

## REVIEW OF *MACROPTERYGIUM* SCHIMPER ("CYCADOPHYTA", PRESUMED BENNETTITALES) AND A NEW SPECIES FROM THE UPPER TRIASSIC OF SONORA, NORTHWESTERN MEXICO

Reinhard Weber\*

### ABSTRACT

The Carnian (and/or Norian?) Santa Clara flora of central Sonora, Mexico, yields a high proportion of bennettitalean leaves. In an earlier paper, *Laurozamites* Weber and Zamudio-Varela was already segregated from *Zamites*. In the present report, a first group of leaves, that might be placed in *Zamites*, *sensu* Watson and Sincock (1992), is assigned to the almost forgotten genus *Macropterygium* Schimper, 1870, subgenus *Macropterygium*. Another lot of specimens from Sonora, previously placed in "*Zamites* cf. *truncatus* Zeiller", are described here as *Macropterygium*, new subgenus *Indozamites*. The genus and subgenera described and discussed here, are placed in the Bennettitales due to the presence of syndetocheilic stomata in the former "*Sphenozamites rogersianus* Fontaine", assigned here to *Macropterygium*, subgenus *Glandulozamites*. It seems that *Macropterygium*, together with some other similar forms and the related genera *Eoginkgoites* and *Sinozamites*, was restricted geographically to western and far-eastern Laurasia.

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

### RESUMEN

La flora de la Formación Santa Clara del Cármino (¿y/o Nórico?) de Sonora central, México, contiene hojas de Bennettitales en gran proporción. En un trabajo previo, se excluyó *Laurozamites* Weber y Zamudio-Varela de *Zamites*. Un grupo adicional de hojas, que podrían ser atribuidas a *Zamites*, *sensu* Watson y Sincock (1992), se asigna aquí al antiguo y casi olvidado género *Macropterygium* Schimper, 1870, subgénero *Macropterygium*. Otro lote de especímenes de Sonora, previamente identificados como "*Zamites* cf. *truncatus* Zeiller", se asigna aquí a *Macropterygium*, subgénero nuevo *Indozamites*. El género y los subgéneros discutidos aquí se adscriben a las Bennettitales, especialmente debido a la presencia de estomas sindetoquélicos en el antiguo "*Sphenozamites rogersianus* Fontaine" (1883), mismo que está asignado aquí a *Macropterygium*, subgénero *Glandulozamites*. Al parecer, *Macropterygium*, con algunos géneros emparentados, tales como *Eoginkgoites* y *Sinozamites*, se encuentra distribuido exclusivamente en las partes occidental y extrema oriental de Laurasia.

Palabras clave: fósiles, plantas vasculares, Bennettitales, hojas, taxa nuevos, Triásico Tardío, Sonora, México, Estados Unidos de América, Austria, Vietnam.

### INTRODUCTION

The Mesozoic "cycadophytes", including chiefly the Bennettitales and Cycadales, are represented worldwide by large numbers of rather diverse leaf types recorded in a voluminous and sometimes perplexing literature. Even today, the fossil "cycadophyte" genera are, for the most part, not defined under the more ideal than practical criterion of whole-plant systematics, and there is no trend to naming the leaves after reproductive organs. The leaves are still placed in form genera that are in some cases sorted out and defined only with difficulty.

Chiefly before paleobotanists had learned to distinguish the Bennettitales and the Cycadales with the help of cuticular anatomy, the description of new "cycad" leaf genera was a rather common endeavor. At about the time detailed research was started on their stomatal organization, that allows to separate both orders more or less accurately (Florin, 1933a, 1933b), an increasingly simplified classification of cycadalean and

bennettitalean leaves was worked out in England mainly by T.M. Harris (1931, 1932, 1969) and his school, but not followed strictly by all regional schools. The British development culminated recently in the monograph on bennettitalean leaves and reproductive organs from the English Wealden, by Watson and Sincock (1992). The generic classification of the leaves, proposed by these authors, is almost exclusively based on macroscopic characters.

Of course, attempts were repeatedly made to define genera not only macroscopically, but also with the aid of cuticular anatomy. Anderson and Anderson (1989), in strict agreement with the main-stream methodology, pointed decidedly in this direction: "We would hazard the guess that the bennettitalean and the fossil cycad fronds could, in significant measure be sorted into natural genera on the basis of cuticle studies; or at least the cuticles would be a significant aid in this regard". Contrary to the above lines, however, T.M. Harris and the British school (Harris, 1969; Watson and Sincock, 1992) found the cuticular characters, though often useful in the delimitation of species, to be of little or no value in the definition of the bennettitalean leaf genera. The latter authors wrote: "The use of cuticle characters is currently limited to the ordinal and

\*Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Delegación Coyoacán, 04510 D.F., México.

specific ranks". Although this will be challenged in the future again and again, a word of caution is necessary. The Andersons' as well as Harris's and Watson and Sincock's views are based on studies of floras with often well preserved cuticles.

In addition, Watson and Sincock (1992) emphasize: "A foliage species without knowledge of its cuticle is almost worthless". However, in the case of research problems requiring the use of the highest possible numbers of fossil species, genera and floras, for example in paleoecological and phytogeographic work, it is at present, and will also in the future be impossible to work only with selected and exceptionally well preserved material. In these research contexts, the usual, non exceptional impression material is still of utmost importance, and its study must be encouraged.

It would be unwise, however, to use parallel classifications for "cycadophyte" leaves lacking cuticles and for those yielding them, not only because most of the traditionally accepted genera were described before the recognition of the diagnostic cycadalean and bennettitalean characters of the cuticles, not only because the syndetocheilic stomatal apparatus has been found occasionally in Cycadales (Schweitzer, personal communication, 1991; Crepet, verbal communication, 1995), but also, because the resulting genera would be form genera anyway.

Watson and Sincock's (1992) classification, that includes the merely Triassic genus *Eoginkgoites* Bock, among others with a wider stratigraphic range, is an essay of universal classification. Regarding their classification, Watson and Sincock (*op. cit.*) wrote: "In the absence of evidence from fructifications a highly artificial and arbitrary series of leaf form-genera is therefore of no practical disadvantage". However, the Cretaceous and later Jurassic leaves seem to fit easily in their genera, but less so the Triassic ones (Axsmith *et al.*, 1995). Watson and Sincock (1992) appear to assume implicitly that the Bennettitales, either as whole plants or only regarding the leaves, showed a constant generic diversity throughout the lifetime of the order. Thereby, the elucidation of the diversification process expected in the Bennettitales during its history which lasted over 100 million years is being hampered.

According to Weber and Zamudio-Varela (1995), several form genera of bennettitalean leaves as adopted by Watson and Sincock (1992) are too comprehensive, for example *Pterophyllum* Brongniart and *Zamites* Brongniart, where the leaves placed here in *Macropterygium* might be referred to. The present paper is a second contribution to the partitioning of *Pterophyllum* and *Zamites*, in order to provide paleobotanists with a number of genera that clearly have not only practical advantages. *Macropterygium* Schimper is taken up again as a useful generic concept. In addition, this genus is discussed as the probable ancestral stock of *Eoginkgoites* Bock.

The assignment of *Macropterygium* to the Bennettitales is orthodox, reinforced by the finding of a syndetocheilic stomatal apparatus in *M. (Glandulozamites) rogersianum*, by Applegate (1956) and in the closely related *Eoginkgoites* (Ash,

1976, 1977). The presence of *Nilssonia*-like epidermal features in *Apoldia tenera* (Compter) Linnell, however, may be taken as contrary evidence. Even though the latter species was never placed in *Macropterygium*, its similarity with this genus might be alleged to disprove generalized assignment of all forms described here, to the Bennettitales. Nevertheless, this is not done here, as long as positive arguments (especially discovery of cycadalean cuticular structure in the species dealt with here) remain unavailable. By the way, *Macropterygium* was not included by Watson and Sincock (1992) in their appendix 1, where many "rejected, redundant or uncertain bennettitalean leaf genera" are listed.

## GEOLOGICAL SETTING, WORKING AREAS AND LOCALITIES

The Late Triassic (Carnian and/or Norian) Santa Clara Formation of Sonora was briefly discussed by the writer in earlier papers (Weber *et al.*, 1980a; Weber, 1985; Weber and Zamudio-Varela, 1995).

The specimens described here were collected between 1973 and 1983 in four working areas and at many localities in eastern central Sonora, listed by Weber (1985, tab. 1). Location maps with locality numbers were published by Weber (1985, figs. 1-5) and Weber and Zamudio-Varela (1995, figs. 1-5). Particular localities will be mentioned in full in the taxonomic descriptions and in the figure captions. The locality numbers appearing after the key IGM-PB are those of the official catalog of paleontological localities of the Instituto de Geología, Universidad Nacional Autónoma de México (CLP-IG-UNAM).

## MATERIAL

About 20 specimens of *Macropterygium (Macropterygium) aff. bronniei* and numerous of *M. (Indozamites) aff. truncatum* were used in this study. Some previously figured specimens of the latter (Weber *et al.*, 1980b, fig. 13, c-g) received new specimen numbers after a reorganization of the Paleontological Museum of the Instituto de Geología. They are mentioned in the descriptive section.

The specimens are mostly preserved as fragmentary impressions and, only rarely, some organic substance is preserved, but according to the very high rank of the coal (anthracite and graphite) of the Santa Clara Formation, these organic remains are generally unsuitable for cuticle studies. In addition, the rocks of this formation were heated locally at many places by a number of independent intrusive events.

## OUTLOOK INTO THE METHODIC CONTEXT OF THIS STUDY

This paper belongs to a project of paleophytogeographical investigations on the Santa Clara flora and other worldwide

(Ladinian)-Carnian-(Norian) floras, based preferentially on the quantitative analysis of presence and absence of genera. Such a project cannot result in the recognition of "natural" distribution areas or provincialism with an exactness higher than the "operativeness" of the underlying generic classification. Weber and Zamudio-Varela (1995) already used the concept of "operative" taxa, not implying that new taxa might be created arbitrarily at the convenience of a particular research context.

The use of too widely defined and heterogeneous form genera such as *Pterophyllum* and *Zamites* is detrimental in such research. Such genera may erroneously be understood as evidence of cosmopolitanism or at least hamper the clear recognition of province boundaries. Distracting, on the other hand, are the "whole-plant" genera, based either on reconstructions of reproductive and vegetative organs including leaves or only on reproductive organs, after which they are named. The distribution areas of these genera are usually unknown or very poorly documented; and they are misleading, when they are thought to be evidence of endemism.

Quantitative paleophytogeographic work using cluster analysis should be centered on the quantitative comparison of genus lists of local (formational) floras, taking into account only those genera based on leaves or leafy axes. In a similar way, generic lists of palynomorphs may be compared and analyzed. The advantages offered by the geographic constancy and wide distribution of plant fossils of this type cannot be ruled out by the disadvantages inherent in their often "artificial" classification. Paleophytogeography can, however, be enhanced, when it is preceded by critical taxonomic work done with the purpose of the best possible recognition of "natural" leaf genera.

Admittedly, this methodical restriction may be considered suspect. Indeed, it seems to be misleading in certain cases or even generally. The Permian Glossopteridales is a good example. The leaves belonging to this order are placed in a low number of form genera which, in addition, are not separated easily in all cases, for instance *Glossopteris* versus *Gangamopteris* (Kovacs-Endrödy, 1985). The corresponding reproductive structures show a higher diversity. However, these are known only from a comparatively low number of local floras and, therefore, probably non-operative in quantitative paleophytogeography. When it is decided to make use of the reproductive structures, doubt comes up, whether male or female structures or both should be used. In the Triassic, the genus *Dicroidium* offers similar problems. Whereas in South Africa, this form genus of corystosperm leaves is defined very comprehensively (Anderson and Anderson, 1983), more conservative South American and Australian palaeobotanists split the *Dicroidium* complex in a number of genera (Frenguelli, 1943; Petriella, 1979; Retallack, 1977; Artabe, 1990). As in the former case, preference might be given to the use of *Umkoasia/Pteruchus*, the reproductive structures of the *Dicroidium* complex. In this case the "male/female doubt" is

easily overcome, but even so, the reproductive structures are only reported from few local floras, and their use in quantitative phytogeography would weaken the method. In this example, the most convenient solution is the use of the more differentiated classification of the leaves, regardless of whether the taxa used are genera or subgenera (Archangelsky, 1970).

## METHOD AND TECHNIQUES

Due to strong tectonic stress, in addition to weathering, large slabs can be collected from only a few localities in the Santa Clara Formation. The leaves described here are very large, and no complete specimens could be collected. Sometimes, the plants are preserved in fine grained rock, and the outline and venation of the leaves are well preserved and contrasted by weathering. Finer details, however, such as "resin or glandular bodies" or cell outlines are rarely observed even with the aid of contrasting techniques (water, kerosene, xylene) for observation under the microscope or in photography.

According to the rather poor preservation of the material, only a few traditional simple techniques could be used. Generally, the slabs were only cleansed with water and a soft brush. This treatment does not damage the impressions due to the hardness and very firm cementation of the rock. The preparation of the fossils was carried out with the help of a percussion tool for metal engraving (Air Scribe, Chicago Pneumatic), which sometimes leaves "rather ugly scars on the matrix" (Cleal, 1991). Needless to say, degagement with needles is usually useless in this material.

