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NEW AND POORLY KNOWN FERNS FROM THE SANTA CLARA FORMATION, LATE TRIASSIC, SONORA, NW MEXICO; III, MARATTIALES. *TRANQUILIA* HERBST—A PANAMERICAN DIMORPHIC GENUS

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ABSTRACT

The dimorphic marattialian fern *Tranquilia whitneyi* (Newberry) Herbst —formerly *"Alethopteris whitneyi* Newberry" and *"Pecopteris falcatus* Emmons"— from the Carnian (and perhaps Norian?) Santa Clara Formation of central Sonora, NW Mexico, is redescribed. Most of the older specimens of this species were either sterile or fertile. The new material from Sonora includes frond fragments with proximally sterile and distally fertile pinnules, which are the definitive proof of dimorphism in this species. The synangia are particularly well preserved in some other specimens. Dimorphous species are rare in the Marattiales. The genus *Tranquilia* was described by Herbst from the Carnian El Tranquilo Group, Argentina. A third species, that seems to be transitional between this genus and *Asterotheca,* occurs in the Carnian flora of the Newark Supergroup, Virginia, USA, where it was reported as *"Asterocarpus virginiensis"* Fontaine 1883 and under a couple of other names. This species is combined here as *Tranquilia virginiensis* (Fontaine) comb. nov. The genus *Tranquilia* has not been recorded outside America.

Key words: Ferns, Late Triassic, Sonora, Mexico.

RESUMEN

Se presenta material nuevo de *Tranquilia whitneyi* (Newberry) Herbst —descrita inicialmente como *"Alethopteris whitneyi* Newberry" y *"Pecopteris falcatus* Emmons"— y recientemente como *"Asterotheca whitneyi* (Newberry) Aguilera", de la Formación Santa Clara (Cárnico ¿y/o Nórico?), Sonora central, NW-México. Hasta la fecha, este helecho marattial dimórfico se conocía casi exclusivamente con base en especímenes completamente fértiles o estériles. El material nuevo incluye algunos fragmentos de frondas con pínulas estériles proximal y fértiles distalmente, con otros que son perfectamente estériles o fértiles. Ésta es la prueba definitiva del dimorfismo. Los sinangios están muy bien preservados en algunos especímenes adicionales. Las especies dimórficas son escasas en las Marattiales. El género *Tranquilia* fue encontrado por Herbst en el Cárnico del Grupo El Tranquilo, Argentina. Una forma aparentemente transicional entre este género y *Asterotheca* se encuentra en la flora cárnica del Supergrupo Newark de Virginia, donde se registró como Asterocarpus virginiensis Fontaine 1883, o bajo algunos otros nombres. Esta especie está combinada aquí como *Tranquilia virginiensis* (Fontaine) comb. nov. Hasta la fecha, el género no se ha registrado fuera de América.

Palabras clave: Helechos, Triásico Tardío, Sonora, México.

INTRODUCTION

Fossil ferns allow valuable insights in the context of community paleoecology. The leaves of many extant ferns usually decay attached to the mother plant, *i.e., in situ.* In addition, many fern leaves loose turgency and shrivel soon after cutting. Certainly, low resistance against water loss was common in ferns of the past as well. Thus, it is reasonable to assume that fronds or fragments of fronds generally did not resist drifting over far distances without suffering major damage, and that well preserved and complete fossil fern fronds are mostly autochthonous or subautochthonous, *i.e.,* they are thought to represent the past plant community once living where they are found now, *i.e.,* they represent often communities *in situ.* This may be true even when the fronds are found in a bed deposited in very short time during flood, for instance after crevasse splay. Conversely, the abscissing leaves of cycadophytes were more easily transported over far distances and they are less trustworthy elements in the reconstruction of paleocommunities.

The paleoecological reconstitution of past land plant communities may be achieved by various qualitative and quantitative approaches that may be combined with petrographic studies of the fossil bearing rocks. When floristic lists of the assemblages at individual collecting sites are compiled and compared with this purpose, it is important to avoid double or multiple recording of whole plants (biological species) under more than one name. A multiple record of a whole plant species may occur when different vegetative organs (leaves, stem, roots) and reproductive organs (male or female cones, seeds, pollen) of a whole plant are placed in different taxa. To avoid this source of error, Weber and students in their work on community paleoecology of the Santa Clara flora (Weber, Trejo-Cruz *et al.*, 1982; Zambrano-García and Weber, 1985) excluded all taxa of reproductive and vegetative structures, except leaves or leafy shoots, from the local floristic lists. Less commonly,

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repeated records may occur when dimorphism or polymorphism of a whole plant species result in the description of more than one paleobotanical taxon even for the same organ. If not excluded from the beginning, such double or multiple records result in biased similarity indexes for pairs of local assemblages. Particularly when the total number of species recorded in a pair of local florules is low, excessively high correlation values will be obtained, when such false couples of species are present.

A clearly dimorphic fern of the Santa Clara flora of Sonora is redescribed here with the purpose of excluding such a fallacious double record. The dimorphism of *Tranquilia whitneyi* had not been considered in the first essay on community paleoecology of the Santa Clara flora (Weber, Trejo-Cruz *et al.,* 1982) on the grounds explained in the caption of fig. 10 b,c,: "Este fragmento sugiere que *Alethopteris whitneyi* puede ser la fronda estéril de un helecho con dimorfismo foliar muy marcado, cuyas frondas fértiles serían el *Pecopteris falcatus* Emmons, ilustrado en la misma figura. Debido a que faltan pruebas adicionales, esta posibilidad no se tomó en cuenta en los conteos ...". The reconstruction was proposed later by Weber (1985b), who assigned *"Alethopteris whitneyi"* and the ill-determined Mexican material of *"Pecopteris falcatus"* together to *"Asterotheca whitneyi"*. This taxonomic decision was not taken into account, however, when the paleofloristic data of our second essay on community paleoecology (Zambrano-García and Weber, 1985) were processed; in that paper, the two mentioned types of fern fronds were still listed as different taxonomic units.

Later on, Herbst (1988) described a new genus, *Tranquilia* Herbst, from the Cañadón Largo Formation, belonging to the Carnian El Tranquilo Group, Argentina, which resembles the Sonoran material not only in morphological details, but also in the dimorphism, which is an important diagnostic feature of this genus. Consequently, Herbst placed the Sonoran species in his genus, naming it *Tranquilia whitneyi* (Newberry) Herbst; but he did not tackle the formidable problem of generic assignment of *"Asterocarpus virginiensis"* Fontaine (1883) from the Late Triassic of Virginia, USA, that had been compared by Fontaine himself and much later by Weber (1985b) with the Sonoran species.

From the beginning of this study, *"Asterocarpus virginiensis"* was thought to be intermediate between *Asterotheca-Pecopteris* and the Mexican species now placed in *Tranquilia,* a difficult situation in paleobotanical taxonomy. Just for this reason, Weber (1985a) had avoided to erect a new genus. In response to the decision of Herbst (1988), mentioned above, a detailed study of the nomenclatural history and of diagnostic characters of the North American species was carried out in order to obtain an objective understanding and a stable taxonomic assignment. In this study it was paramount to base judgements primarily on revised original material, secondly on figured specimens and descriptions, thirdly on previous author's comments about non figured materials, and as marginally as possible on ICBN-centered lawyer's thinking or on pondering of the scientific authority of prior researchers. Therefore, the author examined Fontaine's (1883) original material of *"Asterocarpus"* in the NMNH, Washington.

In 1993 and 1994, well preserved new material of the Sonoran species was collected, including abundant fragments of fronds in which the fertile and the sterile parts are found in organic connection (Plate 1). In 1994, the author saw in the NMNH, Washington, a number of similar specimens from the Santa Clara Formation, collected by Wilson and Rocha, identified as *"Pecopteris falcatus"* and *"cf. Thinnfeldia"* by R. W. Brown (*in* Wilson and Rocha, 1946) in spite of the presence of pinnules with both aspects combined. All these specimens demonstrate the dimorphous character of *Tranquilia whitneyi* beyond doubt.

