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## Later Mesozoic Flora from Maran, Pahang, West Malaysia

### Part 2: Taxonomic Considerations

CHARLES J. SMILEY

*Visiting Fulbright Professor, University of Malaya*(Permanent address: Department of Geology and Geography,  
University of Idaho, Moscow, Idaho, USA)

**Abstract:** A total of 16 plant megafossil species has been identified in the two Maran collections. Five of these are pteridophytes of the genus *Gleichenoides* Kon'no in the family Gleicheniaceae. One is a sphenopsid referred to the genus *Equisetites*. Five are cycadophytes referred to the three genera *Otozamites*, *Ptilophyllum*, and *Zamites*. A single species of conifer in the genus *Frenelopsis* appears to have affinities with the Cupressaceae, and cones of the species were related to the form-genus *Conites* by Kon'no. Two other leaf forms, possibly conifers, are assigned to the genera *?Pelourdea* and *?Nageiopsis*. A possible fruiting body is referred to *?Carpolithes*. No records of Ginkgophytes or of Angiosperms (Dicotyledons) are present in the later Mesozoic (Neocomian) floras of West Malaysia.

#### INTRODUCTION

A comparison between the later Mesozoic floras of West Malaysia, and floras near the Jurassic-Cretaceous boundary from other areas, shows some striking differences in taxonomic composition and in taxonomic diversity. Ferns are commonly one of the dominant kinds of plants in Mesozoic floras, but their record from four study areas in Malaya is a single genus with five very similar species. Conifers are also common and varied elements in Mesozoic floras, yet the Malaysian record is that of a single family represented by one genus and species of common and widespread occurrence; one other conifer of rare occurrence in the northernmost Gagau composite flora has not been found in any of the other study areas. Ginkgophytes are common and varied plants in Mesozoic floras from higher latitudes, yet this plant group has left no record at any of the floral localities in West Malaysia. Angiosperms are extremely rare in rocks older than medial Cretaceous (Albian), and none are present in the early Cretaceous of Malaya. Cycadophytes are represented in Mesozoic floras from all latitudes by a variety of genera and species, and the later Mesozoic record in Malaysia is no exception.

Most of the Maran taxa represent extinct genera and species, and it is doubtful whether any of the Mesozoic taxa have survived unchanged to the present day. Reference of some of the fossil plants to existing families seems reasonably well established, however: *Equisetites* to Equisetaceae; *Gleichenoides* to Gleicheniaceae; and *Frenelopsis* appears to have affinities with the Cupressaceae. The species of *Otozamites*, *Ptilophyllum*, and *Zamites* belong in the plant division Cycadophyta, but they

cannot be referred to any of the existing nine genera of cycads. Following is a list of Maran plants organized systematically:

Sphenopsida

*Equisetites* sp.

Pteridophyta

*Gleichenoides gagauensis* Kon'no

*Gleichenoides pantiensis* Kon'no

*Gleichenoides maranensis* n. sp.

*Gleichenoides serratus?* Kon'no

*Gleichenoides* cf. *stenopinnula* Kon'no

Cycadophyta

*Otozamites gagauensis* Kon'no

*Otozamites malayana* n.sp.

*Ptilophyllum ayobanum* n.sp.

*Zamites* cf. *buchianus* (Ettinghausen) Seward

?*Zamites microphylla* n.sp.

Coniferae

*Frenelopsis malaiana* Kon'no

(*Conites spinulosus* Kon'no)

?Coniferae

?*Pelourdea* cf. *megaphylla* (Phillips) Seward

?*Nageiopsis* cf. *longifolia* Fontaine

Incertae Sedis

?*Carpolithes maranensis* n.sp.

The plant megafossils from Maran are described systematically on the following pages and are figured on Plates 1–5. Figured specimens are housed in the Research Collections, Department of Geology, University of Malaya, Kuala Lumpur, West Malaysia. Specimen numbers are of the Research Collection series, Department of Geology, University of Malaya.

## DESCRIPTIONS OF TAXA

### SPHENOPSIDA

Genus *Equisetites* Sternberg

*Equisetites* sp.