Of course, the studies on foreign materials were mainly done on the basis of published descriptions and illustrations. Original materials were observed in the Smithsonian Institution, National Museum of Natural History, Washington (*Macropterygium* [*Glandulozamites*] *rogersianum*) and the Museum of Natural History at Vienna (*M. [M.] bronni*). The literature on Jurassic floras was not revised thoroughly; hence the results given here may not be extrapolated automatically to the Jurassic.

Owing to the complexity of the taxonomic discussion, the no longer valid species names are quoted here between citation marks, except in the synonymies or in textual quotations from the earlier literature.

The Sonoran specimens are deposited in the Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México. Only figured specimens receive official specimen numbers. These are formed by the sign for the collection, IGM, key of paleobotany, PB, a locality number and, after a hyphen, the specimen number proper.

## SYSTEMATIC PALEOBOTANY

**Order: Bennettiales**

**Form-Genus: *Macropterygium* Schimper, 1870**

**Diagnosis**—Leaf large or medium-sized, petiolate, normally imparipinnate with distinct terminal pinna; whole blade more or less broadly elliptical in shape. Petiole well developed, relatively short, with broadened base. Rachis often very stout, straight. Pinnae attached laterally to rachis, opposite or rarely subopposite to alternate; lowermost pair of pinnae attached at axilar angles of about 90° or more, distally following pairs at decreasing angles to considerably less than 90°; terminal pinna attached to rachis tip, often much wider or, conversely, narrower than the lateral ones; pinnae broadly to narrowly spatulate, pinna base more or less abruptly and symmetrically contracted, rounded to cuneate; in the latter case very narrow at attachment, pinna tip rounded, rounded-truncate, truncate or even slightly emarginate; pinnae medium sized or large to very large, considerably longer than wide. Venation open, subparallel to parallel with numerous dichotomies near pinna base; most veins ending at distal margin. Venation density about 15 to 40 veins/cm.

**Type species of the genus**—*Macropterygium (M.) bronnii* (Schenk) Schimper, 1870.

***Macropterygium* Schimper, 1870**

**Subgenus *Macropterygium* (Schimper) Arber, 1907**

**Diagnosis**—Leaves large, blade subcircular to broadly elliptical in shape, measuring 40 x 40 cm or more, provided with four or slightly more pairs of lateral pinnae and a distinct terminal pinna. Petiole to 1.8 cm in breadth, 10 cm (or more) in length. Rachis stout, 1.5 cm wide and tapering, ending abruptly at base of terminal pinna. Lateral pinnae more or less radially oriented, latero-ventrally and obliquely attached to rachis, spatulate, constricted at subcuneate or rounded base, tip more or less asymmetrically rounded truncate. Lateral pinnae up to 20 cm long and about 8 cm wide, terminal pinnae sometimes wider (about 10 cm). Venation density about 35 veins/cm.

**Type species**—The same as for the genus.

***Macropterygium bronnii* (Schenk) Schimper, 1870**

(Plate 1, figures 1, 2)

**Synonymy:**

- 1858 *Noeggerathia Vogesiaca* (n. g.).- Bronn, 1858, p. 129-130, pl. 6, figs. 1-4 (erroneous specific identification and generic treatment).  
 1865 *Pterophyllum Bronnii*.- Schenk, 1865, p. 18.  
 1870 *Macropterygium Bronnii* (Schenk) Sch.- Schimper, 1870, p. 132-133.

1907 *Pterophyllum Bronni* Schenk.- Arber, 1907, p. 120-124, pl. 18, fig. 1; pl. 19, fig. 4.

1917 *Pterophyllum (Macropterygium) Bronni* Schenk.- Seward, 1917, p. 553-554.

**Excluded record:**

1894 *Pterophyllum Bronnii* Schenk.- Compter, 1894, p. 221, pl. 6.

**Diagnosis**—See Schimper, 1870, p. 132-133.

**Holotype**—Bronn (1858), pl. 6, fig. 1.

On Plate 1, figures 1 and 2, specimens of *Macropterygium bronnii* from the Late Triassic flora of Raibl, Austria, are illustrated here for comparative purposes. Figure 1 (x 0.5) shows probably the best preserved and most complete leaf of this species ever found. It is imparipinnate, with four pairs of opposite lateral pinnae and a distinct terminal one. The inferred shape of the blade was nearly circular. The total width of the leaf is about 40 cm and its length most likely equalled the width. The basal portion of the petiole is lost. Hence, the petiole measured somewhat over 9.5 cm in length and 1.8 cm in maximum width. The rachis is about 8 cm long and about 7 mm wide just below the distalmost lateral pinnae. These and the terminal pinna are attached to the rachis jointly at almost the same point, but they are not fused basally. The terminal pinna is somewhat narrower than the lateral ones. The rachis portions between the lower pinna pairs are about 3 cm in length. The distalmost portions of most pinnae are not preserved, but two lateral pinnae show the tip, which is asymmetrically rounded-truncate. The basalmost pinna at right is about 14 cm in length and strongly oriented towards the leaf base. The axillary angle measures about 160°. The pinnae of the following pair are also attached at an axillary angle of over 90°. Hence the pinnae are arranged nearly radially. The best preserved pinna is the left one of the third pair. It is 21 cm in length and 8 cm in width near the tip. At the left side of the slab, there is an isolated fragment of a pinna tip that very clearly shows the rather delicate parallel and open venation. The venation density in this portion is about 25 veins/cm.

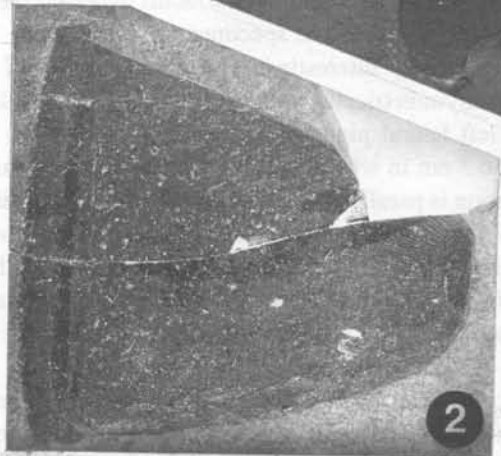
Plate 1, figure 2 (x 1) shows an isolated pinna with coiled distal margin. Seemingly, the leaves of this species and, maybe, of the genus were characterized by circinate venation. In addition, this pinna allows to observe the insertion scar, which is almost 1 cm in width ("along" the rachis) and 3 mm in length (with regard to the longitudinal midline of the pinna).

The holotype of the species proposed above (Bronn, 1858, pl. 6, fig. 1) is less well preserved, but agrees rather

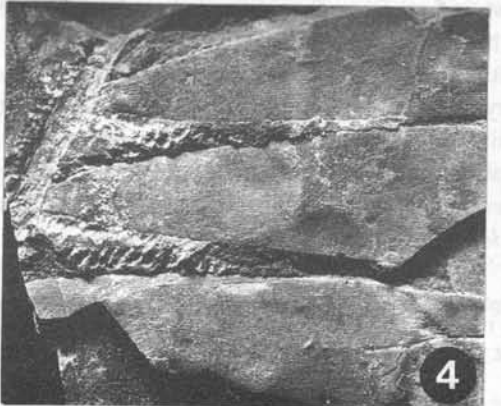
Plate 1. Figures 1, 2—*Macropterygium (Macropterygium) bronnii* Schimper from the Schwarzer Schiefer, Raibl, Austria. 1, Almost complete leaf (specimen 1996B0050, Museum of Natural History, Vienna, Austria. x 0.5. 2, Detached pinna with circinate coiled distal portion. Specimen 1887 IX 51, Museum of Natural History of Vienna. x 1. Figure 3—*Macropterygium (M.)* aff. *bronnii* from Sonora. Loc. 537C El Crucero, Stratum C (specimen IGM-PB-537C-879; x 1). Figure 4—*Macropterygium (Indozamites) mexicanum* n. sp. Pinnae with almost cuneate base. The same fossil on Plate 3, figure 2 (specimen IGM-PB-000-880; x 1; at present, the specimen is lost; the number was given provisionally and does not include the locality number).



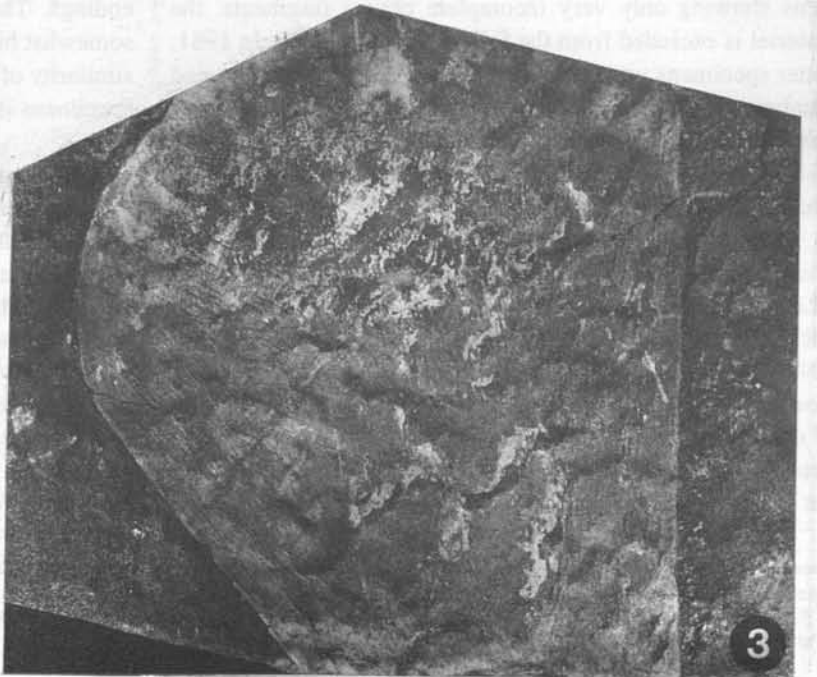
1



2



4



3

closely with the specimen described here. However, its terminal pinna is not preserved and the number of pinnae pairs cannot be counted. The orientation of the uppermost pinnae to the leaf tip suggests that only few pinnae are missing. An additional rather complete specimen described and figured by Arber (1907, pl. 18, fig. 1) as "*Pterophyllum bronni*" resembles the above specimens, but the insertion of the five preserved pinnae is concealed. It is important to mention that after Bronn (1858), the leaf of this species is finely granulated, either "by nature" or by preservation. This might be due, however, to the presence of glandular bodies.

A reconstruction of the leaf of this species is shown in Figure 1, a.

***Macropterygium* cf. *bronnii* (Schenk) Schimper**

(Plate 1, figure 3; Plate 2, figures 1-4; Plate 3, figure 1)