The geological setting of the Santa Clara Formation of central Sonora was outlined by Weber (1985a) and Weber and Zamudio-Varela (1995). Its age is no longer a matter of controversy: Carnian and, perhaps, Norian? (Weber, 1997–1999). The locality that yielded the most important new specimens was discovered in 1993 in the working area 4, La Barranca-Santa Clara (Figure 1) slightly to the southwest from locality Tarahumara

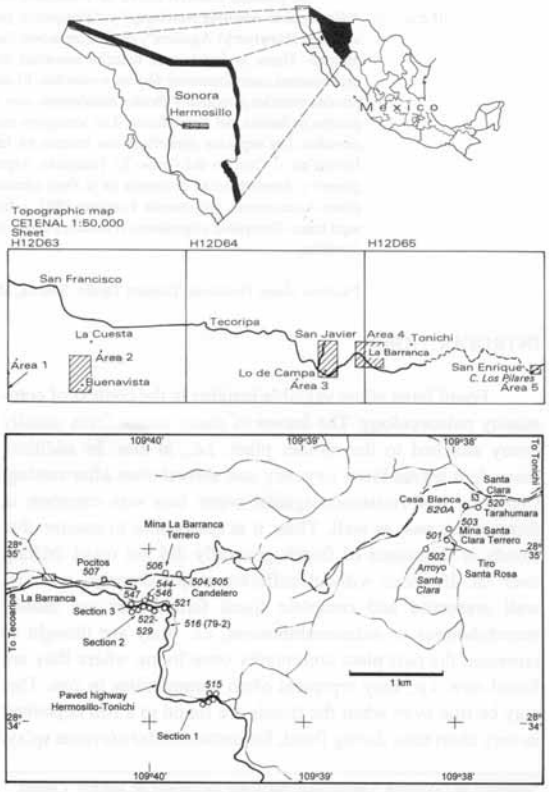


Figure 1. Location map.

(locality 520, CLP-IG-UNAM), left of the usually dry bed of Santa Clara Creek, about 200 m southwest of Casa Blanca. Casa Blanca is a ghost-house of an abandoned mining village, near San Antonio de las Huertas and the Yaqui River, just in the angle at the junction of Arroyo Santa Clara and Arroyo Tarahumara (*cf.* Wilson and Rocha, 1946, pl. 1). In addition, some new specimens collected from roadside talus from La Barranca (loc. 515, CLP-IG-UNAM; see Weber, 1985a, fig. 5) are described here. *Tranquilia whitneyi* is abundant in the surroundings of Casa Blanca, and it is suggested that Wilson and Rocha's (1946) material was also collected from this area.

The material collected by the author and students is deposited in the National Paleontological Collection (Colección Paleontológica Nacional, Instituto de Geología, Universidad Nacional Autónoma de México). The figured specimens received the specimen numbers given in the description and/or in the plate captions. The numbers are composed of a sign of the collection, IGM, followed by PB: paleobotany. After these signs follows the locality number and, after a hyphen, the specimen number. The locality numbers are those of the official catalog of paleontological localities of the Instituto de Geología (CLP-IG-UNAM).

Throughout in this paper, but most often in the discussion of nomenclature, the author uses taxonomic names which are no longer valid. These old names are given between citation marks, except when they appear in a literal quotation given as such in citation marks.

TAXONOMY

Order: Marattiales
Family: Asterothecaceae

Genus: *Tranquilia* Herbst 1988

Diagnosis—Frond very large, dimorphous or polymorphous, at least bipinnate; low order rachis often very wide, rachis of ultimate order of fertile frond portions often alate, wing provided with synangia; pinnules up to over 10 cm long, sterile pinnules alethopterid, more or less decurrent, entire, crenate, pinnatifid or pinnatisect, showing length/width ratio of 5:1 or more; fertile pinnules, if entire, linear, much narrower than sterile pinnules. Main veins of pinnules stout and straight, lateral venation of entire pinnules dichotomous and open, lateral veinlets in sterile pinnae forking twice or thrice, in fertile pinnae once. Combinedly sterile and fertile pinnules, when present, sterile proximally and fertile distally. Synangia attached abaxially, forming one row along each side of pinnule midvein, circular, subcircular or rounded quadrangular, tri- to octosporangiate. Sporangia arranged radially, only partially coalescent or more or less free, rounded at the periphery of synangia.

Type species—*Tranquilia jalfinii* Herbst. Herbst, R., 1988.

Tranquilia whitneyi (Newberry) Herbst 1988
(Plates 1, 2)

1876 *Alethopteris whitneyi*.- Newberry, 1876, p. 145–146, pl. 7, fig. 1, 1a, b.- Silva-Pineda, 1961, p. 16–17, pl. 2, fig. 3, pl. 6, fig. 1, 2.- Weber, Trejo-Cruz *et al.*, 1982, fig. 10a–d; Weber, Zambrano-García and Amozurrutia-Silva, 1982, tab. 2.
1893 *Asterotheca whitneyi* (Newberry).- Aguilera *in* Aguilera and Ordóñez, 1893, p. 14 (only name).- Weber, 1985b, p. 132–135, fig. 4a–e.
1950 *Asterocarpus whitneyi* (Newberry).- Maldonado-Koerdell, 1950, p. 27–28.

Rejected synonyms and misidentifications:
1876 *Pecopteris falcatus* Emmons.- Newberry, 1876, p. 144, pl. 6, fig. 3. Weber, Trejo-Cruz *et al.*, 1982, fig. 10c, e–g; Weber, Zambrano-García and Amozurrutia-Silva, 1982, tab. 2.
1916 *Asterocarpus falcatus* (Emmons) Fontaine.- Humphreys, 1916, p. 76. 1946 cf. *Thinnfeldia*.- R.W. Brown *in* Wilson and Rocha, 1946, p. 28 (only name).
1961 *Taeniopteris auriculata* (Fontaine) Berry.- Silva-Pineda, 1961, p. 19–20, pl. 3, fig. 3–5.
1969 *Cyathoforma carolinensis* (Emmons) Bock.- Bock, 1969, p. 119–127, fig. 190–199.
1982 *Pecopteris falcatus* Emmons.- Weber, Trejo-Cruz *et al.*, 1982, fig. 10c, e–g.

Description—The specimens from the new locality are preserved as impressions in mostly light to middle grey or secondarily brownish mudstone with an important component of fine detritus or in fine-grained sandstone. Venation details are often well preserved in sterile frond fragments. The synangia and sporangia are seen only rarely in the fertile specimens; but sometimes they are preserved as neat three-dimensional replicas, depending on the degree of maturity of the sporangia and on conditions of burial. The following is based almost exclusively on this new material. A previous description containing additional data and details was published by Weber (1985b).
Most specimens of this dimorphous fern represent only the fertile or the sterile parts, but some specimens possess mixed fertile and sterile pinnules. The largest specimen from the new locality (loc. 520A, CLP-IG-UNAM) is shown in Plate 1. Due to the uneven surface of the fossil, which measures 38 cm in maximum width, the picture is not perfectly in focus throughout. It shows a large frond with the adaxial face adpressed to the slab. It is provided with four overlapping pinnulate pinnae attached to a poorly preserved rachis (to the right of the figure). This rachis covers the basalmost parts of the pinnae and measures at least 3 cm in width. In a bipinnate frond, this would be the main rachis. Only the basal 20 cm of the pinnae of last order attached to this rachis are preserved. In addition, there are minor fragments of three more pinnae, one belonging to the same rachis, and the other two, at the lower left of the plate, seem to belong to a second rachis parallel to the preserved one. As this

is most probably correct, the frond was at least tripinnate and very large. Preparation of the distal part of this frond fragment and of the lower order rachis did not uncover the bases and attachment of the pinnae. Hence, the last order pinnae were probably attached to the adaxial face of the rachis at axillary angles of 70 to 75°. The material does not show whether this fern was anadromous or katadromous. However, the decurrent bases of the sterile pinnules in other specimens suggest the latter.