(Plate 5, Figs. 4, 7)

Two incomplete aerial stems of *Equisetites* are present in the upper Maran collection; no representative of this plant group has been found at the lower locality. Specimens referred to the species *E. burchardti* Dunker by Kon'no (1967, p. 141–142, Pl. 27, fig. 1–5) occur in the Gagau composite flora, but it cannot be determined whether they belong in the same species as the Maran fossils. The Maran specimens measure 3.5 mm. wide by 3.3 cm. long (incomplete), and 5 mm. wide by 6 cm. long (incomplete). Nodes that are apparent on the larger stem are spaced at distances of 1.5–2.0 cm.; nodes are not distinct on the smaller one. The ribs and furrows number

about 9 on the smaller stem and about 12 on the larger. Although the other characters seem to equate with the Gagau *E. burchardti*, the greater number of ribs on the Maran specimens may indicate that they are different species. The Maran fossils are not adequate, however, to describe a distinct species differing from the Gagau *Equisetites*.

Hypotypes Nos: 6586, 6587.

Occurrence: Upper Maran locality (5202); ?Gagau composite flora; ?Ulu Endau.

#### PTERIDOPHYTA

Holtum (1966) listed more than 500 species of ferns in the present flora of Malaya distributed among more than 100 genera in 18 families. Ferns are one of the most characteristic plant groups in this region today, resulting from the constantly warm and humid conditions of a tropical rainforest environment. It is most striking to see, therefore, that ferns are taxonomically deficient in Malaysian Mesozoic floras, where they have a known representation of only five species in a single genus (*Gleichenoides* Kon'no) of the family Gleicheniaceae. Ferns are characteristic plants in Mesozoic floras from other parts of the world, however, suggesting that Mesozoic environments in Malaysia were inhospitable for a rich fern population. The taxonomic dearth of Mesozoic ferns, the presence of only Gleicheniaceae that are sun ferns adapted to open environments, the association with small-fronded cycadophytes or with scaly-leaved cupressoid conifers, the consistently few plant taxa represented in each of the several localities that are about evenly-spaced over a distance of more than 200 miles, all point toward an open type of forest in a climate considerably drier than that which now prevails in the Malay region.

#### Family Gleicheniaceae

Holtum (1966, p. 64) noted that in the modern genus *Gleichenia* the round sori contain few and large sporangia that are usually arranged in a single circle. From balsam transfers Kon'no (1967, p. 142) observed in the fossil genus *Gleichenoides* that the circular sori also have few sporangia (usually 6 to 8), and that they are arranged also in a radiate and usually uniseriate pattern. A close relationship between the Mesozoic *Gleichenoides* and the living *Gleichenia* seems apparent, and conforms with the similarities in leaf morphology that can be noted between the Malaysian fossil species and certain "primitive" species of *Gleichenia* that are still living in this part of the world. Arnold (1964, p. 61) noted that the family Gleicheniaceae is thought to have arisen during the Palaeozoic, but that these ferns appear to have "lain low" prior to the Cretaceous. Fronds of *Gleichenoides* are not only important members of later Mesozoic floras in Malaysia, they are the only fern group now known to be represented in Malaysian rocks of this age.

#### Genus *Gleichenoides* Kon'no

At least five species of *Gleichenia*-ferns may be represented in the later Mesozoic flora of Malaysia. Three were described by Kon'no (1967, 1968) from G. Gagau collections, and one other from the Pantii collection. The fifth form is represented in the collection from the upper Maran locality (5202), and is described here as a new species. All species are closely similar in the branching pattern of fronds and pinnae, although one (*G. serratus* Kon'no) may have a somewhat more advanced

system of branching than the others. They are similar also in size and shape of pinnules, and in the characters of sori and sporangia as described by Kon'no. Consistent differences are apparent in the strength of pinna axes, in spacing of pinnae and pinnules, and in the size, shape, and venation of the pinnules.

Several species of *Gleichenia* are still living in Malaya (Holttum, 1966, pp. -72) where they inhabit open ground or forest borders; members of the extant genus are intolerant of the deeper shade of forest floors. The Mesozoic species of *Gleichenoides* have branching systems similar to those which Holttum (p. 62, fig. 14A and 14B) depicted as the most primitive form in the family. This primitive form is represented by the modern Malayan species *G. longissima* and *G. norrisii*, and by the living *G. glauca* of China and Japan.