**Previous reports from Sonora:**

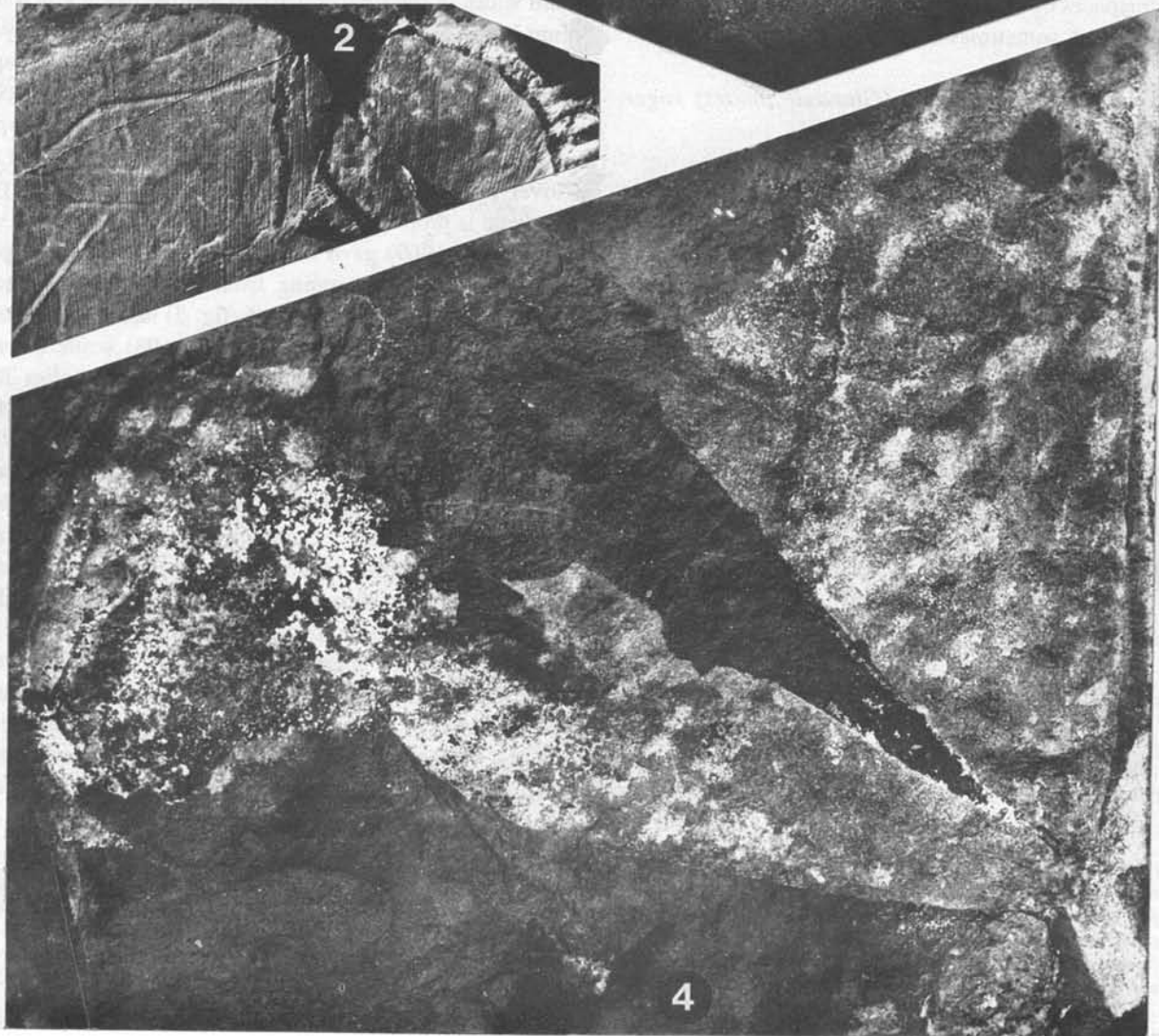
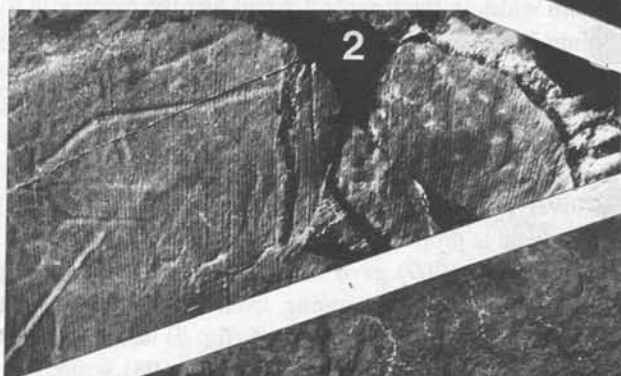
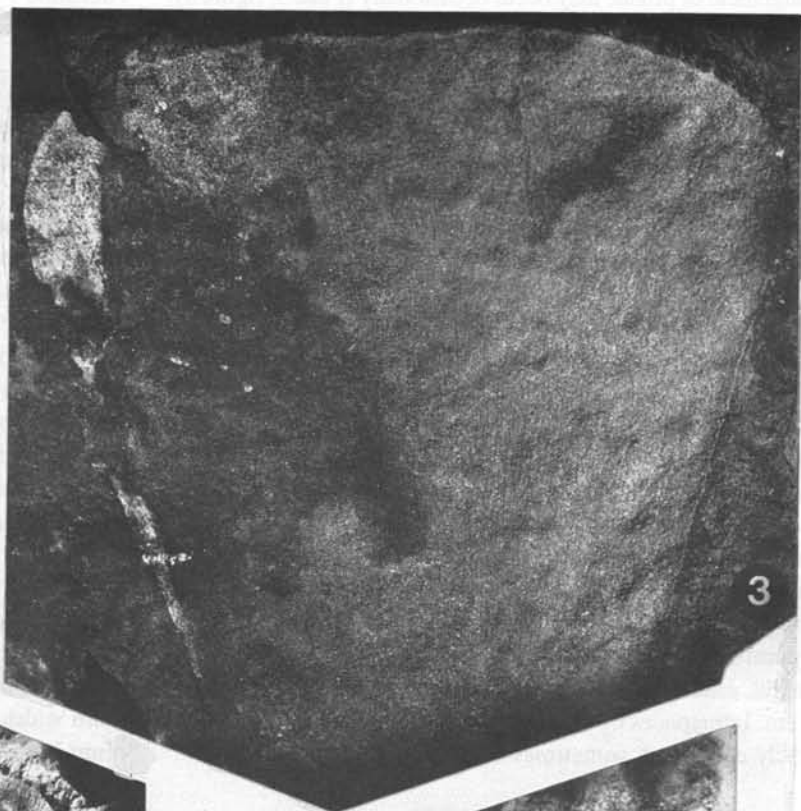
- 1982 *Macropterygium* sp.- Weber, Zambrano-García and Amozurrutia-Silva, 1980b (1982), p. 135, tab. 2 (name only).  
 1985 *Macropterygium* Schimper, sp. A.- Weber, 1985, p. 120, tab. 3 (name only).  
 1985 *Macropterygium* Schimper, sp. B.- Weber, 1985, p. 120, tab. 3 (name only).

**Material and localities**—Specimens probably belonging to this species were collected first by Weber in 1975 in the Santa Rosa locality at the right slope of Santa Clara Creek (loc. 501 CLP-IG-UNAM; see Weber, 1985, fig. 4, tab. 1). Sidney R. Ash, staying at Mexico City in 1980, identified this material as *Eoginkgoites* Bock. Consequently, he correlated the Santa Clara Formation at least in part with his *Eoginkgoites*-zone of the Newark Supergroup, USA (Ash, 1980; cf. Axsmith *et al.*, 1995). However, due to the poor preservation of these specimens showing only very incomplete pinnae fragments, the material is excluded from the following description. In 1981, better specimens were collected by Weber, Torres-Romo and Zambrano-García at four very distant localities: El Salto near San Marcial (sampling area 1, San Marcial; loc. 1003, CLP-IG-UNAM; cf. Weber, 1985, fig. 1), Represa near Arroyo Chamina (loc. 550, CLP-IG-UNAM; Weber, 1985, fig. 2, tab. 1), near Section San Javier No. 3 (loc. 531, CLP-IG-UNAM; Weber, 1985, fig. 3, tab. 1), El Crucero, Stratum C (loc. 537C, CLP-IG-UNAM; Weber, 1985, fig. 5, tab. 1) and at Pozo CRM-SE 55 "Incógnita" Stratum A (loc. 539A, CLP-IG-UNAM; Weber, 1985, fig. 5). The material includes about 15 more or less instructive specimens and a considerable number of minor pinnae fragments. Immediately after these findings, two different species were thought to be present in the material, but no additional specimens could be collected later on.

**Description**—Only two Sonoran specimens show pinnae attached to the rachis. Plate 2, figure 4 (x 1) illustrates the tip of a leaf slightly smaller than the Austrian specimen of *M. bronni* (Plate 1, figure 1). It shows very clearly the free bases of the three crowded distalmost pinnae. Other than in the Austrian specimen, the terminal pinna is wider than the lateral ones and reaches a width of over 10 cm distally, *i. e.*, about twice the width of the neighboring lateral pinna. The angle formed by the lateral margins of the end pinna measures 45°, *i. e.*, about three times the angle found in the Austrian specimen. (The pinna figured in Plate 2, figure 3 has about the same dimensions and proportions. Probably it was also a terminal pinna). The more or less complete ultimate lateral pinna in Plate 2, figure 4 measures 15 cm in length and about 6.5 cm in width, distally; *i. e.*, it is only slightly over half as wide as the terminal pinna. The second leaf fragment with pinnae attached to the rachis is shown in Plate 3, figure 1 (x 0.5). Only two pinnae are preserved, none being the end pinna. This is inferred from the presence of a rachis portion of considerable length below the base of the uppermost pinna. The distal margins of the pinnae are poorly preserved and the latter are likely not preserved in full length. Although the attachment scars of the pinnae are not clearly preserved in this specimen, perhaps two more basal pinnae pairs are missing. The petiole is strongly curved and broken once. From the very base, its width is almost constantly about 2 cm, but it decreases suddenly from the point about 6 cm from the base. This is the transition from the petiole to the rachis. Only 4 cm more distally, the rachis measures only slightly over 1 cm in width. The specimen shown on Plate 2, figures 1 and 2 is very interesting. This distal portion of a lateral pinna is asymmetrically rounded truncate, exactly like the complete left lateral pinna of the Austrian specimen. It reaches about 6.5 cm in width showing well preserved venation. The venation is parallel, open and lacking thickened vein endings. The venation density is about 35 veins/cm, *i. e.*, somewhat higher than in the Austrian specimen. However, the similarity of the lateral pinnae of the Sonoran and the Austrian specimens is striking. The cuticle is unknown.

**Comparison and discussion**—The Sonoran specimens are different from the Austrian one described, in the absolute and relative width of the end pinna. This pinna was found attached only in one specimen from Sonora and Austria. It is well known, that the more common alternately or subalternately pinnate bennettitalean leaves have pseudoterminal pinnae that are rather varying in position and relative dimensions. The mostly opposite pinnation characterizing the materials described here, allows to identify a terminal pinna, even though there are no reasons granting a fundamental difference. In *M.* subgenera *Indozamites* and *Glandulozamites*, a subopposite





arrangement of pinnae may occur occasionally (Plate 3, figure 3). Hence, a high variability of the end pinnae can be expected throughout the genus *Macropterygium*. In addition, there is a slight difference in venation density between the Sonoran and Austrian material. However, the differences between the Sonoran and the Austrian materials are not clear cut and their significance cannot be established with only a couple of specimens at hand. The Sonoran material is poorly preserved and unsuitable to distinguish two species and even less to propose a new one.

***Macropterygium* Schimper, 1870**

**Subgenus *Glandulozamites* (Bock) Weber stat. nov.**

**Diagnosis**—Leaf imparipinnate, elliptic to oblongo-elliptic in shape, large to very large, over 40 cm in width. Rachis wide, straight and stout, abruptly ending at base of terminal pinna. Pinnae mostly opposite, rarely subalternate, attached to rachis at angle of about 90° or less, sessile, broadly spatulate, with rounded to cuneate base and rounded truncate tip, up to 11 cm in width and over 20 cm in length. Venation free, subparallel to parallel, with frequent dichotomies at pinna base, veins straight, ending at pinna margin, venation density about 15 to 20/cm. Interspaces of veins with coarse, subspherical to transversely elongated, sometimes bean-shaped glandular bodies.

**Type species**—*Macropterygium (Glandulozamites) rogersianum* (Fontaine) Weber.

***Macropterygium rogersianum* (Fontaine) Weber comb. nov.**

**Synonymy:**

1883 *Sphenozamites rogersianus* Fontaine.- Fontaine, 1883, p. 80-84, pl. 43, pl. 44, fig. 1, 2, 2, a, 2, b, pl. 45, figs. 1, 2.  
1969 *Glandulozamites punctatus* (Emmons) Bock.- Bock, 1969, p. 194-198, figs. 308-314.

**Excluded record:**

1857 *Calamites punctatus* Emmons.- Emmons, 1857, p. 35, pl. 6, fig. 5.

**Diagnosis**—see Fontaine, 1883, p. 80-81.

**Holotype**—Fontaine, 1883, pl. 45, fig. 1.

**Type locality**—Clover Hill mine, near Winterpock, Virginia, USA.

**Type stratum and age**—Productive Coal Measure Member,

Tuckahoe Formation, Richmond Basin, Newark Supergroup, Late Triassic (early Carnian). See Cornet and Olson (1990).

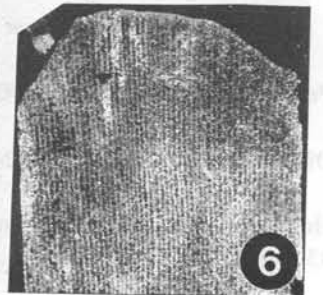
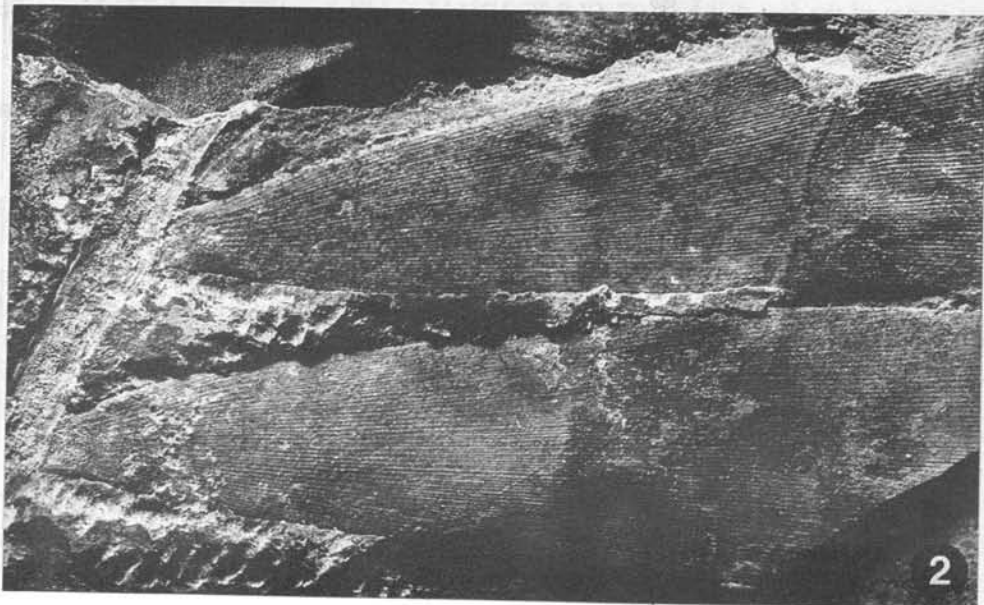
**Derivation of name**—*rogersianum*, in honor of William B. Rogers, Professor of Natural Philosophy, the first U.S. researcher working on the Virginian Late Triassic flora.