The last order rachis is straight from the base and coarsely striate. The striae are probably no surface structures. The rachis measures about 6 mm in maximum width, and tapers toward the apex. The last order pinnae reach about 12 cm in width near their bases. At the lower left corner of the figure, a pinna tip with distally broken terminal pinnule is shown. At less than 10 cm distance from the apex there is an incomplete lateral pinnule of 5 cm in (preserved) length; *i.e.* the width of the pinna at this distance from its apex tip was about 10 cm, or only 2 cm less than at the bases. Hence, the pinnae were neither lanceolate nor narrow triangular, but subparallel-sided with a prominent and narrow terminal pinnule. Only the basalmost 20 cm of these pinnae are preserved, and no decrease in width can be observed along this distance.

The mixed pinnules of this frond are sterile proximally and fertile distally. The transition from the sterile to the fertile parts of the pinnules is more or less abrupt and sometimes slightly asymmetrical. The relative length of the fertile pinnule portions increases from the pinna base to the tip and, corresponding to a slight asymmetry of the pinnae, the fertile portions of the acroscopic pinnules are somewhat longer than those of the basiscopic ones. The synangia are not visible in this specimen. The sterile part of the pinnule measures up to 11 mm in width near the pinnule base, and the sterile part up to 5 mm at base. Both parts are tapering toward the apex.

The new material includes a set of entirely fertile specimens. The largest one of these is not shown here because of its poor preservation (Specimen IGM-PB-520A-1066). It is linear, very slightly tapering pinnules are sessile, attached to the rachis at an angle of 70 to 75°, and about 5 mm wide near the base, but none is complete. The longest pinnule measured over 8.5 cm in length.

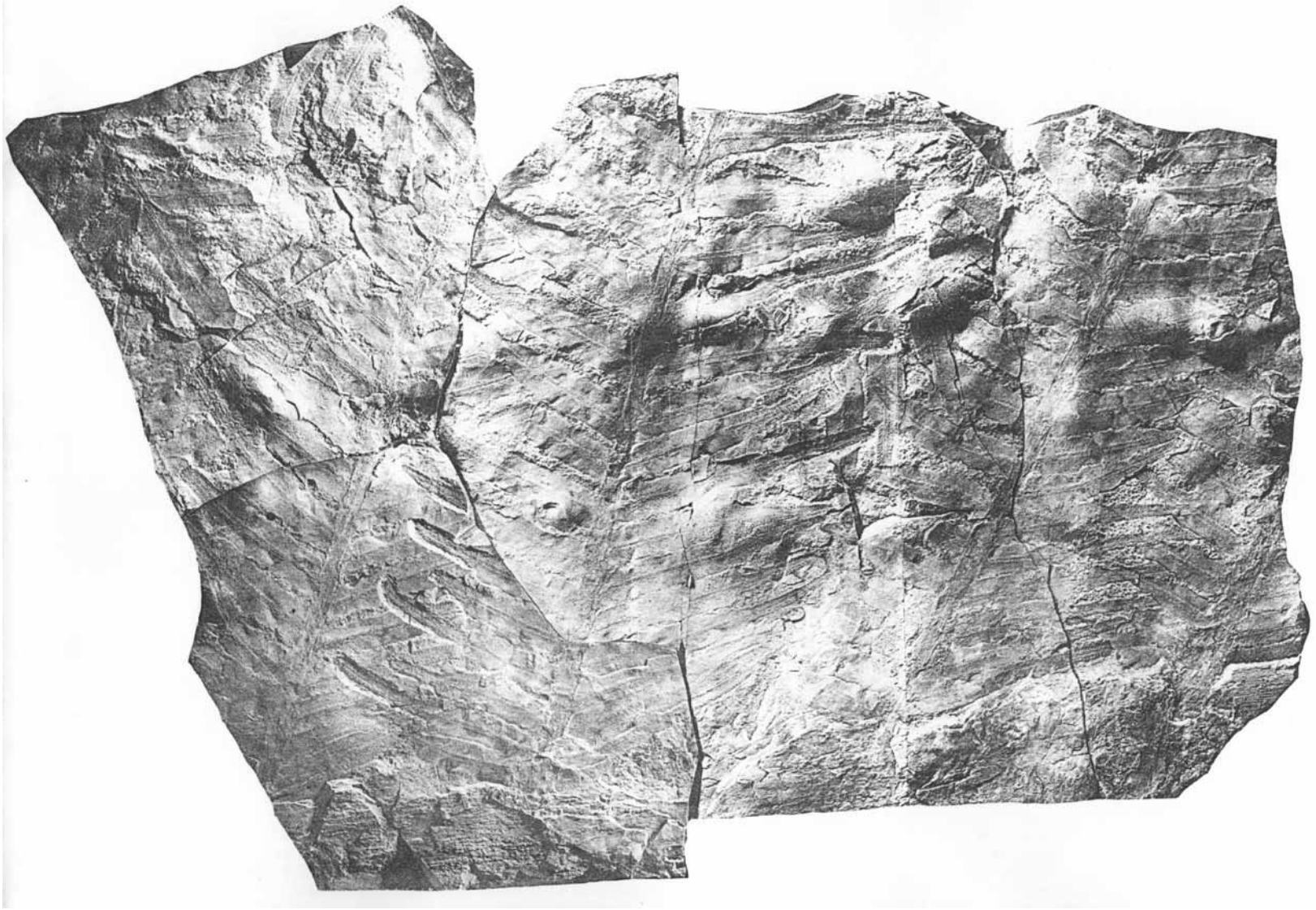
Details of the venation of the fertile pinnule are preserved in a smaller specimen from La Barranca (loc. 515, CLP-IG-UNAM; Plate 2, figures 1 and 2: x2), with the adaxial face exposed. The lateral veinlets branch off from the strong and straight midvein at acute angles (less than 45°) and are very small. The few observed primary veinlets seem to fork once, at least in some cases. At the point of dichotomy, the resulting veinlets are abruptly curved to the pinnule margin, touching it at an angle of about 90°. However, there are also some primary veinlets that appear unbranched and end without touching the margin However, most veinlets can not be traced neatly, because they are concealed by a curved triangular or club-shaped "shadow" of unknown anatomical nature. They might be supporting tissues of the synangia. The specimen does not show the synangia which were doubtless present in life.

Conversely, the specimens in Plate 2, figures 3 and 4, were fossilized in such a way that they show the abaxial face of the frond with synangia in positive replica. The specimen shown in figure 3 bears well preserved synangia at left, but at right, these are almost invisible due to differential fossilization. Such differences in appearance should, hence, not be used to speculate about the "upside down or downside down" burial of the fronds. Contrary to the description by Weber (1985), the pinnules of the specimen shown in figure 4 are more or less decurrent, but this is not easily observed, because the resulting wings are attached and restricted in width to the adaxial face of the pinna rachis and concealed by the rachis. Nevertheless, at some points, the synangia of the wing are visible as shadows on the rachis.

The synangia are arranged in two regular straight rows touching the pinnule midvein and covering the wings of the pinnule blade almost completely. Only very narrow marginal zones of the blade, of about 0.7 mm in width, are not covered. No indusia or indusium-like structures were observed. Many synangia are tridimensionally preserved and are often not exactly circular in outline as a result of non horizontal burial of the frond. The more or less free sporangia are grouped in a circle around the central base or receptacle, and are angular in shape to the center and rounded outwards. Those observed in the specimen of Plate 2 (figures 5–8: x3; figure 9: x5) are still closed and mostly do not show a preformed apparatus of dehiscence. However, in some sporangia there is a longitudinal line suggestive of such a structure at the outer face of the synangium. None of the photographs published here shows such a line. No annuli were observed. The number of sporangia per synangium seems to vary between five and eight, most frequently six. The synangia measure 1.6 mm in diameter. Hence, the sporangia are up to 0.8 mm radially. The length of the sporangia remains unknown.