In the Mesozoic deposits near Maran, Pahang, the species of *Gleichenoides* appear to be stratigraphically restricted. The species *G. pantiensis* is a co-dominant with the cupressoid conifer *Frenelopsis*, both in the lower Maran florule and in the Panti collection from south Johore. None of these taxa has been found at the upper Maran locality (5202) where *G. gagauensis* and *G. maranensis* (n.sp.) have been identified. The fern species *G. gagauensis* is co-dominant with the cycadophytes *Otozamites* and *Ptilophyllum* at the upper Maran locality; none of these Maran taxa has been found at the lower Maran locality, nor have they been identified in the collection from the Panti area.

The fossil species identified by Kon'no may be difficult to distinguish from fragmentary or poorly-preserved material. The Maran specimens are adequate to see some distinguishing characters by which four species are identified and one other is given provisional reference.

*Gleichenoides gagauensis* Kon'no  
(Pl. 3, Figs. 2, 3, 4)

*Gleichenoides gagauensis* Kon'no, Geology and Paleontology of Southeast Asia, 4, pp. 140-141, Pl. 24, Fig. 8, 1968. *Gleichenites (Gleichenoides) gagauensis* Kon'no Geology and Paleontology of Southeast Asia, 3, pp. 146-147, Pl. 25, Figs. 1-3, 1967.

Several specimens of penultimate and ultimate pinnae of *G. gagauensis* are present in the upper Maran florule (5202), where it is a co-dominant with the cycadophytes *Otozamites* and *Ptilophyllum*. The species is distinguished from *G. pantiensis*, which is present in the lower Maran florule (5201), by closer spacing of pinnae and pinnules, by a slight lobation that is apparent on some of the pinnules, by a near-uniformity in size of pinnules at the base of ultimate pinnae, and by the more slender and flexible pinna axes. *G. gagauensis* differs from the new species *G. maranensis* with which it is associated in having distinctly broader, flexible, penultimate pinnae, and more openly-spaced ultimate pinnae and pinnules.

*G. gagauensis* is present in the composite flora from the Gagau area about 85 miles north of the Maran site. Although the species has not yet been recognized in the preliminary sample collections from the Ulu Endau area about 85 miles southeast of Maran, the dominance of cycadophytes in the present Ulu Endau collections suggests that more extensive collecting will show *G. gagauensis* to be an associated form there as it is in the upper Maran florule. *G. gagauensis* is not present in the lower Maran florule, where *G. pantiensis* occurs in association with conifers rather than with cycadophytes. Nor has it been found in the collection from the Panti area

about 145 miles southeast of Maran, where *G. pantiensis* is found in association with conifers as it is in the lower Maran florule, and where cycadophytes are also lacking.

Hypotypes Nos: 6559, 6560, 6561.

Occurrence: Upper Maran locality (5202); Gagau composite flora.

*Gleichenoides pantiensis* Kon'no  
(Pl. 1, Figs. 1, 2, 3)

*Gleichenoides pantiensis* Kon'no, Geology and Paleontology of Southeast Asia, 4, p. 140, 1968.

*Gleichenites (Gleichenoides) pantiensis* Kon'no, Geology and Paleontology of Southeast Asia, 3, pp. 147–148, Pl. 25, Figs. 4–6; Pl. 26, Fig. 5b, 1967.

Several specimens of penultimate and ultimate pinnae of *G. pantiensis* are present in the lower Maran florule (5201), where it is a co-dominant with the conifer *Frenelopsis*. The species is distinguished from *G. gagauensis*, which is present in the upper Maran florule (5202), by the more rigid and more widely-spaced pinnae, by the entire-margined pinnules, and by the significant size difference of basal pinnules on ultimate pinnae. *G. pantiensis* differs from *G. maranensis* in having more widely-spaced pinnae and pinnules, and by the size difference of basae pinnules on the ultimate pinnae.

*G. pantiensis* was described originally from specimens in the Panti collection, where it is associated with conifers as in the lower Maran florule. It has not been identified in the composite Gagau flora, or in association with cycadophytes in the upper Maran florule, and its presence in the cycadophyte-dominated Ulu Endau collections is not known at present.

Hypotypes Nos: 6538, 6539, 6540.

Occurrence: Lower Maran locality (5201); Panti area.