**Comparison and discussion**—This species is based on the material described by Fontaine (1883) from Clover Hill, near Winterpock. Whereas Fontaine received his material from miners, Bock (1969) collected from the old dumps of the same mine. He pointed out that his specimens, especially the leaves preserved with rachis, are considerably smaller, than those of Fontaine (*op. cit.*): "...the pivotal ones are medium sized fronds, the apex of one showing a stem (*sic*) of 12 cm length with several well preserved pinnae up to 16 cm long, one of which is complete". "...Moreover, an astounding dimorphism appears to have plagued this single type". Bock does not explain the latter comment. In his redescription of the species, obviously he took into account the characters observed in Fontaine's (1883) and his own material. His own material differs from Fontaine's in its much narrower pinnae (maximum width in the figures 2.7 cm) and the much less rounded pinna bases. Even though the "dimorphism" observed by Bock does not seem to be intraspecific, no new species is proposed here for Bock's specimens, because these are lost (Axsmith, personal communication, 1996). The presence of two species is not impossible, since about six coal beds were found in the Clover Hill mine. This is also the reason why no type palaeodeme is proposed here for the species.

Bock (1969) gave to his *Glandulozamites* the specific epithet "*punctatus*", coming from a fragmentary specimen figured by Emmons (1857, pl. 6, fig. 5) under the name "*Calamites punctatus*". Fontaine (1883, p. 98) wrote about this figure: "It is clearly a fragment of *Sphenozamites Rogersianus*". Later, however, Wanner and Fontaine (1900) remarked: "In view of the fact that Professor Fontaine did not find at Williams College the specimen figured by Emmons in his American Geology, Part VI, pl. 6, fig. 5, and described on p. 35 under the name *Calamites punctatus*, considered to belong to this species...it is not thought best to enter that form in the synonymy, especially as its earlier date would have involved a change of nomenclature". The present writer heartily agrees with Wanner and Fontaine (1900; not quoted by Bock, 1969), because Emmons's specimen is indeed unsuitable as holotype. Even the generic identity of this specimen and *Macropterygium (Glandulozamites) rogersianum* may be challenged. In his synonymy, Bock (1969) refers to a

Plate 3. Figure 1—*Macropterygium (Macropterygium)* aff. *bronni* from Sonora. Loc. Pozo CRM SE-55 (specimen IGM-PB-539A-884 a; x 0.5). Figures 2-6—*Macropterygium (Indozamites) mexicanum* sp. nov. (all enlarged); 2, same specimen as in Plate 1, figure 4; venation: dark dots near the base of the more distal pinna are preservational artifacts; glandular bodies are visible at the distal end of the basal pinna (specimen IGM-PB-000-880; x 2). 3, Detached fragments; venation, glandular bodies as distinct units (right-hand fragment), rosary-like aspect of veins (left fragment), photographed under xylene. Loc. La Barranca, Section 1 (specimen IGM-PB-515-545; x 3). 4-6, Enlarged fragments of detached pinnae; apparent transverse veins between longitudinal veins, preservational artifact; 4 and 6, Loc. Camino Tule-Chamina (specimen IGM-PB-509-885a, b; x 2); 5, Loc. Camino El Tule-Chamina (specimen IGM-PB-509-886; x 2).





"*Taeniopteris*" species reported by Newberry (1876) from the Santa Clara Formation of Sonora. This specimen in fact shows a granular texture somewhat like that of subgenus *Glandulozamites*, but it was recognized by the present author as *Cycadolepis* aff. *wettsteinii* Kräusel (Weber *et al.*, 1980b, fig. 11, d). Confusions such as this one give a strong warning against the use of fragmentary specimens as holotypes.

A reconstruction of the leaf of this species, based on figures by Fontaine (1883) is shown in Figure 1, c.

### *Macropterygium* Schimper

#### Subgenus *Indozamites* Weber subgen. nov.

**Diagnosis**—Only leaf known. Leaf elliptic to oblong-elliptic, large, to about 20 cm in width. Rachis slender, straight. Pinnae attached to rachis at angle of 90° or less, sessile, oblong-spatulate, with symmetrically contracted, cuneate to rounded base and rounded, truncate or even truncate-emarginate tip. Venation open, subparallel to parallel, dichotomizing frequently near pinna base, veins fine, venation density about 40/cm. Interspaces of veinlets with small circular or subcircular (often not preserved) glandular bodies. Cuticle unknown.

**Type species**—*Macropterygium* (*Indozamites*) *truncatum* (Zeiller) Weber. R. Zeiller, (1902-) 1903, p. 166-167, pl. 43, figs. 3-6.

**Derivation of name**—*Indo-*: subgenus found in "West India" and East India (Indochina), but not in India properly; *-zamites*: resembling *Zamia*.

**Discussion**—The type species was assigned by Zeiller (1902-1903) to *Zamites*, even though he clearly recognized its uniqueness in this genus, regarding the truncate pinnae: "...cette espèce diffère de toutes les autres espèces à moi connues de *Zamites* par la forme de ses folioles, brusquement tronquées à leur sommet". He was aware of the fact that he widened the generic diagnosis even with regard to the very wide one adopted by Seward (1917). Zeiller compared the species with "*Sphenozamites rogersianus* Fontaine", now *Macropterygium* (*Glandulozamites*) *rogersianum*, remarking that the generic placement of the latter species by Fontaine (1883) "ne laisse pas, d'ailleurs, d'être discutable". However, he discarded the possibility of affinity between his "*Z. truncatus*" and Fontaine's species.

#### *Macropterygium truncatum* (Zeiller) Weber comb. nov.

**Previous record**—(1902-) 1903 *Zamites truncatus* Zeiller.

**Diagnosis**—see Zeiller, (1902-) 1903, p. 166.

**Holotype**—The specimen figured by Zeiller, (1902-) 1903, pl. 43, fig. 4, 4, a.

**Type locality**—Hongay Mine, eastern valley of l'Oeuf, Shaft Léonice, Vietnam.

**Age**—Late Triassic.

#### *Macropterygium mexicanum* Weber sp. nov.

(Plate 1, figure 4; Plate 3, figures 2-6; Plate 4; Plate 5)

#### Previous records from Sonora:

- 1961 *Zamites truncatus* Zeiller.- Silva-Pineda, 1961, p. 23-24, pl. 5, fig. 4.
- 1961 *Zamites* sp., cf. *Z. megaphyllum* (Phillips) Seward.- Silva-Pineda, 1961, p. 22-23, pl. 5, fig. 3 (erroneous identification).
- 1961 *Zamites megaphyllum* (Phillips) Seward.- Silva-Pineda, 1961, pl. 5, fig. 3 (only in the figure caption; erroneous identification).
- 1982 *Zamites* cf. *truncatus* Zeiller.- Weber and others, 1980 (1982)a, tab. 2.
- 1982 *Zamites* cf. *truncatus* Zeiller.- Weber and others, 1980 (1982)b, figs. 1, 2, 13, c-g.
- 1985 *Zamites* cf. *truncatus* Zeiller.- Weber, 1985, tab. 2.

**Diagnosis**—*Indozamites* with large leaves and pinnae. Leaves about 20 cm in width; pinnae about 10 cm in length and 3 cm in width.

**Holotype**—Specimen IGM-PB-521B-889 (Plate 5, figure 1) from loc. 521B, CLP-IG-UNAM.

**Type palaeodeme**—All specimens belonging to this species from the type locality.

**Type locality**—Hermosillo-Tonichi highway, approx. Km 152, La Barranca Section 2 (measured by Potter *et al.*, 1980), Unit 42, "LB 3 stratum" and "Semillas" stratum (loc. 521B and C, CLP-IG-UNAM; see Weber, 1985, fig. 4, tab. 1), road-cut; 28°34'40"N/109°40'06"W, Sonora, Mexico.

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

**Derivation of name**—*mexicanum*: a species found in Mexico.

**Description**—This species is a rather common element in the Santa Clara flora. However, at most localities only detached pinnae were found. Hence, it is likely that at least some pinnae were shed when the leaves grew old. For the same reason, in most more or less complete leaves at least some basal pinnae are missing. This hampers obviously the reconstruction of the shape of the whole leaf.

Plate 5, figure 1, shows a specimen with petiole. The rachis is 3 mm wide immediately after the first pinnae, and along the preserved length of 9 cm, it tapers only slightly. In

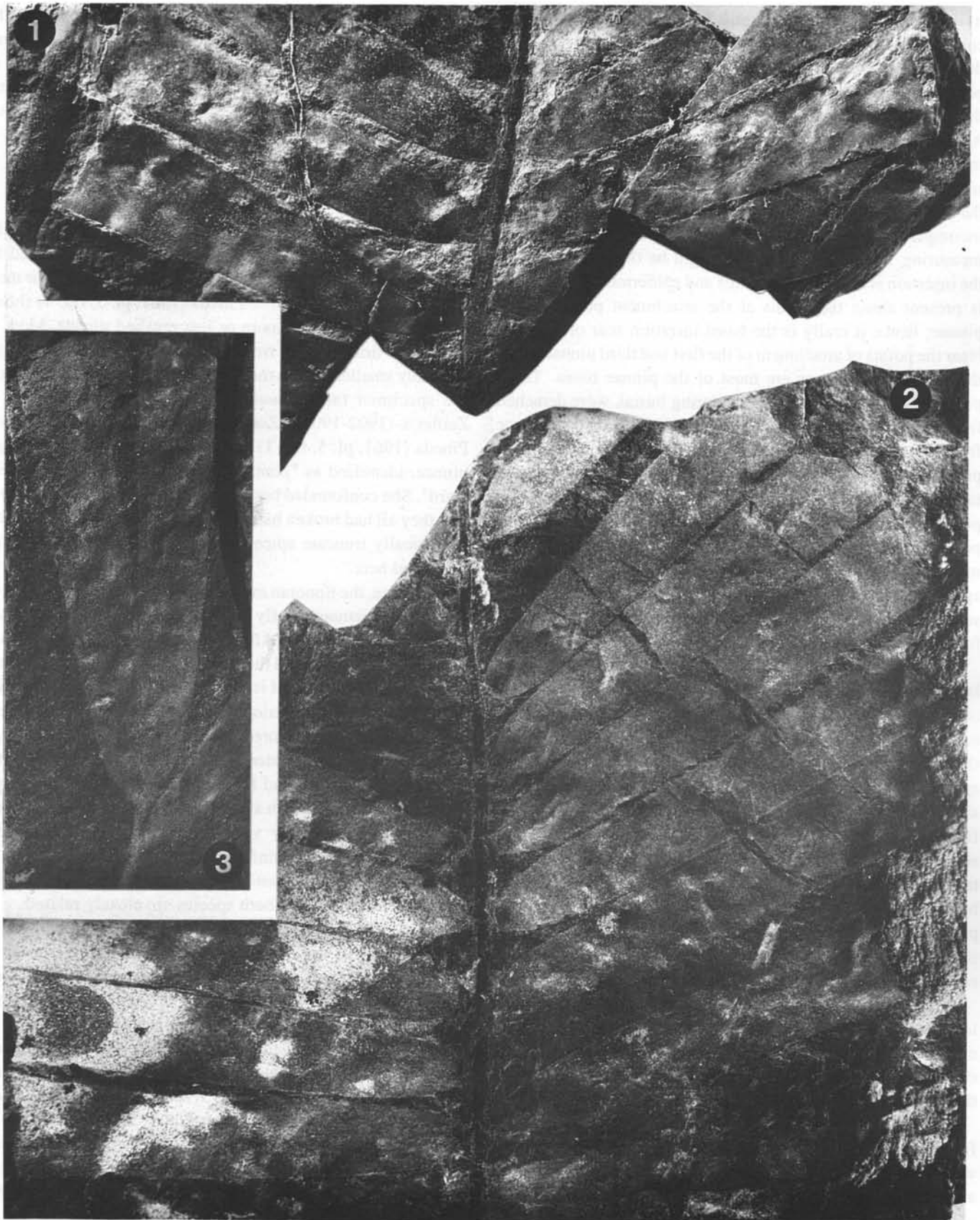


Plate 4. Figures 1-3—*Macropterygium* (*Indozamites*) *mexicanum* sp. nov. (all x 1). 1, Proximal fragment of large leaf. Loc. La Barranca, Section 2, Unit 42 (specimen IGM-PB-521-887). 2, Distal fragment of large leaf. Loc. La Barranca, Section 2, Unit 42 (specimen IGM-PB-521-888). 3, Distalmost portion of normal leaf. Loc. Arroyo Chamina, southern slope (specimen IGM-PB-543-889).

its distalmost part it measures still 2.5 cm in width. Hence, the considerable increase in width from the first pair of pinnae to the base proves that this segment of the central axis is the petiole, and that the basalmost pair of pinnae is preserved in this case. The petiole is about 3.3 cm long and 5 to 6 mm wide. At the very base it is widened suddenly to slightly less than 10 mm at the base, there is a transversal subelliptical insertion scar, measuring about 7 x 2.5 mm. This might be the scar of the conductive tissue. Excentrically around this, there is an incomplete much larger outline of sub-hexangular shape, measuring 11 mm in width, that might be the true outline of the insertion scar, including cortex and epidermis. No such scar is present along the rachis at the attachment points of the pinnae; hence it really is the basal insertion scar of the leaf. Near the points of attachment of the first and third pinnae pairs, the rachis is broken as are most of the pinnae bases. These probably did not resist the stress during burial, were detached from the rachis, and the pinnae glided away to some distance from the rachis. This character suggests that the leaves were probably not flat in life, *i. e.*, the pinnae were attached to the rachis at an angle of less than 180° between the pinnae of a pair, measured in a plane perpendicular to the rachis. The pinnae of this specimen show rather abruptly contracted, almost rounded bases, and one pinna has a slightly emarginate apex. The leaf shows traces of rootlets growing along its surface after burial, *i. e.*, the sediment enclosing the leaf is a fossil soil.