The form and proportions of the synangia and sporangia cannot be described exactly on the basis of compression material. However, no synangia are seen in lateral view. It can be inferred that they were not flexible at the base, and could not be tilted. Hence, they were probably broadest and more or less flattened at the base, and were perhaps wider than long. The form of the sporangia was similar to that of the inner divisions of an orange cut transversally in two halves. The center of the synangia shows variable aspects, but the receptacle was distally covered by the sporangia in most cases. Only rarely, there is a very small, subcircular, protruding body that might be the tip of a receptacle or central column.

Plate 1. *Tranquilia whitneyi* (Newberry) Herbst. Large fragment of frond with combined sterile and fertile pinnules. Specimen IGM-PB-520-1064; Loc. Tarahumara, bed A, no. 520 CLP-IG-UNAM (x1).



The sediment replicas of the sporangia may fall away individually under harsh conditions of preparation, for instance when cleansing with a hard brush. This, in addition to the non-circular outline of the synangia and the sometimes disordered arrangement of the individual sporangia, suggests that they were free or only partially coalescent in life. The sporangia are considered eusporangiate on the basis of their dimensions and absence of an annulus.

Comparison—See under *Tranquilia virginiensis.*

Paleoecological comment (modified after Weber, 1985b)—*Tranquilia whitneyi* belonged to a group of species growing in habitats intermediate between the riversides and the interfluvial swamps (Weber, Trejo-Cruz *et al.,* 1982; Zambrano-García and Weber, 1985). However, the species assigned to this group in the analysis of paleocommunities might also be considered as ecologically vague. Its association with beds of coarse or middle-grained sandstone or coal seams is rare, but association with shale or mudstone is very common. There is a preferential association with sediments poor or very poor in dispersed organic matter. Nevertheless, the species likely preferred dryer and oxygen-richer sediments than *Asterotheca santaclareae* which is most common in dark and fine-grained strata associated in some cases with coal seams (*cf.* Weber, Trejo-Cruz *et al.,* 1982; Zambrano-García and Weber, 1985).

Distribution—The species is most common in the surroundings of Casa Blanca, Santa Clara and La Barranca, Section 1 and Section 2, whereas it is almost completely absent in the working areas of San Enrique or Los Pilares and San Javier (*cf.* Weber, 1985a, fig. 3–5; Weber and Zamudio-Varela, 1995, fig. 3–5).

Tranquilia virginiensis (Fontaine) comb. nov.

1883 *Asterocarpus virginiensis* Fontaine (incl. *A. v.* var. *obtusilobus*).- Fontaine, 1883, p. 41–46, pl. 19, fig. 2–5; pl. 20, fig. 1, 2, pl. 21, fig. 1–4, pl. 22, fig. 1–3, pl. 23, fig. 1–4, pl. 24, fig. 1–5, pl. 25, fig. 1.
1900 *Asterocarpus falcatus* (Emmons).- Ward *in* Wanner and Fontaine *in* Ward, 1900, p. 282–283, pl. 38, fig. 5, 6; Fontaine *in* Ward, 1900.

Rejected synonyms and misidentifications:
1856 *Pecopteris falcatus* Emm.- Emmons, 1856, p. 327, pl. 4, fig. 9.
1856 *Pecopteris carolinensis* Emm.- Emmons, 1856, p. 327, pl. 4, figs. 1, 2.
1857 *Pecopteris carolinensis* Emm.- Emmons, 1857, p. 100–101, text-fig. 68, pl. 4, fig. 1, 2.
1883 *Asterocarpus platyrachis* Fontaine.- Fontaine, 1883, p. 46–47, *partim,* pl. 25, fig. 6.
1969 *Cyathoforma carolinensis* (Emmons) n. comb.- Bock, 1969, p. 119–127, fig. 190–199.

Diagnosis—See Fontaine, 1883, p. 41.

Holotype—USNM 312587 (Fontaine, 1883, pl. 23, fig. 1).

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

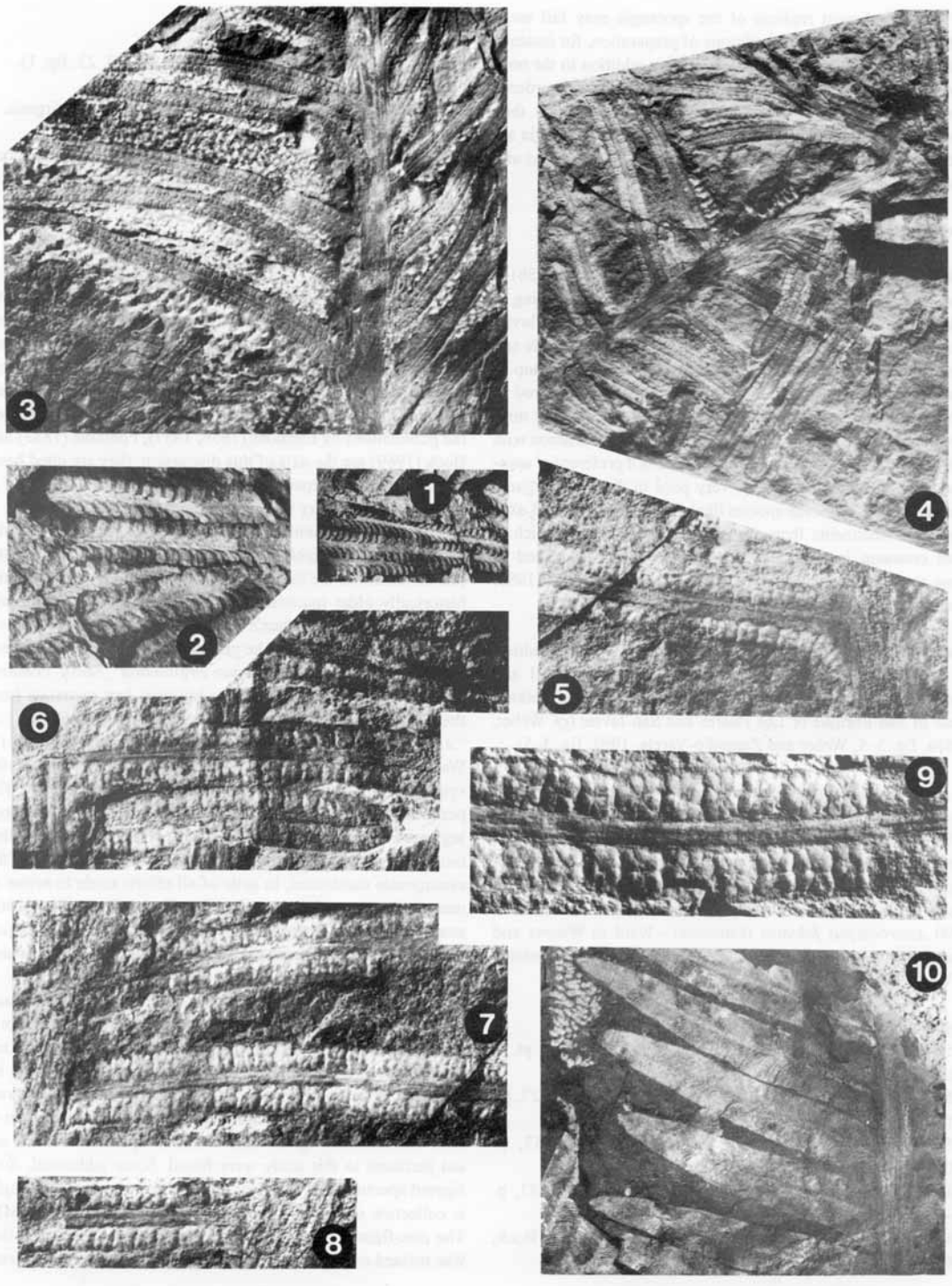
Type stratum and age—Productive Coal Measure Member, Tuckahoe Formation, Richmond Basin, Newark Supergroup, Late Triassic (early Carnian). See Cornet and Olsen (1990).