*Gleichenoides maranensis* new species  
(Pl. 3, Figs. 1, 5)

Description: Portion of frond with rachis, 12 penultimate pinnae on one side, parts of seven pinnae on other; rachis firm, straight, preserved portion tapering from width of 2 mm. near middle of specimen to 1 mm. apically; preserved length of frond 12 cm.; width about 15 cm. in basal portion tapering to about 7 cm. apically. Penultimate pinnae alternately attached at intervals of about 12 mm., departing at angles of 90° on one side and 65°–70° on the other; base of pinnae decurrent on rachis; axis firm, straight, about 0.5–0.7 mm. wide at base, tapering gradually to about 0.1 mm. at apex; length about 7.5 cm. in basal portion of frond, gradually diminishing to 4 cm. or less in upper portion; width of pinnae 1 cm. near base of frond, sides parallel for about two-thirds distance to apex, then gradually narrowing to acute apex composed of a single lanceolate pinnule; pinnae near apex of frond with same shape, but proportionately smaller. Ultimate pinnae alternately disposed on penultimate axis, decurrent, about 26 on each side of axis, spaced at intervals of about 1.5 mm., almost touching adjacent ones but never overlapping; proximal pinnae departing from penultimate axis at angles of 80°–90°, distal pinnae departing

at angles of 50°–60°; axis slender but firm, straight, or tip of ultimate pinnae gently flexed toward penultimate apex; width 2–3 mm., narrowing gradually to an acute apex composed of a single pinnule. Pinnules usually obovate, sometimes ovate-lanceolate, with rounded or acute apex, about 1 mm. long and 0.3–0.5 mm. wide, narrowing at base which is decurrent on axis of pinna; pinnules alternately disposed, 6 or 7 on each side of pinna axis, and a single apical pinnule; pinnules nearly touching adjacent ones, but never overlapping; basal pinnules about equal in size; pinnules departing at angle of about 60° near base, angle becoming more acute toward apex of ultimate pinna; midvein straight, sometimes with tip flexed slightly toward pinna apex; secondary veins obscure.

Discussion: The sum of the characters gives this species the appearance of having a large and fairly rigid frond. The straight, narrowly-lanceolate penultimate pinnae, with closely-spaced ultimate pinnae and pinnules, provide a strikingly different appearance from any other species of *Gleichenoides* that has been described to date. This and other species of *Gleichenoides* from the Mesozoic of Malaysia are quite similar to some modern species of *Gleichenia* (*G. longissima* and *G. norrisii*) which are represented in Malaysian floras of open or forest border sites. A comparable open-forest environment for the Mesozoic *Gleichenoides* may be indicated also by the relatively small leaves, and the few kinds, of other plant taxa with which it is associated at each of the several fossil localities.

Holotype No: 6558.

Occurrence: Upper Maran locality (5202).

*Gleichenoides serratus?* Kon'no  
(Pl. 1, Figs. 5, 6, 7)

*Gleichenoides serratus* Kon'no, *Geology and Paleontology of Southeast Asia*, 4, pp. 141–142, Pl. 24, Figs. 5–7, 1968.

*G. serratus?* is represented in the lower Maran florule by several pinnae. The relatively broad and coarsely-serrate pinnules are distinguishing features. One of the Maran specimens has a barren rachis preserved for a length of about 4 cm., with alternate side branches of about equal strength, spaced about 2.2 cm. apart, and departing from the main rachis at angles of about 50°; the basal 1.5 cm. of the side branches is also barren, before giving rise on the distal side to a pinna that is twice more divided. Another specimen shows a side branch with the twice-divided pinna, and with the pinnules having coarsely-serrate margins as in the species *G. serratus*.

The frond of *G. serratus?* thus appears to be at least quadri-pinnate, with a stout branching framework, and a fairly open frond. The frond pattern appears to be somewhat more advanced than the other species of *Gleichenoides*, and not unlike the pattern of the living *Gleichenia microphylla* which Holttum (1966, pp. 62–63, Fig. 14B) has illustrated in his figure of comparative frond diagrams for the modern genus.

Hypotypes Nos: 6542, 6543, 6544.

Occurrence: Lower Maran locality (5201); Gagau composite flora.

*Gleichenoides* cf. *stenopinnula* Kon'no  
(Pl. 1, Fig. 4)

*Gleichenites* (*Gleichenoides*) *stenopinnula* Kon'no, *Geology and Paleontology of Southeast Asia*, 3, pp. 148–150, Pl. 25, Figs. 7 and 8, 1967.

*Gleichenoides stenopinnula* Kon'no, *Geology and Paleontology of Southeast Asia*, 4, p. 140, 1968.