Plate 4, figure 2 shows a more apical fragment of a very large leaf with slender rachis, 2.5 to 2 mm wide along a length of almost 14 cm; *i. e.*, the rachis tapers very slightly from the base to the apex, suggesting that the leaves were much longer than is seen in the specimens. The pinnae are opposite and apparently attached to the rachis at angles that differ on both sides of the rachis. This suggests again that the leaves were not flat in life. Several pinnae of the right side of the leaf show subcircular to rounded triangular insertion scars at some distance from the rachis. Again, this indicates, that they are broken and drifted away from the rachis. All apices of the pinnae are damaged and incomplete. The widest rachis, 6 mm, is found in the leaf of Plate 5, figure 4. Its granular texture results from the coarse grain of the sediment.

A further important specimen (Plate 4, figure 3) shows a leaf apex with three pinnae. The pinnae are seemingly alternate. However, the middle pinna is clearly attached to the apex of the rachis at a distance of about 3 mm from the insertion of the basally following, left lateral pinna.

The fossil illustrated in Plate 1, figure 4 and Plate 3, figure 2 (x 2) shows the cuneate bases of two pinnae and the venation. However, the small dark dots on the pinnae surfaces are not the glandular bodies characterizing this species. In this

specimen, the rock is dotted throughout by weathering. The spherical to transversely elongate glandular bodies are very clearly seen in Plate 3, figure 3 (x 3). This figure shows, as well, that these structures often appear to connect neighboring veins, suggesting transverse anastomosis of the venation which, in fact, does not exist.

A reconstruction of a leaf of this species is shown in Figure 1, b.

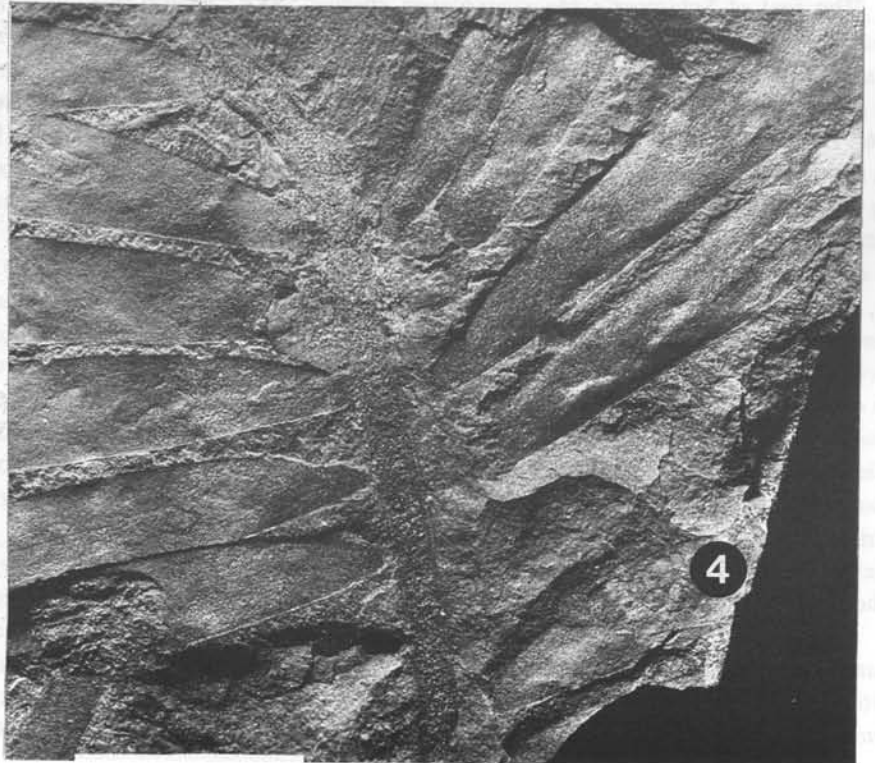
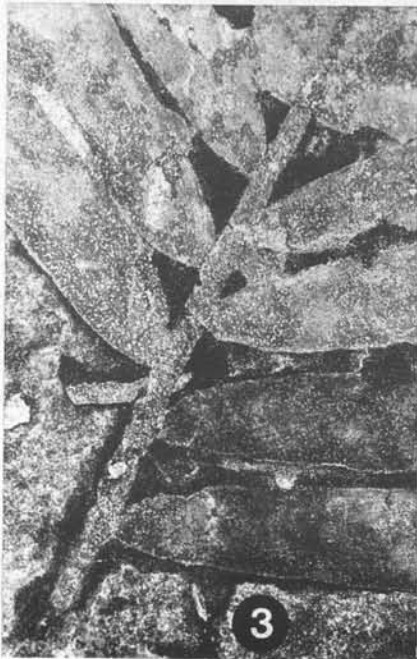
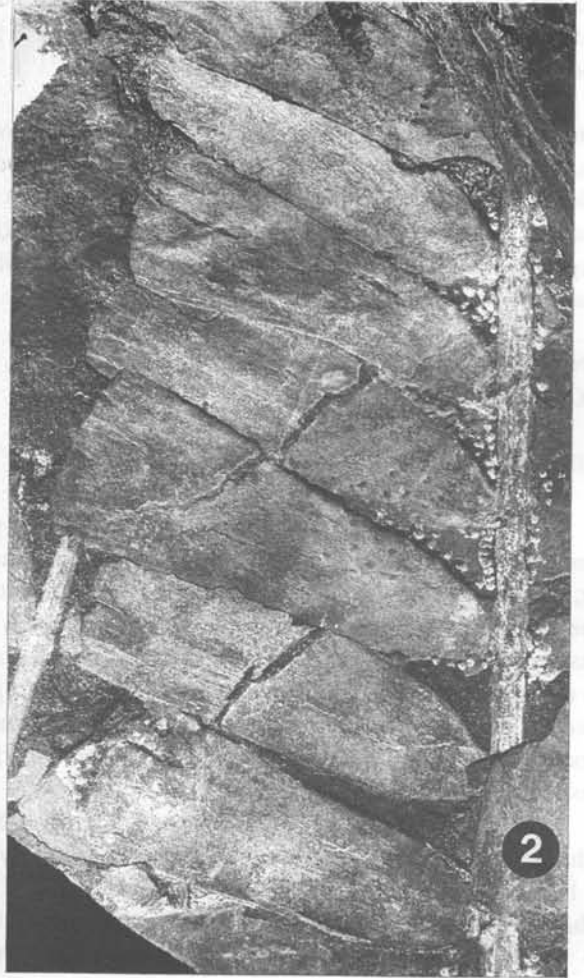
**Comparison**—This species resembles only the forms discussed in the present paper. It was previously described by Silva-Pineda (1961) from the Santa Clara Formation. The most complete specimen of Silva-Pineda (1961, pl. 5, fig. 4) shows mostly incomplete and more or less crushed pinnae. Most of them have drifted away from the rachis. The pinnae are considerably smaller than in the specimens described here. Hence, the specimen falls almost into the dimensional range of Zeiller's (1902-1903) "*Zamites truncatus*". However, Silva-Pineda (1961, pl. 5, fig. 3) described also considerably larger pinnae, identified as "*Zamites cf. megaphyllus* (Phillips) Seward". She confounded base and apex of the pinnae and stated that they all had broken bases. These "broken bases" are in fact the apically truncate apices of typical pinnae of the species described here.

Hence, the Sonoran material differs from Zeiller's specimens from Vietnam chiefly in dimensions. The Sonoran leaves are considerably larger. After Zeiller, the width of the leaves did not exceed 9 cm, and the pinnae were no longer than 5 cm. Even though his material is very poor, there is no overlapping of both species in dimensional ranges. The similarity between the detached pinnae figured by Zeiller (*op. cit.*, pl. 43, figs. 4-6) and the Sonoran material is higher than that between the latter and Zeiller's frond fragment (pl. 43, fig. 3) showing a well preserved pinna with almost parallel margins. In addition, the paleogeographically very significant distance between Sonora and Vietnam reinforces the specific segregation of *Macropterygium (Indozamites) mexicanum*. There remains little doubt, however, that both species are closely related.

**Paleoecological observations**—If all remains, the more or less complete leaves and the detached pinnae are considered, *Macropterygium (Indozamites) mexicanum* belongs to the most constant species of the Santa Clara flora, making it of little value in community paleoecology. However, the detached pinnae were probably often transported and are found now in allochthonous deposit. When only the more or less complete leaves are taken into account, the species shows a trend to belong to assemblages associated with well drained, energy-rich habitats. This observation was not verified in previous paleoecological studies, because no difference was

Plate 5. Figures 1-4—*Macropterygium (Macropterygium) mexicanum* sp. nov. (all x 1). 1, Holotype. Proximal fragment of normal leaf with petiole. Pinnae mostly detached and slightly drifted away from insertion. Loc. La Barranca, Section 2, Unit 42, Stratum B (specimen IGM-PB-521B-890). 2, Proximal fragment of leaf with relatively short pinnae. Same loc. as figure 1 (specimen IGM-PB-521B-891). 3 and 4, Fragments of leaves with narrow, subcuneate pinnae. 3, Same loc. as figure 1 (specimen IGM-PB-521B-542a). 4, Loc. Cerro El Candelero Stratum 2 (specimen IGM-PB-505-892).







made for statistical purposes between detached pinnae and frond fragments (Weber *et al.*, 1980b; Zambrano-García and Weber, 1985).

**Phytogeographic significance**—According to current knowledge, *Macropterygium*, subgenus *Indozamites* is restricted to southeastern Asia (Vietnam) and Mexico, suggesting the existence of transpacific phytogeographic relations. In Mexico, the species ranges into the Middle Jurassic of Oaxaca (Silva-Pineda, 1969, pl. 11, figs. 3, 4).

## GENERAL DISCUSSION AND COMPARISON OF *MACROPTERYGIUM*

### TYPIFICATION

In 1870, Schimper erected *Macropterygium* for two previously known and quite different species. The genus, however, was not accepted by later writers for a long time, but the name was occasionally used at subgeneric level. Jongmans and Dijkstra (1960) listed no references of *Macropterygium* species described after Schimper, but Andrews (1955, 1970) indexed the genus, and Bock (1969) adopted it, adding a number of more or less out of tune species from the North American Triassic, which are excluded here.

According to the usage of the time, Schimper (1870) neither proposed a type species nor did he choose holotypes, and later authors also did not, except Andrews (1955). If one wishes to use the genus *Macropterygium*, however, one of the two species included by Schimper (1870) must be the type species.

The first of Schimper's *Macropterygium* species, "*M. Bronnii* (Schenk) Sch.", had been described from the Late Triassic flora of Raibl, Austria, by Bronn (1858), who identified it as "*Noeggerathia vogesiaca* Schimper and Mougeot 1844". By the way, Bronn erroneously stated *Noeggerathia* to be a new genus. In fact, it had been erected already by Sternberg (1822; *fide* Andrews, 1970). Regarding this generic assignment, Arber (1907) wrote: "It remains to be pointed out, that detached pinnae of this frond especially when fragmentary, are likely to be mistaken for the leaves of *Cordaites* and other genera in which the nervation is closely similar, but which are simple leaves, spirally arranged on branches. They also strongly resemble detached leaflets of the Upper Carboniferous genus *Noeggerathia*,...". In *Noeggerathia*, however, the leaves (not pinnae), are strictly alternate, and it seems now reasonably sure that this genus and the *Noeggerathiopsida* are restricted to the Palaeozoic. Bronn's material was renamed by Schenk (1865) as "*Pterophyllum Bronnii*", and finally placed in the new genus *Macropterygium* by Schimper (1870).