Derivation of name—From the State of Virginia, U.S.A.

Delimitation of the species—The swarm of names ("synonyms") and interpretations called to order around *"Asterocarpus virginiensis"* Fontaine (1883) by several authors is studied here carefully to choose the best holotype and diagnosis which, in turn, must support the name and taxonomic assignment of *Tranquilia virginiensis,* as erected here. Because the publications by Emmons (1856, 1857), Fontaine (1883) and Bock (1969) are the axis of this discussion, they are cited herein mostly without repeating the year of publication. The year is given when necessary to avoid misunderstandings.

From the beginning, *"Asterocarpus virginiensis"* and the corresponding available original material was favored by the present author as the basic reference in this study, but not so the historically older material of Emmons. This choice was predetermined by the author's general consent with Fontaine's selection of the specimens he placed or did not place in his very variable species. *"Asterocarpus virginiensis" sensu* Fontaine (1883) was mixed up later with additional fern materials from the United States of America—see the synonymy of *"Asterocarpus falcatus"* by Ward *in* Wanner and Fontaine (*in* Ward, 1900)—and moreover, with a Mexican record—see the synonymy of *"Cyathoforma carolinensis"* by Bock (1969). The pertinent original materials, as far as available, and the changing taxonomic interpretations confirm, or at least suggest, that more than one vegetatively similar species were confused in the synonymies mentioned. In spite of all efforts made to revise as many original specimens as possible, the present author is still unable to offer a perfectly objective, fossil-based and conjecture-free sorting of these species for several circumstances and botanical reasons.

Circumstancial constraints are often encountered in studies involving "antique" materials, *i.e.* old collections: In the present case, many original specimens of earlier workers could not be located. The specimens from North Carolina illustrated by Emmons, reviewed by Fontaine (1883) and revised and redrawn under his supervision (Fontaine *in* Ward, 1900), were sought in the NMNH, Washington. Only about 15 specimens which are not pertinent to this study were found. Some additional, non-figured specimens of Emmons's material are in the stratigraphic collection of the Smithsonian Institution at Silver Hill, MD. The non-figured part, *i.e.* the bulk of Emmons's material that was revised and mentioned by Fontaine (*in* Ward, 1900) seems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to be lost or does "no longer exist" (Cornet and Olsen, 1990). No such material is housed at Williams College, Williamstown, at present (Cox, personal communication, 1998). Unfortunately, it was never adequately figured. The material figured by Fontaine as *"Asterocarpus virginiensis"* is housed in the NMNH, but the set is incomplete at present. Additional figured specimens are thought to be misplaced in Fontaine's very rich non figured material at Silver Hill. The pertinent specimens of Bock are all lost (Spamer, 1995). Furthermore, many of the North American Triassic plant specimens described before Fontaine were badly fragmented small pieces, and most illustrations before Bock were drawings. Fontaine had larger specimens, but they are not as well preserved as his plate drawings suggest. As far as the author is aware, after 1900 only Bock published new specimens from the USA pertinent to the present study. He illustrated his paper with photographs. The drawings published up till 1900 are sometimes inaccurate or poor in detail. Those of Emmons have repeatedly been criticised in the literature, whereas Fontaine's drawings of his Virginian material are rich in omissions or in additions to the actually preserved plant fragments as confirmed by the author.

In addition, no previous author proposed any holotype—neither lectotype nor neotype—for *"Asterocarpus virginiensis"*.

The botanical difficulties faced in this study are the following: the earlier authors disagreed regarding the number of species actually present in the pertinent materials. Furthermore, the presence of records of *Phlebopteris*, formerly *"Laccopteris" auct.* in the synonymies mentioned above, and the alternative assignments of the whole complex either to *Asterotheca,* formerly *"Asterocarpus" auct.* (Wanner and Fontaine *in* Ward, 1900), of the Marattiales, or to *"Cyathoforma"* of the Cyatheaceae (Bock) are based on different interpretations of the sporangial clusters (synangia or sori?) which, in turn, reflect the poor preservation of the reproductive structures studied by most of the earlier authors. The best and most intriguing illustrations of fertile specimens published until now were those in Bock (1969, fig. 195–198). Whose interpretation of the sporangial clusters was best is more easily asked than answered.

Rejected synonymizations—Before the botanical affinity of *"Asterocarpus virginiensis"* is discussed, it is attempted here to exclude a number of fallacious or insecure additions and, thus, to reject some previous synonymizations. The above name given to the fern by Fontaine was changed first by Ward *(in* Wanner and Fontaine *in* Ward, 1900) upon synonymization with the prior *"Pecopteris falcatus"* Emmons 1856, once Emmon's original collection had been rediscovered in 1898. Ward emphasised the specific identity of Emmons's figured specimens (1856, pl. 4, fig. 5, 9)—and of additional non figured specimens in Emmons's collection—with *"Asterocarpus virginiensis"* and combined both as *"Asterocarpus falcatus"*. Apparently, this change was imposed to Fontaine rather imperiously, even though Ward painstakingly tried to prove that Fontaine himself was responsible for this change, publishing a letter written by Fontaine in 1890 in which this possibility seemed to be suggested (Ward, 1900: 271; Ward *in* Fontaine; Ward *in* Wanner and Fontaine; both *in* Ward, 1900; authorship for synonymies in these papers claimed by Ward, 1900: 277).

Under this circumstance, it is intriguing that the specimens figured by Emmons (1856, 1857) and reproduced by Fontaine (1883) in his first revision, and those chosen for illustration of *"Asterocarpus falcatus"* by Fontaine (*in* Ward, 1900, pl. 38, fig. 5, 6) in his second revision of Emmons's collection are not the same. Perhaps, the specimens figured by Emmons were already lost by the turn of the century, hundred years ago. Despite its importance, the fertile specimen shown by Emmons (1856, pl. 4, fig. 9) and Fontaine (1883, pl. 48, fig. 6) was not illustrated again in 1900. Fontaine (1883) had suggested, but not proposed formally, that *"Pecopteris falcatus"* "is probably a *Laccopteris"* and "might properly be called *Laccopteris Emmonsi*". The use of the latter name by Fontaine (1883) in the caption of plate 48 does not render it valid and it is not listed here as a synonym. Perhaps in 1900, at least Fontaine still felt that the mentioned fertile specimen could not belong to *"Asterocarpus"* even though he explained it otherwise in his description. The present writer finds difficult to agree with Fontaine's (*in* Ward, 1900) explanation because it contradicts his own prior—and good—interpretation of the fertile specimens of *"Asterocarpus virginiensis"* (Fontaine, 1883). The fertile specimen of Emmons was reproduced again by Bock (1969, fig. 221a), who placed it in his *Phlebopteris falcata* (Emmons) Bock 1962. This species was, in turn, considered as identical with *Ph. smithii* (Daugherty) Arnold, by Ash and collaborators (1982), except the just mentioned fertile specimen. The history of synonymizations shows that there is a kind of agreement on the taxonomic placement of this fertile specimen in *Phlebopteris* and the Matoniaceae, though Ash and collaborators (1982) did not consecrate it: "The fossil *Pecopteris falcata* Emmons (1856) with which *Phlebopteris smithii* was synonymized (Bock, 1969) is apparently lost. . . . The fossil might have been the remains of a pinna of *Phlebopteris* as Bock (1969) thought, but it could just as well have been the remains of a bipinnate fern leaf as Emmons (1856) and Ward (1900) thought". Both specimens of Emmons's are judged herewith as not determinable.