A few isolated fragments of ultimate pinnae in the lower Maran florule contain relatively large and lanceolate pinnules some of which have sharply-toothed margins. The specimens resemble the species *G. stenopinnula* in these characters, rather than *G. pantiensis* with which they are associated at this locality. The fossil material is adequate to place in the genus *Gleichenoides*, but is not adequate to place definitely in the species *G. stenopinnula*. The specimens may as well represent a deviant form of *G. pantiensis*, the dominant fern in the lower Maran florule. The long slender pinnules do, however, represent a form different from specimens that are more positively identified from either Maran locality, and match most closely the Gagau species *G. stenopinnula*.

Hypotype No: 6541.

Occurrence: Lower Maran locality (5201); Gagau composite flora.

#### CYCADOPHYTA

In the Maran section, Cycadophytes are known only from the upper locality (5202), where they are the dominant and characteristic fossils. They are also the dominant plants in Ulu Endau collections, and are present in the Gagau composite flora. None has yet been found at either the lower Maran or Panti locality, where cupressoid conifers hold a position of dominance similar to that of cycadophytes at the other localities.

The upper Maran cycadophytes appear to be of two general types: (1) fronds complete with persistent pinnae, and (2) isolated pinnae that were deciduous or otherwise readily detached from the rachis. Type (1) is represented by species of *Otozamites* and *Ptilophyllum*; type (2) is represented by species of *Zamites*.

Modern cycadophytes are restricted to subtropical or tropical zones of the earth, and distribution of the group approaches the temperate zones at latitudes of about 30 degrees. They are found also in conditions approaching the temperate in higher elevations within the tropics and subtropics. Living cycads occur commonly in exposed well-drained environments such as open slopes; but they are not restricted to such a habitat, and some species live even in moist densely-forested sites. The occurrence of the Maran cycadophytes in fairly coarse sandy matrix, their association with few other plant taxa, and the presence of sun-ferns (*Gleicheniaceae*) as the only ferns and as co-dominants in the flora, suggest that the later Mesozoic cycadophytes of the southern Malay Peninsula occupied an open well-drained environment as seems most typical of their modern counterparts.

At present cycadophytes are represented in Asia by the genus *Cycas*, which ranges from Australia northward to China and southern Japan. In the southern Malay Peninsula, the species *C. circinalis* typically inhabits open sandy environments

near the coast, *C. siamensis* inhabits open cliff faces of limestone hills and *C. rumphii* is found in interior mountainous areas where it inhabits the protected sites of forest floors. The lower elevation cycads of Malaysia are thus inhabitants of open and well-drained sites, an environment that seems probable also for the Malaysian cycadophytes of the Mesozoic. In northwestern Thailand, the author recently has seen small cycads, probably of the species *Cycas siamensis*, as common plants on the more open forest floors, especially where locally well-drained or poor soils occur. The climate of northwestern Thailand, about 15° in latitude north of the Malayan fossil localities, has a distinct dry season of several months duration; the cycads grow on the floor of a deciduous forest where trees are fairly widely spaced and of few taxa locally (commonly dipterocarps, teak and clumps of bamboo).

#### Genus *Otozamites* Braun

The genus *Otozamites* is a common representative in middle Mesozoic floras, with a wide geographic distribution in upper Triassic, Jurassic, and lower Cretaceous times (Seward, 1917, 3, pp. 537–545). The alternate pinnae, attached obliquely to the rachis by a portion of a slightly asymmetrical rounded base, with a low length-width ratio, obtuse to rounded apex, and spreading veins, are characters distinguishing the genus in the Maran collections. Maran species of *Otozamites* are further distinguished from associated specimens of *Ptilophyllum* by a marked asymmetry of fronds, a stronger and unflexed rachis, broader pinnae with rounded rather than acute apex, distinctly alternate rather than subopposite to opposite attachment of pinnae, and a near-right angled departure of the pinnae at least on one side of the frond rather than more acute on both sides as in *Ptilophyllum*.

The 60 specimens of *Otozamites* in the upper Maran collection show a considerable variation in characters, but they can be separated into two general forms: (1) *O. malayana* n.sp.: the pinnae are short and broad, of uniform size and shape for much of the length of the frond, and are commonly at or near right angles to the rachis; the frond itself is slender, straight, symmetrical or nearly so, with sides essentially parallel for most of its length, and with an abruptly-rounded apex and base; (2) *O. gagauensis* Kon'no; the pinnae are much longer at least in the middle portion of the frond, are commonly falcate and curving proximally, depart at a somewhat more acute angle on one side of the rachis than the other giving the frond a distinctly asymmetrical appearance; the frond ends taper more gradually than in *O. malayana*, to a rounded base, and to an apex that is terminated by a single pinna.