The second species referred to *Macropterygium* by Schimper (1870) had been described originally by Schenk (1865) as *Pterophyllum giganteum*. Schimper called it "*Macropterygium Schenkii* Schimp.", even though the epithet

*giganteum* was not preoccupied in *Pterophyllum* before Schenk (1865; *cf.* Jongmans and Dijkstra, 1963). The formally correct name in Schimper's context could have been "*Macropterygium giganteum* (Schenk) Schimper". Later on, this species was assigned to "*Zamites grandis*" by Arber (1907); but Arber (1909) dropped this change, because he found that the British material assigned to this species did not really belong to *Zamites*. Since the two species included in *Macropterygium* by Schimper are thought to be generically distinct, the second one is excluded here. Its valid name is still *Pterophyllum giganteum* Schenk. The specimen figured by Schenk (1865, pl. 2, fig. 2) is chosen here as its holotype.

In short, *Macropterygium bronnii* (Schenk) Schimper was discovered at first, and Andrews (1955) was right, selecting it as type species of the genus. The specimen figured by Bronn (1858, pl. 4, fig. 1) is chosen here as the holotype of this species.

### DIAGNOSTIC VALUE AND PALEOBIOLOGICAL MEANING OF SOME CHARACTERS

In many diagnoses or descriptions of the species discussed here and the related genera, the insertion of the pinnae is considered a useful, or at least interesting feature. Regarding *Macropterygium bronnii*, Arber (1907) suggested in agreement with the type specimen figured by Bronn (1858), that the rachis does not show any kind of callosity at the insertion of pinnae. However, the specimen figured here (Plate 1, figure 1) shows that they are attached obliquely to the upper or ventral face of the rachis. The outline of the scars is not well preserved. In the Sonoran specimen compared here with the former species (Plate 3, figure 1), oblique insertion of two pinnae to the ventral face of the rachis is clearly observed, but no callosities are present. After Fontaine (1883), the pinnae of *Macropterygium (Glandulozamites) rogersianum* possess a very short pedicel obliquely attached, "somewhat within the margins of the stem". Bock (1969), in the material assigned here to *M. (Gl.) punctatum*, observed "small, oval callosities up to 5 mm wide near the upper margin of rachis...serving as attachment for pinnae bases". The oblique attachment is very clearly shown in his fig. 313. In agreement with these observations, it is tempting to propose that the pinnae were mostly twisted at the base to get oriented in a more or less flat lamina. This twisting is clearly visible in the leaf of Plate 1, figure 1. The pinnae of *M. (Indozamites) truncatum* are attached to the upper (ventral) face of rachis and thickened at base. The rachis has a callosity at this point. The Sonoran material placed in the subgenus, however, does not show these features owing to poor preservation.

These observations, together with the rarity of leaves with all pinnae preserved and attached, added to the very frequent occurrence of detached pinnae, suggest that the pinnae of this genus had preformed abscission structures, and that shedding of pinnae was a normal biological character of the group, which seems to be a really important character.

"Glandular bodies" have been found not only in a number of bennettitalean leaf genera, but also in the cycadalean *Nilssonia*, especially in *Nilssonia polymorpha* Schenk (Weber, 1968, pl. 12, fig. 117). Schenk (1867, pl. 29, figs. 1, a, 2, a) figured these bodies and interpreted them as fertile structures. Nevertheless, they are mentioned here in the diagnosis of two subgenera. They were not observed beyond doubt in *Macropterygium*, subgen. *typicum*. The interpretation of these dark dots found in the interspaces of the veins, was controversial for long time after their discovery. Fontaine (1883), regarding *M. (Glandulozamites) rogersianum* stated: The granulation "...is composed of globular prominences or dots which do not seem to be anything but a fine granulation of the epidermis" and "does not appear to be anything like fructification". He added: "Sometimes, owing to distortion from pressure, these dot-like elevations are drawn out into little bars which extend from nerve to nerve and look like transverse nerves". Seward (1917) believed the dots to be papillae. Bock (1952) regarded them as glandular bodies, but later (1969), on the basis of his material of *M. (Gl.) punctatum*, conjectured after detailed description: "The whole device appears to be of protective nature, which may include water or gaseous regulations. It may discourage insects and fungus growth, which constitute a quite obvious danger to Triassic, broad-leaved cycadeans". The terms "glandular bodies" or "resin-bodies" are used here in a rather conventional sense. It is most important, however, that no transverse veins are present in these forms.

#### MACROPTERYGIUM AND PTEROPHYLLUM

In accordance with the above mentioned classification of bennettitalean leaf genera by Watson and Sincock (1992), presented by these authors in the form of a key and several emended diagnosis, *Pterophyllum* is characterized by linear leaves and pinnae that are more or less symmetrically expanded at attachment or, if not, show lateral margins running parallel, or almost so, to the rachis. In the first case, the pinnae may be slightly narrowed near the base. Additionally, in the literature exists a more or less flexible consensus regarding the pinnae of *Pterophyllum* to possess subparallel margins from the base to the tip. In no way can forms like those placed here in *Macropterygium*, be assigned to *Pterophyllum*, not only because their pinnae are strongly spatulate, but also because the whole leaf is elliptical or even subcircular in shape. Admittedly, however, there are some species that seem to be intermediate between *Macropterygium* and *Pterophyllum*.

On the basis of material housed at that time in Munich, *Macropterygium bronniei* has been redescribed under the older name "*Pterophyllum bronniei* Schenk", by Arber (1907), even though he recognized that this species did not agree with the generic diagnosis of *Pterophyllum*, given by Brongniart (1828), Schimper (1870) and Zeiller (1903) regarding the pinnae shape. He even compared this species with "*Sphenozamites rogersianus* Fontaine 1883": "Fontaine's figures do

not, however, agree very well with the Austrian specimen, though Stur (1888) has gone so far as to say that both are specifically identical".

Some years later, Seward (1917) wrote about these plants: "*Pterophyllum Bronniei* and *P. Rogersianum* might be placed in Schimper's genus *Macropterygium*, though another Raibl species, originally described by Schenk as *Pterophyllum giganteum* and referred by Schimper to *M.*, has much longer and relatively narrow pinnae and agrees more closely with *Pterophyllum* as the genus is usually defined. In order to emphasize the distinctive features of *Pterophyllum Bronniei* and Fontaine's Virginian species they may conveniently be spoken of as *Pterophyllum (Macropterygium) Bronniei* and *Pterophyllum (Macropterygium) Rogersianum*".

#### MACROPTERYGIUM AND SPHENOZAMITES

Watson and Sincock (1992) defined *Sphenozamites* Brongniart in their generic key for bennettitalean leaf genera as follows: "Pinnae obliquely rhomboid or diamond-shaped; attached laterally to rachis". It is clear that none of the species of *Macropterygium* reviewed here agrees with this definition. Besides the spatulate pinnae shape, the mostly opposite attachment of the pinnae is a prominent character of the latter genus. According to the more detailed diagnosis of *Sphenozamites* given by Wesley (1958), this genus has alternate pinnae in addition to the bennettitalean stomatal apparatus.

In the above discussion, it was pointed out that Seward (1917) already proposed to exclude Schimper's species "*Macropterygium schenkii*" from *M.* accepted by him as a subgenus. In contrast to Arber (1907), however, he included "*Sphenozamites rogersianus* Fontaine", the later "*Glandulozamites punctatus* Bock 1969". This strengthens the above choice of *Macropterygium bronniei* as type species of this genus.

In his review of *Sphenozamites*, Wesley (1958) pointed out that it might be best to take up again Schimper's generic name *Macropterygium* for "*Sphenozamites rogersianus* Fontaine". He wrote: "I am certain that Seward was not correct in using the name *Pterophyllum*, since that genus is characterized by pinnae which are not contracted at their insertions on the rachis, but his suggestion that Schimper's genus *Macropterygium*, which has the pinnae contracted at their insertions, might be used seems to me to be a more suitable suggestion".

Consequently, Bock (1969) was unfortunate, placing in *Macropterygium* a number of species not closely related with anyone included by Schimper, and less so with the type species *M. bronniei*. Only one of those included by Bock, "*M. grandifolium* (Fontaine) Bock", resembles "*M. schenkii* Schimper" regarding the pinna outline. A second one, "*M. spatulatum* (Emmons) Bock", also compares rather weakly with the same species, proposed above for exclusion from *Macropterygium*. Bock (1969) obviously overlooked the selection of the type species of *M.* by Andrews (1955), and added confusion to the nomenclature of bennettitalean leaves.

## MACROPTERYGIUM AND ZAMITES

Zamites is quite widely defined by Watson and Sincock (1992; cf. Weber and Zamudio-Varela, 1995): In this genus the pinnae have symmetrically contracted, more or less rounded to cuneate bases. After these researchers, the shape of the pinnae has no diagnostic value in *Z.* However, the present author considers best to return to Harris's (1969) diagnosis of *Z.*: "Leaf simply pinnate, pinnae attached to upper side of 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, dichotomising but not anastomosing; ending in pinna margins and apex. Cuticle...".

According to this diagnosis, the species of *Macropterygium* discussed here cannot be placed in *Zamites*. As to the conflict between the Watson and Sincock's (1992) classification and the one intended here, a new genus collecting all species of *Zamites*, *sensu* Watson and Sincock not belonging to *Zamites*, *sensu* Harris (1969), *Laurozamites* and *Macropterygium* might be erected. *Parazamites* might be the name of such a genus.

## THE SUBGENERA OF MACROPTERYGIUM

As stated above, Bock (1969) was partially right, removing the former "*Sphenozamites rogersianus* Fontaine" from this genus through the new combination "*Glandulozamites punctatus* (Emmons) Bock". However, the large glandular bodies observed in this species are considered here to be of insufficient diagnostic weight for erecting a genus, especially because glandular bodies are also present in subgen. *Indozamites* proposed here. *Glandulozamites* can be accepted at subgeneric level, since regarding the pinna shape it resembles *Macropterygium* subgen. *Macropterygium*, but in the leaf form and number of pinnae, it is closer to subgen. *Indozamites*. Certainly, several earlier authors had already proposed to group *M. brononii* with "*Sphenozamites rogersianus*" in one subgenus (Seward, 1917; Wesley, 1958). But it was unfortunate to place them as members of subgen. *Macropterygium* in *Pterophyllum*.

The subgenus *Indozamites* is proposed here, because the two species assigned to it are clearly related to subgen. *Macropterygium* and *Glandulozamites*, but also markedly distinct regarding the pinna dimensions and proportions. The characters distinguishing these subgenera are in general terms considered too trivial for establishing three genera.

## MACROPTERYGIUM AND EOGINKGOITES

The leaf of *Macropterygium brononii* illustrated here (Plate 1, figure 1) and the one figured by Arber (1907, pl. 18, fig. 1) show that this species possesses a low number (only about 10 or slightly more) of very large broadly spatulate

pinnae attached to a comparatively short rachis. The leaves of *Eoginkgoites* are also characterized by a very short rachis. A further similarity lies in the crowded grouping of the distalmost pinnae in *Macropterygium* (*Macropterygium*) and in *Eoginkgoites*. In other characters, however, *M.* and *E.* do not agree. Especially, the basal fusion of the distalmost group of pinnae and marginal veins or rims often present in *E.* are not shared by *M.*, except perhaps subgen. *Glandulozamites*. Fontaine (1883) repeatedly mentioned and underscored the presence of rims at the pinnae margins of his "*Sphenozamites rogersianus*". Anastomosing veins are known only in *Eoginkgoites*. A more detailed comparison of these genera is not given here due to the poor preservation of the material from Sonora. However, the Sonoran specimens of *Macropterygium* in no instance show pinnae with marginal vein or rim, and neither terminal thickenings nor anastomosis of the veins have been observed. The most proximal pinnae of *E.* are attached to the rachis at an axillar angle much lower than 90°, whereas in *M.*, it measures normally about 90° or more. Consequently, *Eoginkgoites* is considered here a valid genus closely related to *Macropterygium*.

The short rachis shared by *Macropterygium*, subgenera *Macropterygium* and *Eoginkgoites* is doubtless a derived character with regard to other coeval bennettitaleans. In the latter genus, this reduction or compaction of the rachis is even stronger than in the first genus, indicating an evolutionary tendency to short and broad leaves in the group of bennettitalean leaf genera discussed here. The above mentioned additional diagnostic characters of *E.* are probably derived with respect to *M.* and other pinnate bennettitalean leaf genera. Hence, *Macropterygium* is thought to be the ancestral stock of *Eoginkgoites*.

A reconstruction of a leaf of *Eoginkgoites* is shown in Figure 1, d.

## SPECIES EXCLUDED FROM MACROPTERYGIUM

"*Macropterygium schenkii* Schimper" (1870, p. 133) = *Pterophyllum giganteum* Schenk (1865: 18-19, pl., 2 fig. 2) is excluded, because its pinnae, though spatulate in shape, are attached to the rachis with broadened, not strongly contracted base. The preservation (or quality of the illustration) does not allow to generalize these observations. The pinnae of this species are narrowly spatulate and truncate as in *M.* (*Indozamites*), but the minimum pinna width at base is 7 mm, *i. e.*, more than one third of the maximum pinna width of 20 mm.