Plate 2. *Tranquilia whitneyi* (Newberry) Herbst. Completely fertile or sterile frond fragments. Figures 1, 2, Fertile pinnules with weakly visible secondary veinlets. Specimen IGM-PB-515-1065; Loc. La Barranca, Sección 1; no. 515 CLP-IG-UNAM), *1,* (x1), *2* (x2). Figure 3, Fertile specimen with synangia well preserved at left and almost invisible at right. Specimen IGM-PB-520A-1067, Loc. Tarahumara, Bed 1; no. 520A CLP-IG-UNAM (x1). Figures 4-9, Fertile specimen with neatly preserved synangia. Specimen IGM-PB-520A-1068, Loc. Tarahumara, Bed 1; no. 520A CLP-IG- UNAM (x1), *4,* (x1); *5-8,* (aprox. x3); *9,* (aprox. x6). Figure 10, Sterile specimen. Specimen IGM-PB-520A-1069, Loc. Tarahumara, Bed 1; no. 520A CLP-IG- UNAM (x1).

Fontaine (*in* Ward, 1900, pl. 38, fig. 5, 6) illustrated, instead of Emmons's figured specimens, two more fossils from Emmons's non figured material to show two types of pinnae of the sterile fronds mentioned in his description: "While the long, slender pinnules are most common in Emmons's specimens, some of them show the short, very obtuse pinnules that are more common in the Virginia forms". Emmons's collection apparently lacked frond fragments with crenate or pinnatifid pinnules, *i.e.,* transitional forms showing the addition of another order of small pinnules. Such transitional forms are well represented in Fontaine's material from Virginia. Their absence in Emmons's collection is inferred. However, Fontaine's *(in* Ward, 1900) writing suggests that the ranges of variation of the fronds from North Carolina (Emmons) and Virginia (Fontaine) were not the same and more different than Ward's imperious emphasis allows to assume. After the author's revision of the pertinent literature, all sterile frond fragments of *"Pecopteris falcatus"* figured by Emmons, and of *"Asterocarpus falcatus",* figured by Fontaine (*in* Ward, 1900), cannot be placed in *"Asterocarpus virginiensis"* with full confidence.

The above conclusions based on the revision of the prior literature are not free of conjecture. Therefore, the author tried to re-study the corresponding original materials. The sterile material of *"Pecopteris falcatus",* collected by Emmons, is said to have been very rich (Fontaine *in* Ward, 1900): "Many specimens of a large fern are in Emmons's collection which prove to be identical with *Asterocarpus virginiensis...*". Unfortunately, this rich material was not found by the author, and the particular specimens figured by Emmons (1856, 1857; reproduced by Fontaine, 1883) and Fontaine (*in* Ward, 1900) could not be located in the NMNH. In the stratigraphic collection at Silver Hill, MD, however, there are four non-figured specimens of the Emmons collection (numbers 8269, 8270, and 8279, part and counterpart), labeled as *"Asterocarpus falcatus",* but none of these can be placed in *"Asterocarpus virginiensis"* with any degree of confidence.

Since Emmons's figured original specimens are lost, and none of the figures of *"Pecopteris falcatus"* of Emmons (1856, 1857) are suitable as the holotype of a species embracing *"Asterocarpus virginiensis" sensu* Fontaine (1883), the use of the epithet *"falcatus"* for this fern is not adopted here even against Ward's authority.

The name *"Asterocarpus falcatus"* was changed in turn by Bock. Since he thought Emmons's *"Pecopteris falcatus"* to be *Phlebopteris,* he considered the epithet *falcatus* as preoccupied, and chose instead the epithet *carolinensis,* derived from *"Pecopteris carolinensis"* Emmons (1857, text-fig. 68; *non* 1856; pl. 4, fig. 1, 2). In addition, Bock postulated a cyatheaceous affinity of this fern, and the former *"Asterocarpus virginiensis"* became *"Cyathoforma carolinensis"* (Emmons) Bock, new combination, which is not valid from a merely legal point of view. However, this will not be used here to evade the analysis of Bock's synonymization.

Fontaine had suggested that *Laccopteris carolinensis* might be the best name of Emmons's *"Pecopteris carolinensis"* (Emmons, 1856, pl. 4, fig. 1, 2, 1857, text-fig. 68). Again, he did not adopt formally this change of name: "It is clearly a *Laccopteris,* and most probably is identical with *Laccopteris elegans,* Presl. If not, it should be called *Laccopteris Carolinensis".* When redrawing the figures "without, it must be confessed, any artistic improvement" (Ward, 1900: 169), Fontaine (1883, pl. 49, figs 12, 12a) reduced the number of sporangia per sporangial cluster from about 10 drawn by Emmons to about eight or even less. Fontaine had not seen Emmons's specimens at that time, but he discussed them later together with *P. falcatus* (Fontaine *in* Ward, 1900): "The different appearance of the sori in the forms regarded by Emmons as different species is due to the fact that the sori of the supposed *P. falcatus* are seen with the upper surface of the frond presented uppermost, while in the forms given as *P. carolinensis* they are presented with the lower surface of the frond uppermost and show their true character, which is that of *"Asterocarpus virginiensis*". This was Ward's and, hence, Fontaine's "choice" in 1900, and contradicts again the observations by Fontaine (1883) on different appearances of fertile *"Asterocarpus virginiensis",* depending on burial or preservation. But Bock made a different proposal. He considered Emmons's specimens of 1856 as *Phlebopteris,* but not so the specimen figured by Emmons in 1857 (text-fig. 68), which he thought to be conspecific with *"Asterocarpus virginiensis".* To add more confusion, Bock synonymized Emmons's *"Pecopteris carolinensis"* not only with his *"Cyathoforma carolinensis"* but also with his *"Phlebopteris falcata"* nov. comb.; and the years of publication of Emmons's papers are misprinted as 1956 and 1957 in Bock's synonymy of *"C. carolinensis".* The very disappointing status of *"Pecopteris carolinensis"* as poorly recorded in the literature as it is, and as no longer existing in collections, lead Ash and collaborators (1992) to take no notice of it. Between the foregoing lines it is hidden somewhere why the name *"Cyathoforma carolinensis"* might not only be non-valid, but also illegitimate. The specimen of Emmons (1857, text-fig. 68) is too poor, too fragmentary and too badly drawn to be identified at all using the figure.

None of Emmons's (1856, 1857) original specimens of *Pecopteris carolinensis* could be located in the NMNH, Washington.

The foregoing lines contain a warning to accept the overall synonymization of *"Pecopteris carolinensis"* with *"Asterocarpus falcatus"* by Ward (*in* Wanner and Fontaine *in* Ward, 1900) as definitive, or to select the holotype of the fern under discussion among Emmons's (1856 or 1857) figures of *"Pecopteris carolinensis".* In conclusion, the present author does not adopt the epithet *"carolinensis"* now against Bock.

Consequently, the epithet *virginiensis* given to the species by Fontaine (1883) is considered legitimate and is revalidated here. A holotype selected from Fontaine's (1883) material of *"Asterocarpus virginiensis"* is proposed above.