Although 15 specimens can be referred to *Otozamites malayana* and most of the remainder are referred to *O. gagauensis*, a few have characters that are intermediate between the two extremes or combine characters that are distinctive of one or the other. The presence of two distinct leaf forms; with intermediate types having a combination or an overlapping of characters, might represent a single species with characters varying perhaps in accordance with position on the plant, or with degree of maturity or time of individual frond maturity, or with slight local differences in ecology. They might, on the other hand, represent closely-related but distinct taxonomic entities, of a species or possibly a varietal level. Because the two extremes in leaf form are quite consistent, and only a few are of intermediate type, the Maran specimens will be considered here as distinct morphologic entities that may or may not represent separate species. If they are in fact separate species, they would appear to be very closely related.



*Otozamites gagauensis* Kon'no

(Pl. 4 Figs. 1b, 1c, 2, 10)

*Otozamites gagauensis* Kon'no, Geology and Paleontology of Southeast Asia, 4, pp. 142–143, Pl. 25, Figs. 5–7, 1968.

The species *O. gagauensis* was recently described by Kon'no from two specimens in the Gagau composite flora. The Gagau specimens are in close agreement with the long-pinnaed form from the Maran locality in size, shape, and asymmetry of the frond, and in size, shape, number, and method of attachment of the pinnae. Kon'no (1967) had earlier examined three other specimens in the Ulu Endau collection and had described them as *Ptilophyllum* cf. *pterophylloides* (Yokoyama) Kon'no. One of the Ulu Endau specimens (his Pl. 27, Fig. 7) appears indistinguishable from *Otozamites gagauensis* both in the Maran collection and in the Gagau composite flora. Kon'no's Figs. 6 and 8 of Pl. 27 (1967) appear to have the characters of *Ptilophyllum*: pinnae apparently attached by the whole base that is decurrent on the rachis, and what appear to be parallel rather than spreading veins. The Ulu Endau collection may, therefore, contain both *Otozamites gagauensis* and *Ptilophyllum* as in the upper Maran collection.

Hypotypes Nos: 6565, 6567.

Occurrence: Upper Maran locality (5202); ?Ulu Endau; Gagau composite flora.

*Otozamites malayana* n.sp.

(Pl. 4 Figs. 1a, 4; Pl. 5, Figs. 1b, 10a, 11–14)

Description: Frond straight, sides parallel except near base and apex, apex rather abruptly rounded and terminating in a single pinna, base on one specimen appearing to be abruptly rounded, mature width 12–14 mm., length unknown, 5 cm. maximum preserved and probably much longer; rachis stout, width about 1 mm. in middle portion of larger specimens, rarely flexed and then only slightly so. Pinnae distinctly alternate, attached obliquely to top of rachis by a part of base, departing from rachis at wide angles approaching 90°, angle of departure may be slightly more acute on one side of rachis than on the other but not typically so, spaced at about 4 pinnae per cm. on mature fronds; pinnae commonly ovate to ovate-lanceolate, sides parallel, abruptly rounded apex and base, base nearly symmetrical, occasionally slightly auriculate on side nearer frond apex; on mature fronds, pinnae vary from a length of 6–8 mm. with a length:width ratio of 2:1, rarely to a length of 8–10 mm. with a length:width ratio of 4:1; veins distinctly spreading toward margins on ovate pinnae, spreading only at base and parallel apically on more slender pinnae; shorter pinnae straight, longer pinnae either straight or slightly curved toward base of frond.

This leaf form is subordinate numerically to *Otozamites gagauensis* in the upper Maran collection. It is not at present known in the Gagau composite flora or in the Ulu Endau flora, where *Otozamites gagauensis* would appear to be represented alone.

Holotype No: 6563; Paratypes Nos: 6564, 6579, 6580, 6581, 6582, 6583, 6584.

Occurrence: Upper Maran locality (5202).

Genus *Ptilophyllum* Morris*Ptilophyllum ayobanum* n.sp.