"*Macropterygium grandifolium* (Fontaine) Bock" (1969, p. 179-184, figs. 278-282) = *Ctenophyllum grandifolium* Fontaine (1883, p. 73-76, pl. 39, figs. 1-3, a, pl. 40, 41, 42, fig. 1, 1, a, b) and *Ct. giganteum* Fontaine (1883, p. 76-77, pl. 39, fig. 5). This species, according to the figures given by Fontaine has very long pinnae with almost parallel lateral margins attached to rachis with broadened bases and lacking a basal constriction. Fontaine's *Ct. giganteum* is in our opinion a non identifiable

fragment. Bock's specimen (1969, figs. 278-280) seems to be specifically identical, although the pinnae are somewhat more widened from the base to the non preserved tip of the pinnae.

"*Macropterygium angustum* (Braun) Bock" (1969, p. 187-192, figs. 295-304) is a potpourri of unrelated bennettitalean leaves not belonging to the genus discussed here. No further details are given here because a major number of species was lumped together by Bock (1969) under this name.

"*Macropterygium spatulatum* (Emmons) Bock" (1969, p. 103-194, figs 305-307) = *Pterozamites spatulatus* Emmons (1857, p. 120, fig. 88). The pinnae of this species are very narrow and slightly lanceolate, but not spatulate. No basal constriction is seen in Emmons original figure. Bock's specimen is probably specifically distinct from Emmon's. *Ctenophyllum truncatum* Fontaine (1883, p. 68-69, pl. 38, figs. 3-5) is specifically distinct, although Bock (1969) includes it in his synonymy of "*M. spatulatum*". None of these specimens can reasonably be placed in *Macropterygium*.

"*Macropterygium vestitum* Bock" (1969, p. 184-186, figs. 283-294) has very long parallel-sided pinnae. Bock's fig. 291 shows a rachis with some fragmentary, non constricted pinnae bases with parallel margins. It does not fit the genus *Macropterygium* as defined here.

#### RECORDS RESEMBLING BUT NOT PLACED HERE IN *MACROPTERYGIUM*

In the literature, there are several records of species resembling the forms included here in *Macropterygium*, but they are either not adequately preserved to grant the assignment to this genus, or, in one case, contrary evidence is available.

*Sinozamites leeiana* Sze (1956) from the upper part of the Late Triassic Yenchang Formation of northern Shensi, China, resembles *Macropterygium* in the opposite to subopposite attachment of the pinnae. Sze (1956, pl. 39, fig. 2) figured a specimen with one spatulate (or broken?) pinna with truncate apex resembling *M. (Indozamites) truncatus* Zeiller closely. However, the more complete, typical specimens are characterized by a dentate pinna apex (Sze, 1956, pl. 39, fig. 3) and the not perfectly entire pinna margins (pl. 39, figs. 1, 1, a). In addition, sharply pointed toothlets seem to be present at the vein endings along the distal parts of the lateral pinna margins, but in part these teeth appear to be preservational artifacts. In several bennettitalean leaf genera, showing normally pinnae with entire margins, species with dentate margins or pinnae tips are occasionally found. One example is *Pterophyllum spinosum* Person and Delevoryas (1982, pl. 10, fig. 52), from the Middle Jurassic of Oaxaca, Mexico. A second case is a not yet formally described species assignable to *Anomozamites* from the Santa Clara Formation of Sonora (Weber, 1985). The generic identifications of these species are not discussed here.

*Sphenozamites changi* Sze (1956) from the Late Triassic Yenchang Formation of northern Shensi, China, resembles

*Macropterygium*, subgenera *Macropterygium* and *Glandulozamites* in its very wide pinnae. Yet these are much shorter than in *M.*: The length/width ratio is about 2 or even less, and the distal margin is very asymmetrical, so that the original assignment of the species to *Sphenozamites* seems to be reasonable. However, the leaves are suggestive of a close relationship between this species and *Macropterygium*.

*Apoldia tenera* (Compter) Linnell was reported originally as "*Sphenozamites tener*" by Compter (1883) from the lower Keuper of Thuringia, central Germany, on the basis of very fragmentary material. Compter (1894) reported this species once again, figuring (pl. 4, fig. 3) an additional leaf fragment with three pairs of opposite pinnae attached to a rather slender rachis. The pinnae are very wide, basally fan-shaped, but the apices are missing and the form of the complete pinnae is unknown. The material was re-examined by Linnell (1932), who found a close resemblance with *Nilssonia* regarding the stomatal apparatus and proposed the genus *Apoldia* for such leaves. No additional material has been found in the German Keuper up till now (Kelber and Hansch, 1995). Although this species resembles *Macropterygium* in macroscopic characters, it cannot be assigned to this genus or to the Bennettiales either.

#### GEOGRAPHIC DISTRIBUTION OF *MACROPTERYGIUM*

As far as the author's acquaintance reaches, the genus is distributed in eastern Asia, North America and central Europe, during the Late Triassic. Only in Mexico, it does reach the Middle Jurassic. The Late Triassic Paleopacific Ocean was bridged over by *Macropterygium (Indozamites)*. By the way, it should be mentioned that two additional rather closely related bennettitalean genera, *Laurozamites* Weber and Zamudio-Varela (1995) and *Sinoctenis* Sze (1931) have jointly a comparable distribution. These genera are distinct only in that the first one shows normally pinnae with both basicopic and acroscopic auricles, whereas the second possesses only acroscopic auricles, even though slight expansions of the basicopic pinna corner may also be observed occasionally (Barale and Zhou, 1988). North America and Europe were not separated by an ocean during the Late Triassic. The simultaneous occurrence of *M. (Macropterygium)* in Sonora and Austria is, hence, less intriguing. The genus is missing all over southern and eastern Europe, Russian Asia and neighboring countries (Dobruskina, 1994). It is absent as well from Gondwana, at least during the Late Triassic.

In addition, the above mentioned species doubtfully related to and not placed in *Macropterygium* all have been found within the distributional area of this genus.

#### OUTLOOK INTO CULTURAL HISTORY

About 30 years ago, the writer visited the Museum of Natural History (Naturhistorisches Museum), Vienna, where

he saw the excellent specimen discussed above, labeled as "*Pterophyllum Bronni* Schenk", from the Late Triassic Flora of Raibl (Plate 1, figure 1). The specimen had been figured previously in a guide book of that museum (Anonymous, 1964, fig. 5), but was never described, although it had certainly been collected in the past century. As pointed out earlier in this paper, this specimen belongs to *Macropterygium* (*Macropterygium*) *bronnii* (Schenk) Schimper.

In 1975, the writer collected the first fragmentary specimens, which he hesitated to identify as *Macropterygium* (or as ginkgoalean leaves), from the Santa Clara Formation of Sonora (Weber, 1985). At that time, he noticed the resemblance between a palm-like "cycad" tree in a painting by José María Velasco showing Triassic vegetation in the Geological Museum (Museo de Geología), Mexico City, the mentioned Vienna specimen and the Sonoran material. Several years later, in 1981, together with his students he discovered some new localities in Sonora with better preserved remains of *Macropterygium*, described here as *M. aff. bronnii*.

In 1989, the writer was visited by the art historian María Elena Altamirano Piolle of the UNAM, who worked on a monograph on the slightly romantic Mexican realist painter José María Velasco (Altamirano-Piolle, 1993). She asked him to explain for her book the set of paleontological landscape reconstructions by Velasco decorating the entrance hall of the old building of the Geological Institute (formerly Instituto Geológico de México, now Museo de Geología, Instituto de Geología, UNAM), Mexico City. In addition, M.E. Altamirano Piolle, a descendent of Velasco, mentioned that in the personal archive of the painter, owned by her, she had found a set of photographic post-cards of the *belle époque* after paintings by Josef Hoffmann, Vienna, that resemble Velasco's paintings very closely (Altamirano-Piolle, 1993, figs. 510-532). Obviously, Velasco had drafted most of his paintings after these post-cards.

Two points allowed the assumption that the original paintings by Hoffmann were in the Museum of Natural History, Vienna, at the beginning of the century: Firstly, the eminent Mexican geologist José G. Aguilera had attended the IXth International Geological Congress at Vienna, 1903. Probably, he had obtained the post-cards there, and later forwarded them to Velasco, scientific artist (1880-1910) at the National Museum (Museo Nacional), Mexico City, in order to copy them for the planned building of the Geological Institute. The building was opened to the public in 1906, on the occasion of the Xth International Geological Congress. Secondly, the writer remembered the similarity mentioned above, between the palm-like tree represented by Velasco and Hoffmann in their Triassic landscapes, the *Macropterygium* specimen of the Museum of Natural History, Vienna, and the Sonoran material of *Macropterygium*. As could be verified through a written request to the Vienna museum, the Hoffmann paintings are indeed there since 1882/89 (Nebehay, personal communication, 1989). In addition, Stefan Nebehay forwarded a published

explanatory text by Josef Hoffmann (late 19th century; without year) to the writer. Regarding his fourth comprehensive painting (Vollbild), the life picture of the Triassic vegetation, Hoffmann mentioned *Pterophyllum Bronni*. So, it was proven that *Macropterygium* had been represented in a painting housed in the Geological Museum at Mexico City long before it was found as a fossil in the Santa Clara Formation.

During a later visit to Vienna, in 1991, the writer saw the paintings by Hoffmann in the Dinosaur-room (Saal X) of the Museum of Natural History, and examined once again the specimen of *Macropterygium bronnii* mentioned above. Later on, Johanna Eder-Kovar kindly sent a photograph of this excellent specimen (Plate 1, figure 1). These memorable confabulations of art work and paleobotany, rendered the *Macropterygium* problem even more worthwhile.

#### ACKNOWLEDGMENTS

Many persons furthered this work during many years, but not all of them can be named here. The writer is especially indebted to Alfonso Torres-Romo, Ricardo Trejo-Cruz, Ángel Zambrano-García and Adriana Hurtado-Cortés, who collected some of the finest specimens studied here. Armando Altamira, Héctor Hernández-Campos and Johanna Eder Kovar were very helpful in the elaboration or obtention of photographs. Several institutions helped to finance the project. In the last years, the Dirección General de Asuntos del Personal Académico, Universidad Nacional Autónoma de México, financed this work through the grant IN-205392. The paper was reviewed by Drs. Sergio Archangelsky and Tatsuki Kimura. Their comments are gratefully acknowledged here. Errors that may survive in the paper, however, are full responsibility of the writer.

#### BIBLIOGRAPHICAL REFERENCES

- Altamirano-Piolle, M.E., 1993, José María Velasco. Paisajes de luz, horizontes de modernidad, in Homenaje Nacional José María Velasco (1840-1912). Con prólogo de Xavier Moyssén e introducción por Fausto Ramírez: Museo Nacional de Arte, México, D.F., v. I, p. 1-283; v. II, p. 291-555, 623 fig. (exhibition catalog).
- Anderson, J.M., and Anderson, Heidi-M., 1983, Palaeoflora of southern Africa-Molteno Formation (Triassic)—v. 1, Part 1, Introduction; Part 2, *Dicroidium*: Balkema, Rotterdam, Botanical Research Institute, v. 1, pt. 2, 227 p., 223 pl.
- 1989, Palaeoflora of southern Africa-Molteno Formation (Triassic); Gymnosperms (excluding *Dicroidium*): Balkema, Rotterdam, Botanical Research Institute, v. 2, 567 p., 331 pl.
- Andrews, H.N., Jr., 1955, Index of generic names of fossil plants, 1820-1950: U.S. Geological Survey Bulletin 1013, 262 p.
- 1970, Index of generic names of fossil plants, 1820-1965: U.S. Geological Survey Bulletin 1300, 354 p.
- Anonymous, 1964, Eine Besichtigung der geologisch-paläontologischen Sammlung, in Bachmayer, Friedrich, ed., Schätze im Boden. Bilder aus Österreichs geologischer Vergangenheit: Vienna, Veröff. Naturhistorisches Museum, v. 5, p. 8-19.
- Applegate, S.P., 1956, Additions and review of the paleobiology of the Triassic of Virginia: Virginia, University of Virginia, M. Sc. thesis, 224 p., 68 text-fig., 53 pl. (unpublished).



