically isolated and represent "good" taxa. The new genus *Laurozamites* was in a phase of very active speciation at Late Triassic time. The question whether the distinguished taxa are useful and operative in phytogeographic and paleoecological studies can be answered at present only in the latter context.

Laurozamites fragilis is one of the most constant species of the Santa Clara taphoflora. According to Zambrano-García and Weber (1985), it was collected from 21 of the 37 sampled strata. *Asterotheca santaclarae* Weber is also a constant species—14 of 37 strata—and characterizes interdistributary, perhaps swampy flood plains. The two species are found together at nine of these localities, but only in one stratum are they both abundant. Generally, in strata where one or other is abundant, the other is rare, or both are rare. Other species closely linked to swampy habitats, like *Taeniopteris elegans* Newberry— found in six strata, three with *Laurozamites fragilis*—present no better linkage with *L. fragilis*. On the other hand, the species of the channel-related paleohabitats do not show a closer association with *L. fragilis*. *Phyllotheca?* sp. A, for example, is found in 11 strata, but together with *L. fragilis* only in five of these. Only at one locality are both species really abundant. Hence, although *L. fragilis* has low pearsonian indices with all other species of the Santa Clara taphoflora, due to its high

constancy it probably was neither a species of the most swampy nor of the most channel-related paleohabitats.

Laurozamites pima is much less constant than *L. fragilis*—11 of 37 strata; abundant only in four. Weber and coworkers (1980a) and Zambrano-García and Weber (1985) recognized that this species belongs to a recurrent group, which excludes the taxa of the interdistributary paleohabitats. It probably grew best in channel-related paleoenvironments. *L. pima* was found together with *Asterotheca santaclarae* only in two strata, and only in one of them were both species abundant.

Laurozamites yaqui is found at very few localities. According to the previous literature and our field observations, it may belong to swampy interdistributary paleohabitats, and *L. tarahumara* var. *tarahumara* may have played a similar part. Nothing can be said about the other varieties of the species.

In conclusion, only *Laurozamites pima* can at present be taken as a good paleoenvironmmental index species.

THE PALEOPHYTOGEOGRAPHICAL ROLE OF *LAUROZAMITES*

Fossil floras of Late Triassic, especially Carnian and Norian age, are widely scattered all around the world. Amozurrutia-Silva (1985), in a paleophytogeographical study on the Carnian floras, was able to compile information on 32 regional floras of that age. Her work has not been published so far, because traditional and regional differences in the use of many generic names could not be overcome. Most troubling among these names are those of old, well-known form genera, such as *Cladophlebis* and *Taeniopteris*, the already discussed bennettitalean leaf genera, *Desmiophyllum, Brachyphyllum, Pagiophyllum, Elatocladus*, etc., on one hand, and those of monotypic genera with local distribution, like *Ischnophyton*, on the other. When phytogeographic relationships between regional floras are calculated on a presence-absence basis, names such as *Zamites*, conceived for very wide "artificial" groups, will diminish the differences between provinces, and names of the kind of *Ischnophyton* will erroneously highlight the peculiarity of local floras, and consequently hamper the delimitation of provinces. Much attention must be paid to the improvement of paleobotanical taxonomy and nomenclature with this and similar purposes in mind.

LAUROZAMITES *IN THE NORTH AMERICAN TRIASSIC*

In the previous chapters, a number of species from the United States of America have been placed in the new genus *Laurozamites*. One further species, *Zamites occidentalis*, which was described by Newberry (1876) from Abiquiu, New Mexico, and mentioned here in the comparisons of *Laurozamites pima*, also possibly belongs to the new genus, but this cannot be confirmed on the basis of the figures given by Newberry (*op. cit.*). Together with the Sonoran species, *L. powellii* and *L. macombii*, which are mainly found in the southwestern United States, form the bulk of the genus, which

seems to be much less diverse and outstanding in the Triassic of eastern North America.

No species assignable to *Laurozamites* is recorded in the most comprehensive monograph on the Virginia Triassic (Fontaine, 1883). Applegate (1956), in his study on Triassic plants and fish from Virginia, did not alter this picture. No such leaves were reported by Emmons (1856, 1857) nor Fontaine (1900) in the Triassic floras of North Carolina. Only recently was *Ischnophyton iconicum* described from North Carolina. Earlier in this paper, the authors proposed the name *Laurozamites paraiconicus* for the detached leaves of this plant. Bock (1969) includes the only record of *Otozamites powellii* (Fontaine), now *Laurozamites powellii*, and *O. dentalina* Bock, from Pennsylvania. The latter species may belong to *Laurozamites*, but the published illustrations do not help in the new combination. The original material of Bock must be considered lost. *Laurozamites* is not common in eastern North America, much less common than in Mexico and the southwestern United States, but in fact seems to occur in the plant-bearing non-marine deposits of the Late Triassic all over North America.

After an intensive literature search on worldwide Late Triassic floras, *Laurozamites* was not found by the present authors to be known outside North America. Their compilation, however, does not cover so far floras much older or much younger than Carnian in age. It was out of the scope of this study to scan the literature on Jurassic floras. Nevertheless, it is worthwhile to mention here again the record of what seems to be a species of *Laurozamites*, reported from North Africa—Sudan—under the name *Pterophyllum nubiense* Lejal-Nicol. This plant has been found in a sequence that ranges from Permian to Early Jurassic age, and is considered Jurassic in age (Lejal-Nicol, 1984). No further record of doubtless *Laurozamites* is known to the authors from any Jurassic flora.

At present, *Laurozamites* is considered a North American genus, at least for the Late Triassic.

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