(Pl. 4, Figs. 3, 8, 9; Pl. 5, Fig. 3)

Description: Fronds symmetrical, with flexible rachis, at least 7.2 cm. long, 2.4 cm. wide at widest part, widest portion in middle of frond, tapering gradually toward obtuse or narrowly rounded base, and toward apex that is obtuse or acute and is terminated by a single pinna; pinnae linear, straight or slightly falcate, 14 mm. long and 2 mm. wide in middle part of frond, sides parallel for most of length and narrowing to an acute apex; base of pinnae apparently straight or slightly rounded, decurrent, attached to upper surface of rachis but not obliquely, departing suboppositely to oppositely, rarely distinctly alternate, departing at same angle from both sides of rachis, angle of departure changing gradually from near 90° at base of frond to about 45° in middle portion to about 30° near apex, spaced about 3 per cm. in middle portion of larger fronds; veins parallel from base, 8 or 9 per pinna.

The 15 Maran specimens that are referred to this species may be distinguished from fronds of *Otozamites* in the collection by the flexible rachis, symmetrical frond, slender pinnae, decurrent attachment, and parallel venation. The specimens appear to fall within the variable composite group of *Ptilophyllum pecten* (Phillips) Seward, and also show a close resemblance to *P. pterophylloides* (Yokoyama) Kon'no from the early Cretaceous of Japan. The combination of characters of the Maran fronds is not an exact match for previously described species, or for Kon'no's species of *P. cf. pterophylloides* from the Ulu Endau flora, and is thus described as new. The species is named in honour of Mohammad Ayob of the University of Malaya who mapped the Maran area, measured the sections, and located the fossil beds.

Holotype No: 6569; Paratypes Nos: 6573, 6574, 6585.

Occurrence: Upper Maran locality (5202), ?Ulu Endau.

Genus *Zamites* Brongniart

The genus *Zamites* appears to be represented in the upper Maran collection by two types of isolated pinnae; (1) a larger lanceolate form that is broadest near the middle, narrowing gradually in both directions to a rounded apex and a slender petiole-like base; and (2) a much smaller, obovate form with an abruptly rounded apex and a narrowly acute base. The lanceolate form appears to be present also in the Gagau composite flora as illustrated by Kon'no (1968, Pl. 24, Fig. 4), a specimen that was identified as a very small leaf of his *Pelourdea cf. megaphylla*. The figured specimen appears indistinguishable from medium-sized pinnae of the upper Maran *Zamites*. In the Maran section, ?*Pelourdea* is common at the lower locality where the leaves are all large and lance-shaped, and where no specimens similar to Kon'no's Fig. 4 cited above or to the upper Maran *Zamites* have been found. The Maran records suggest, therefore, that the larger ?*Pelourdea* and the smaller *Zamites* leaf forms are distinct entities both taxonomically and stratigraphically.

Kon'no illustrated (1967, Pl. 27, Fig. 13-15) some Gagau fossils having a size and shape similar to the Maran *Zamites*, but he identified them as *Nageiopsis?* spp. because of their different venation pattern. In *Zamites* the veins are more crowded, are parallel with the margin, and converge toward the apex; in *Nageiopsis* the veins are fewer and more widely spaced, do not converge toward the apex, but rather ter-

minate at the margin of the lamina. In the Maran section, *?Nageiopsis* sp. occurs at the lower locality at a stratigraphic level different from that of *Zamites*; and although the fragmentary specimens suggest a size and shape like that of *Zamites*, their venation is different and they appear to represent the species of *?Nageiopsis* illustrated by Kon'no from the Gagau composite flora.

*Zamites* cf. *buchianus* (Ettinghausen) Seward  
(Pl. 4, Fig. 1d; Pl. 5, Figs. 1a, 2, 6b, 10c)

*Zamites* cf. *buchianus* (Ettinghausen) Seward: Kon'no, *Geology and Paleontology of Southeast Asia*, 4, Pl. 24, Fig. 4, 1968.

It is difficult to determine from the specimens available whether the Maran fossils should be referred to the species *Z. buchianus* or to a new species that is probably a very close relative. The larger lanceolate pinnae in the upper Maran collection fall well within the range of all characters that have been ascribed to this "Wealden and Lower Cretaceous" species as illustrated and described by Seward (1917, p. 535, Fig. 601-C; p. 536-537). Similar fossils from East Asia, Europe, and North America appear to represent a Lower Cretaceous taxonomic complex in which species are difficult to distinguish on the basis of leaf morphology alone. The more than 40 Maran specimens, mostly pinnae fragments, are thus referred provisionally to *Z. buchianus*, to indicate that they are apparently representatives of this widespread Lower Cretaceous group of cycadophytes.