- Arber, E.A. Newell, 1907, On Triassic species of the Genera *Zamites* and *Pterophyllum*—Types of fronds belonging to the Cycadophyta: Transactions, Linnean Society, 2nd Ser. Botany, v. 7, p. 109-127, pl. 17-19.
- 1909, On the affinities of the Triassic plant *Yuccites vogesiacus* Schimp. and Mougeot: Geological Magazine [V], v. 6, p. 11-14.
- Archangelsky, Sergio, 1970, Fundamentos de Paleobotánica: La Plata, Argentina, Universidad Nacional de La Plata, Fac. Ciencias Nat. y Mus., Ser. Técnica y Didáctica, no. 11, 347 p., 22 pl.
- Artabe, A.E., 1990, Revalidación del género triásico *Zuberia* Frenguelli 1943, Familia Corystospermaceae: La Plata, Argentina, Universidad Nacional de La Plata, Fac. Ciencias Nat. y Mus., Revista del Museo de la Plata (N. S.), v. 9, Paleontología 55, p. 145-155, 2 pl.
- Ash, S.R., 1976, The systematic position of *Eoginkgoites*: American Journal of Botany, v. 63, no. 10, p. 1327-1331.
- 1977, An unusual bennettitalean leaf from the Upper Triassic of the south-western United States: Palaeontology, v. 20, p. 641-659, pl. 77-79.
- 1980, Upper Triassic floral zones of North America, in Dilcher, D.L., and Taylor, T.H., eds., Biostratigraphy of fossil plants—Successional and paleoecological analysis: Stroudsburg, Dowden, Hutchinson and Ross, p. 153-170.
- Axsmith, B.J.; Taylor, T.N.; Delevoryas, Theodore; and Hope, R.C., 1995, A new species of *Eoginkgoites* from the Upper Triassic of Northern Carolina, USA: Review of Palaeobotany and Palynology, v. 85, p. 189-198.
- Barale, Georges, and Zhou Zhiyan, 1988, On the presence of the genus *Sinoctenis* Sze in the Upper Triassic flora from Vietnam: Revue de Paléobiologie, v. 7, no. 1, p. 25-32, 2 pl.
- Bock, Wilhelm, 1952, New eastern Triassic Ginkgos (New Jersey-Pennsylvania): Bulletin of the Wagner Free Institute of Sciences of Philadelphia, v. 29, p. 9-14.
- 1969, The American Triassic flora and global distribution: Geological Center Research Series, nos. 3-4, 406 p.
- Brongniart, Adolphe de, 1828, Prodrome d'une histoire des végétaux fossiles: Levrault, Paris, Strasbourg, VIII, 212 p. (also in Dictionnaire Univ. Hist. Nat., v. 56, p. 16-212).
- Bronn, H., 1858, Beiträge zur triassischen Fauna und Flora der bituminösen Schiefer von Raibl. Neues Jahrb. Min., Geognost. Geol. u. Petrefakten, p. 129-130, pl. 6.
- Cleal, C.J., ed., 1991, Plant fossils in geological investigation. The Paleozoic—Introduction: New York, Ellis Horwood, p. 13-33.
- Compter, Gustav, 1883, Zur fossilen Flora der Lettenkohle Ostthüringens: Zeitschrift Naturwiss., v. 56, 29 p.
- 1894, Die fossile Flora des unteren Keupers von Ostthüringen: Zeitschrift Naturwiss., v. 83, no. 2, p. 205-230.
- Comet, B., and Olson, P.E., 1990, Early to middle Carnian (Triassic) flora and fauna of the Richmond and Taylorsville basins, Virginia and Maryland, U.S.A.: Virginia Museum of Natural History, Guidebook 1, 83 p., 4 phot. pl.
- Dobruskina, I.A., 1994, Triassic floras of Eurasia: Österreichische Akademie der Wissenschaften Schriften. Erdwiss. Kommission, v. 10, Springer Verlag Wien, New York, 422 p.
- Emmons, Ebenezer, 1857, Albany, N.Y., American Geology, pt. 6, v. 3, 155 p.
- Florin, Rudolf, 1933a, Die Spaltöffnungsapparate der *Williamsonia*-, *Williamsoniella*- und *Wielandiella*-Blüten (Bennettitales): Arkiv f. Botanik, v. 25A, p. 1-20, 1 pl.
- 1933b, Studien über die Cycadales des Mesozoikums nebst Erörterungen über die Spaltöffnungsapparate der Bennettitales: K. Svensk Vetenskapssakad. Handl., 3, v. 12, no. 5, p. 1-134, 16 pl.
- Fontaine, W.M., 1883, Contributions to the knowledge of the older Mesozoic flora of Virginia: U.S. Geological Survey, Monograph, v. 6, 144 p., 56 pl.
- Frenguelli, Joaquín, 1943, Reseña crítica de los géneros atribuidos a la "Serie de *Thinnfeldia*": La Plata, Argentina, Universidad Nacional de La Plata, Revista, n. s. geología, v. 2, p. 225-342.
- Harris, T.M., 1931, The fossil flora of Scoresby Sound, east Greenland—Part 2. Description of seed plants *incertae sedis* together with a discussion of certain cycadophyte cuticles: Meddelelser om Groenland, v. 85, no. 2, 112 p., 9 pl.
- 1932, The fossil flora of Scoresby Sound, east Greenland—Part 3. Caytoniales and Bennettitales: Meddelelser om Groenland, v. 85, no. 5, 133 p., 19 pl.
- 1969, The Yorkshire Jurassic flora—Part 3. Bennettitales: London, British Museum (Natural History), Publication 675, 186 p., 69 text-fig., 7 pl.
- Hoffmann, Josef, s. a., Erläuterung zu den Gemälden—Die Bildungs-Epochen der Erde und Charakterbilder für Asien und Central-Afrika: Wien, Verlag von Josef Hoffmann, 13 p.
- Jongmans, Willem, and Dijkstra, S.J., 1960, Filicales, Pteridospermae, Cycadales. 17, in Jongmans, Willem, ed., Fossilium Catalogus. II—Plantae: Junk, s'Gravenhage, pars 44, p. 1453-1596.
- 1963, Filicales, Pteridospermae, Cycadales. 29, in Jongmans, Willem, ed., Fossilium Catalogus. II—Plantae: Junk, s'Gravenhage., pars 56, p. 1453-1596.
- Kelber, K.P., and Hansch, Wolfgang, 1995, Keuperpflanzen. Die Enträtselung einer über 200 Millionen alten Flora: Städtische Museen Heilbronn (exhibition catalog), museo 11, p. 1-157, 300 fig.
- Kovács-Endrödy, Éva, 1985, The *Gangamopteris* story: Annals of the Geological Survey, Republic of South Africa, v. 19, p. 73-77.
- Linnell, Tore, 1932, Zur Morphologie und Systematik triassischer Cycadophyten. I. Die Gattung *Sphenozamites* BRONGN: Svensk Bot. Tidskr., v. 27, no. 3, p. 241-263.
- Newberry, J.S., 1876, Report of the exploring expedition from Santa Fe, New Mexico, to the junction of the Grand and Green rivers of the Great Colorado of the West in 1859: U.S. Army and Engineers Department, Geological Report, p. 137-148, 8 pl.
- Person, C.P., and Delevoryas, Theodore, 1982, The Middle Jurassic flora of Oaxaca, Mexico: Palaeontographica, Abteilung B, v. 180, p. 82-119, 11 text-fig., 10 pl.
- Petriella, Bruno, 1979, Sinopsis de las Corystospermaceae (Corystospermales, Pteridospermophyta) de Argentina. I. Hojas: Ameghiniana, v. 16, nos. 1-2, p. 81-102.
- Potter, P.E., and coworkers, 1980, Breve informe de actividades ...: Hermosillo, Sonora, Dirección Min. Geol. Energ., Gobierno Estado de Sonora, private report, 6 p., enclosures (unpublished).
- Retallack, G.J., 1977, Reconstructing Triassic vegetation of eastern Australasia—A new approach for the biostratigraphy of Gondwanaland: Alcheringa, v. 1, p. 247-277, and Microfiche supplement Alcheringa-fiche I, G1-G116 (distributed in print by Univ. New England, Geol. Dept., Armidale, NSW).
- Schenk, August, 1865, Ueber die Flora der schwarzen Schiefer von Raibl: Würzburger Naturwiss. Zeitschrift, v. 6, p. 10-20.
- 1867, Die fossile Flora der Grenzschichten des Keupers und Lias Frankens. Text, 232 p.; Atlas, VI, p., 45 pl. Wiesbaden (1865-1867). (Dates of publication of the fascicles: see Kilpper, 1964, Palaeontographica, Abt. B, v. 114, p. 73).
- Schimper, W.P., 1869-1874, Traité de paléontologie végétale, 3 v. and atlas: Paris, Baillière. V. 1. 1869, IV, 740 p.; v. 2. 1870-1872, IV, 968 p.; v. 3. 1874, IV, 896 p.; 1874. Atlas (quoted as Schimper, 1870).
- Seward, A.C., 1917, Fossil Plants: Cambridge, Cambridge University Press, v. 3, 656 p.
- Silva-Pineda, Alicia, 1961, Paleontología del Triásico Superior de Sonora. Parte 2. Flora fósil de la Formación Santa Clara (Cármico) Estado de Sonora, in Alencáster de Cserna, Gloria, ed., Paleontología del Triásico Superior de Sonora: Universidad Nacional Autónoma de México, Instituto de Geología, Paleontología Mexicana 11, pt. 2, 36 p., 6 pl.
- 1969, Plantas fósiles del Jurásico Medio de Tecamatlán, Estado de Puebla, in Paleobotánica y Geología de Tecamatlán, Estado de Puebla: Universidad Nacional Autónoma de México, Instituto de Geología, Paleontología Mexicana 27, pt. 1, p. 2-38, 19 pl.
- Stur, Dionys, 1888, Die Lunzer-Lettenkohlen-Flora in den older Mesozoic beds of the coal-field of eastern Virginia: Verhandlungen der Geologischen Bundesanstalt (Wien), no. 10, p. 203-217.
- Sze, H.J., 1931, Beiträge zur liassischen Flora von China: Shanghai, National Research Institute of Geology, Memoirs, v. 12, 85 p.
- 1956, Older Mesozoic plants from the Yenchang Formation, northern Shensi: Acta Palaeontologia Sinica, whole Number 139, New Ser. A, n. 5, 217 p., 56 pl. (in Chinese and English).

- Wanner, E.T., and Fontaine, W.M., 1900, Triassic flora of York County, Pennsylvania, in Ward, L.F., ed., Status of the Mesozoic floras of the United States: Washington, D.C., Geological Survey, Annual Report 20, v. 2, p. 233-255.
- Watson, Joan, and Sincock, C.A., 1992, *Bennettitales of the English Wealden*: London, Monograph Palaeontographical Society, 228 p., 23 pls. (Publ. No. 588, part of vol. 145 for 1991).
- Weber, Reinhard, 1968, Die fossile Flora der Rhät-Lias-Übergangsschichten von Bayreuth (Oberfranken) unter besonderer Berücksichtigung der Coenologie: Erlanger Geologische Abhandlungen v. 72, 73 p., 14 text-fig., 17 pl.
- Weber, Reinhard, 1985, Las plantas fósiles de la Formación Santa Clara (Triásico Tardío, Sonora, México)—Estado actual de las investigaciones, in Weber, Reinhard, ed., Tercer Congreso Latinoamericano de Paleontología, Simposio sobre floras del Triásico Tardío, su fitogeografía y paleoecología: Universidad Nacional Autónoma de México, Instituto de Geología, Congreso Latinoamericano de Paleontología, 3, Oaxtepec, Mor., México, Memoria, p. 107-124.
- Weber, Reinhard; Trejo-Cruz, Ricardo; Torres-Romo, Alfonso; and García-Padilla, Antonio, 1980a (1982), Hipótesis de trabajo acerca de la paleoecología de comunidades de la taoflora Santa Clara del Triásico Tardío de Sonora: Universidad Nacional Autónoma de México, Instituto de Geología, Revista, v. 4, no. 2, p. 138-154.
- Weber, Reinhard; Zambrano-García, Ángel; and Amozurrutia-Silva, Flor, 1980b (1982), Nuevas contribuciones al conocimiento de la taoflora de la Formación Santa Clara (Triásico Tardío), Sonora: Universidad Nacional Autónoma de México, Instituto de Geología, Revista, v. 4, no. 2, p. 125-137.
- Weber, Reinhard, and Zamudio-Varela, Graciela, 1995, *Laurozamites*, a new genus and new species of bennettitalean leaves from the Late Triassic of North America: Universidad Nacional Autónoma de México, Instituto de Geología, Revista Mexicana de Ciencias Geológicas, v. 12, no. 1, p. 68-93.
- Wesley, Alan, 1958 (1960), Contributions to the knowledge of the flora of the grey limestones of Veneto—Part II. A revision of the *flora fossilis formationis Oolithicae* of de Zigno: Padova, Italy, Università di Padova, Istituto Geologico et Mineral., v. 21, p. 1-57, 3 pl.
- Zambrano-García y Weber, Reinhard, 1985, Nuevo ensayo de un panorama de la paleoecología de comunidades de la taoflora Santa Clara (Triásico Tardío, Sonora), in Weber, Reinhard, ed., Simposio sobre floras del Triásico Tardío, su fitogeografía y paleoecología: Universidad Nacional Autónoma de México, Instituto de Geología, Congreso Latinoamericano de Paleontología, 3, Oaxtepec, Mor., México, Memoria, p. 153-163, 4 tab.
- Zeiller, René, 1902-1903, Flore fossile des gîtes du charbon du Tonkin, in *Études des gîtes minéraux de la France: Colonies Françaises*, 320 p. (1903), Atlas (1902).

Manuscript received: March 18, 1996.

Corrected manuscript received: May 31, 1996.

Manuscript accepted: August 3, 1996.