Before discussing the right generic name of the studied species, some additional synonyms listed by Bock will be checked. As the only European entry, Bock (1969: 119) recorded *Asterotheca merianii,* an unquestionable marattialian fern with tetrasporangiate synangia (Bhardwaj and Singh, 1957), just because Stur (1888), Krasser (1909) and even Hirmer (1927) had considered the European and the American species to be identical. Cornet and Olsen (1990) rejected this synonymization, which they deemed approved by Bock who, on the contrary, had been right to reject it due to a misidentification. Bock had explained: "The detailed evidence produced, clearly established that *Pecopteris meriani* or *Asterotheca meriani*, is distinctly different from *Cyathoforma carolinensis*." Stur's name leads, by the way, to remember a form of *Asterotheca merianii* from Lunz, Austria, called *Asterotheca intermedia* (Stur, 1885) which was never figured. Krasser (1909) in Latin briefness remarked on this form: *"pars media folii et apex folii A. Merianii teste Stur!"*. Upon examination of the original material in Vienna (Naturhistorisches Museum; Geologische Bundesanstalt), the present author was impressed by the resemblance of this form and *"Asterocarpus virginiensis"* at least in vegetative aspects, and thought it to be transitional between *Asterotheca merianii* and *"Asterotheca virginiensis"*, but closer to the former than to the latter. After the discovery of the new fertile material from Sonora, it seems to be clear now that such a comparison does not help to understand the taxonomic position of the American species. Bock was wrong, however, when he recorded in his synonymy the fertile frond of the Mexican *Tranquilia whitneyi* under the older name *"Alethopteris whitneyi"*. This synonymization, could perhaps seem correct at that time because of the poor quality of the Mexican material figured prior to 1969 (Newberry, 1876; Silva-Pineda, 1961) although Fontaine (1883) as a fine observer had avoided to propose synonymy despite that he had noticed the resemblance of both forms, and despite the fact that Newberry (1876) had already transferred the name *"Pecopteris falcatus"* to the Mexican material. It may be added that the present writer is still inclined to consider *"Asterocarpus virginiensis"* as an intermediate species between more typical *Asterotheca* and *Tranquilia whitneyi*; but closer to *Tranquilia* than to *Asterotheca.* Maybe, even this fixed idea does not help to understand the natural affinity of these plants.

Family assignment—The smoke screen of discussion on nomenclature cannot conceal the crossfire of contradictory botanical interpretations behind it.

To which fern family and order belongs the species studied here? This question is meaningless as long as it remains unclear whether *"Asterocarpus virginiensis"* and *"Cyathoforma carolinensis"* are really the same plant, as suggested by the considerable vegetative similarity of both materials.

However, the strong dimorphism that is very clear in *Tranquilia whitneyi* and the slightly weaker dimorphism of Fontaine's *"Asterocarpus virginiensis"* is neither documented in Bock's illustrations nor stated clearly in writing. He reports only a moderate polymorphism. This contention is specified in two contradictory versions, after which the frond is either provided with "distinct sterile and fertile pinnae"—in the redescription (Bock, 1969, p. 124)—or with "pinnules divided distinctly into fertile and sterile segments" (p. 122). Since the dimorphism can be appreciated clearly only in a minor part of Fontaine's frond specimens, no specific difference can be constructed using the apparent absence of dimorphism in Bock's specimens. But the arrangement of sporangial clusters might allow one to do so.

Among his figures of *"Asterocarpus virginiensis"*, Fontaine (1883, pl. 22, fig. 2) showed a fragment of a frond with pinnules that are only distally fertile along about 1/3 of their length. The middle and basal portions of the pinnules are sterile. This specimen was seen by the author in the NMNH, Washington, and the correctness of the figure is confirmed. Thus, the sporangial clusters clearly occupy the distal part of the pinnules as in *Tranquilia whitneyi* from Sonora or as in many species of *Asterotheca,* as distinguished from the reconstruction of *"Cyathoforma carolinensis"* given by Bock (1969, fig. 195, upper sketch). In this drawing, the sporangial clusters occupy only the basal and middle part of the pinnules whereas the apices are sterile. This difference might be deemed important enough to indicate that at least Bock's fertile material was not conspecific with Fontaine's (1883). But Bock's drawings might be inaccurate. For instance, one of the pinnules in his drawing is totally sterile, although the corresponding photograph (fig. 196) does not show any sterile pinnule. Sterile pinnules in just this position next to the fertile ones might never have existed in Bock's lost material. According to the reconstruction, the photograph shows in the upper left corner pinnules which seem to be sterile distally, and some other pinnules are apparently sterile at base. The preservation of the sporangial clusters, however, is unequal in different parts of the frond fragment, and clusters of sporangia were most probably present along the whole length of the pinnules before fossilization. Although the photograph does not show this neatly, no specific difference between Fontaine's (1883) and Bock's (1969) material can be constructed using the arrangement of the sporangial clusters. But the sporangial clusters themselves might allow one to do so.

The original description of *"Asterocarpus virginiensis"* by Fontaine (1883) could imply at that time the assignment to the Marattiales with eusporangiate sori or synangia, as Strasburger (1874, *fide* Seward, 1910) had suggested such an affinity, or perhaps to the Gleicheniaceae, with leptosporangiate sori (*cf.* Bock, 1969). The first interpretation was at least implicitly accepted by Ward (1900) and, among others, by Weber (1985a). Due to the absence of annuli, the sporangial clusters shown by Fontaine (1883, pl. 23, fig. 4, 4a; pl. 24, fig. 2, 2a) or those figured by Bock (1969, fig. 195–199) can not be interpreted as matoniaceous sori. Bock, however, interpreted the sporangial clusters in his material of *"Cyathoforma carolinensis"* as cyatheaceous sori. Consequently, he placed the whole complex of *"Asterocarpus"* described by Fontaine from

the Triassic of eastern North America—except *"Asterocarpus platyrachis", partim*—in the Cyatheaceae. This general contention goes too far, even though Bock (1969) reinforced it with his description of *Cyathocaulis carolinensis. "Cyathoforma carolinensis"* was illustrated by Bock with rather well preserved fertile specimens that allowed the observation of "nearly globose" large sporangial clusters covered sometimes by what he understood as indusia (Bock, 1969, fig. 195, 198). The indusia shown in his reconstruction (fig. 195) seem to be attached to the pinnule blade at the outline of the cluster. They are completely closed, and show a narrow fold crossing the apex of the "sorus" with a minute central protrusion, *i.e.*, they might be cyatheaceous indeed. The same drawing shows clusters lacking indusia. Some of them have intact sporangia, but in others, the sporangia are open and empty. Do cyatheaceous sporangia look like these after spore dispersal? As a result of Bock's interpretation, one stands between two fires: either Fontaine's and Bock's materials are different species, or at least one of these authors misinterpreted the material.

The latter point is here discussed further. Fontaine (1883, pl. 23, fig. 4a; pl. 24, fig. 2a) published two drawings of specimens with rather convincing marattialean synangia. Regrettably, the present author was not able to observe synangia as well preserved as these in any specimen of *"Asterocarpus virginiensis",* although Fontaine's original material in the NMNH was examined repeatedly. The absence of fertile specimens with clearly visible synangia in his material renders it impossible to check the exactness of his drawings. In accordance with the principle *in dubio pro reo* it is assumed here that Fontaine's drawings are reasonably accurate. To prove that the materials of both authors were conspecific, fire-proof evidence against Bock's interpretation has to be offered. Since Bock's original specimens are lost (Spamer, 1995) this can hardly be achieved, but it can be tried with the weak help of Bock's photographs (Bock, 1969, fig. 195–199). The sporangial clusters in Bock (1969, figs. 196–198) differ in fact from those drawn by Fontaine, though Bock's reconstructed "sori" with missing indusium and intact sporangia (Bock, 1969, fig. 195) resemble the "synangia" of *"Asterocarpus virginiensis"*. The sporangial clusters shown by Bock are arranged in nearly straight rows in the specimen of figs. 197 and 198, but are in disorder in fig. 196, due to incipient differentiation of an additional order of pinnules. The closed indusia, as shown in the drawn reconstruction, are hardly seen in the photograph magnified x12 (fig. 198). The illumination of the same fossil is better in fig. 197, but the low x3 magnification renders a sound examination difficult. Fig. 198 shows three rows of sporangial clusters. Some of them seem to be crossed by a pair of subparallel or more or less diverging lines or by what might be understood as slits between pairs of opposite indusial valves (for example right row: uppermost; middle row: lowermost and, less convincingly, left row: central cluster). Others seem to present cross or star-shaped slits between more irregular indusial lobes (right row: central, and, less clearly, middle row: uppermost cluster). The individual clusters measure about 0.8 to 1.5 mm in largest diameter, whereas Bock (1969) in his description speaks of about 0.7 mm wide, nearly globose containers. If the sporangia were arranged as Bock suggested in his drawing (1969, fig. 195), they measured about 0.4 to 0.7 mm in maximum width, thus exceeding most probably the dimensional range of cyatheacous leptosporangia. However, it is impossible to count or measure them in Bock's photographs because their outlines are not seen. Many of the clusters appear globose, indeed; but in others, the outline is provided with slightly protruding swellings that seem to correspond to sporangia. Bock's interpretation of his observations is not the only possible one. The following alternative interpretation, which is as hypothetical as Bock's, requires that the sporangia were more closely coalescent in the immature synangia than is the case in the Mexican *Tranquilia whitneyi.* His photographs might represent frond fragments with almost mature synangia. In some of them the sporangia are still firmly united and the synangia looked circular, but in others the sporangia begin to segregate and are more rounded. The first fissures between the drying sporangia are what Bock understood as slits between indusial valves, and the clusters with cross or star-shaped "slits" show a more advanced degree of sporangial separation. The following points speak not very strongly against Bock's (1969) weak interpretation: (1) The sporangia as drawn by Bock are too large for the leptosporangiate ferns, except perhaps the Schizaeaceae with the sporangia not arranged in sori. (2) The sporangia were not clearly observed by Bock and, consequently, no annulus was observed. (3) The presence of an indusium is not unequivocal. However, since the principle of *in dubio pro reo* is in force, he may have been right.

Hence, one may conclude that Fontaine's and Bock's materials were not conspecific. If this is assumed to be true, the whole taxonomic treatment of Bock's *"Cyathoforma carolinensis"* is ill-settled. On the other hand, Fontaine might have been wrong, though he is protected by *in dubio pro reo.* To support Fontaine, indirect evidence must be used:

Comparison—The vegetative characters of the dimorphous *Tranquilia whitneyi* can all be observed in certain specimens of *"Asterocarpus virginiensis"* as well, and some of the latter might even be confused with *T. whitneyi. "A. virginiensis",* however, shows polymorphism. The range of variability of this species is clearly higher than that of *T. whitneyi,* and it might even be suspected that Fontaine's *"Asterocarpus virginiensis"* embraces more than one species. The author checked the latter during the revision of Fontaine's original material. The supposition could not be confirmed and it was therefore stated above, that the author agrees with Fontaine's selection of specimens assigned and not assigned to *"Asterocarpus virginiensis".*

The dissection of the frond is the most variable character. The pinnules of the Sonoran species are all entire-margined. Presumedly, they are a result of complete lateral conation of phyletically prior smaller pinnules of the *Pecopteris*-type, as illustrated by the *Pecopteris-Ptychocarpus unitus-Fascipteris*

series. Fronds that might be transitional between *T. whitneyi* and *Asterotheca santaclarae* (Weber, 1985b) are absolutely absent from the Sonoran material. According to Fontaine (1883), in sterile fronds of *"Asterocarpus virginiensis"*, the pinnules are entire, pinnatifid, more deeply dissected or almost compound of pinnules of a higher order, as in "var. *obtusilobus,* but a complete separation of the pinnule lobes is not achieved because the more separate they become, the more decurrent they are and the more clearly they are united basally by wings of the rachis. On the contrary, the fertile pinnules of *"Asterocarpus virginiensis"* often show entire margins. Hence, the Sonoran and the Virginian species are very similar in the fronds with entire pinnules, but they are distinct inasfar as only the Virginian species can posses and, in fact, often possesses dissected pinnules. Since the Sonoran and the Viriginian species are compared here to stress their similarity, but not the well known differences, only the fronds with entire pinnules are compared in the following lines.

As described above, the fronds of *Tranquilia whitneyi* are clearly dimorphous. The same dimorphism can be observed in the pertinent specimens figured by Fontaine (1883), pl. 22, 23, fig. 3, with large sterile pinnules, and pl. 23, figs. 1, 4, showing large fertile pinnules. The latter are linear and much narrower than the sterile ones, just as in *Tranquilia whitneyi.* Of particular interest are the mixed sterile and fertile pinnules of the frond fragment figured by Fontaine (pl. 22, fig. 2). It shows that the sporangial clusters of this species are concentrated at the pinnule apex, when the pinnule is only partially fertile, just as in *Tranquilia whitneyi.* Fontaine writes: "Plate 22, fig. 2 gives the form presented by pinnules which are fructified only at the ends. The rest of the pinnule has the usual nervation and other characters of the large sterile pinnules".

The fertile pinnules of *T. virginiensis* are strongly decurrent, as shown by Fontaine (pl. 23, fig. 1, 4); consequently, the last order rachis is winged, *i.e.*, it presents conspicuous fertile seams of lamina on both sides. These wings are nearly laterally attached to the rachis. In *T. whitneyi,* the Sonoran species, these wings had not been observed previously, but they were found in the new material from Sonora described above. The wings are attached to the rachis more adaxially and are usually not visible in the impression material.

Fontaine (1883) as a fine observer described the fertile pinnules of *"Asterocarpus virginiensis"* carefully. He emphasised especially the differences in the aspect of the sori, depending on burial: "...the rounded sorus and its strong nerve, when pressed against the thick, dense leaf-substance of the pinnules, do not present a sharp outline of the separate parts when seen from the upper side, but the sorus and nerve produce a club-shaped prominence...". This recalls the above observations on the secondary venation in fertile specimens of *Tranquilia whitneyi.* The present author examined a large number of fertile specimens of *"Asterocarpus virginiensis"*, but the preservation does not facilitate the recognition of the secondary veins which are very often concealed by coaly remains of the synangia. However, there is without doubt a similarity between both species in this aspect.

The sporangial clusters of *Tranquilia whitneyi* with their normally six very large, annulus-free sporangia are interpreted as eusporangiate synangia without hesitation and resemble those drawn by Fontaine (1883, pl. 23, fig. 4a and pl. 24, fig. 2a). Nothing indicates that they might be cyatheaceous sori.

In conclusion, the Sonoran species *Tranquilia whitneyi* and the Virginian *"Asterocarpus virginiensis"* are very similar and are deemed congeneric. Moreover, it can be deduced now that Fontaine's drawings of the synangia of *"A. virginiensis"* are correct or almost correct. Hence, the name *Tranquilia virginiensis* (Fontaine) nov. comb. is proposed here for the Virginian species.

"Cyathoforma carolinensis" (Emmons) Bock is not considered as a synonym of *Tranquilia virginiensis,* though Bock's material might be conspecific with *T. virginiensis*, and furthermore something might be wrong in the interpretation of the sporangial clusters by Bock (1969). However, he is protected by *in dubio pro reo. "Cyathoforma"* is not revalidated herein. Perhaps, before the valid publication of the correct and legitimate generic name *Tranquilia* by Herbst (1988), it was still possible to save Bock's generic name *"Cyathoforma"*, but since it implies a taxonomic interpretation which may not withstand deeper scrutiny it was a lucky strike that Bock forgot to typify the genus and the species he had proposed and which, consequently, are not validly published.

GENERAL DISCUSSION

No additional species of *Tranquilia* were found by Herbst (1988) or by the present writer in the literature or in collections. The only record of a similar form is that compared by Kelber (1990, fig. 67; also *in* Kelber and Hansch, 1995, fig. 124) with the invalidly published, so-called *Bernoullia franconica* Frentzen 1926 from the Lettenkohle (Lower Keuper, Ladinian) of Franconia, Germany. The specimen is completely fertile and agrees more or less closely with the fertile material of *Tranquilia* described here. However, the synangia seem to be larger and are less regularly arranged along the pinnule midveins. No sterile frond fragments were found along with the fertile specimen figured by Kelber. Thus, the dimorphic nature of *Tranquilia* is not documented in the Franconian material, which cannot still be placed in this genus. The genus *Bernouillia* itself does not compare closely with the material decribed here. *Tranquilia* apparently remains unknown outside America.

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