The Maran pinnae are typically about 7 cm. long, and are 1 cm. wide near the middle of the lamina. Largest pinnae measure more than 9 cm. long by 1.5 cm. wide; smallest pinnae measure about 0.4 cm. wide, and have an estimated length of about 3-4 cm. based on incomplete specimens. The pinnae are widest near the middle, narrowing gradually toward both ends; the apex is narrowly rounded; the base is constricted to a petiole-like shape that appears to be abruptly terminated as if along an abscissal line. The veins are fine, crowded, bifurcating near the base, parallel, converging apically as the lamina narrows, and 24-26 in number in the middle portion of the pinna.

In its living state, complete fronds of *Z. cf. buchianus* would probably represent the largest foliar organs known to have occurred in the Mesozoic vegetation of the Maran area.

Hypotype Nos: 6568, 6575, 6576, 6577, 6578.

Occurrence: Upper Maran locality (5202); Gagau composite flora.

*?Zamites microphylla* n.sp.  
(Pl. 5, Figs. 6a, 7-9, 10b)

Description: Isolated pinnae, apex round, base narrowly acute and almost petiole-like; size ranging from 10 mm. long by 4 mm. wide to 15 mm. long by 5 mm. wide; veins sub-parallel, bifurcating near base, slightly spreading apically parallel to margins, abruptly converging at apex, 2 basal veins dichotomously forking and re-forking to a maximum of 12 in distal half of lamina; attachment to rachis apparently by narrow petiole-like base, probably deciduous, attachment and rachis otherwise unknown.

Discussion: This small-leaved species, represented by more than 20 specimens in the upper Maran collection, appears to have the generic characters of the species *Z. cf. buchianus* with which it is associated. The consistently obovate shape, and venation pattern are characters by which the species *?Z. microphylla* can be distinguished.

Holotype No: 6592; Paratypes Nos: 6589, 6590, 6591, 6593.

Occurrence: Upper Maran locality (5202).

#### CONIFERAE

A single species of cupressoid conifer, *Frenelopsis malaiana* Kon'no (1967, 1968), is abundantly represented at the lower Maran locality, in the Panti collection, and in the Gagau composite flora. The species was described originally from Gagau and Panti specimens. Some attached and isolated female cones which Kon'no named *Conites spinulosus* are organs produced by *F. malaiana*. The foliage shoots show a wide variation in characters of stems and leaves, a variation that is apparent in the lower Maran collection as well as in the collection from Gagau and Panti. Kon'no described another species of cupressoid conifer, based on a single Gagau specimen, as *Cupressinocladus acuminifolia* (1968, p. 144–147, Pl. 25, Fig. 1B and 4); the specimen is in close proximity to a shoot of *F. malaiana* and on the same bedding surface. Although the ultimate branches are alternate as in *Frenelopsis*, a part of the branching system appears to be opposite; and the leaves are a little more slender and spreading than is typical of *F. malaiana*. The shape and attachment of leaves on the ultimate branches of *F. malaiana* may, however, approach that shown on Kon'no's specimen of *C. acuminifolia*. It has not been clearly demonstrated that the single Gagau shoot of *C. acuminifolia* is other than a variant of *Frenelopsis* with which it is closely associated in the Gagau sediments. It seems more likely to the present author to be a young terminal shoot of *F. malaiana* than a single specimen of an entirely different genus.

Other conifers, or possible conifers, are of few kinds and rare in later Mesozoic floras from Malaysia. A possible exception may be the large blade-like leaves in the Gagau and lower Maran collections which Kon'no referred to the genus *Pelourdea*, a form that may represent a Mesozoic relict of the Cordaiteae (Seward, 1917, 3, p. 277–281); however, the Gagau and lower Maran specimens are incomplete, and their affinities are not clearly demonstrated. A few fragmentary conifer shoots with needle-like leaves are present in the Gagau composite flora, and were identified as *Sphenolepis cf. kurriana* by Kon'no (1968, p. 150). A few lanceolate leaves referred to *?Nageiopsis* sp. are present in the Gagau and lower Maran collections; if they are of this genus, they may represent a Mesozoic conifer whose affinities are uncertain but may be with the Araucariaceae.

Thus the common and widespread conifer in later Mesozoic rocks of Malaysia is the cupressoid species *Frenelopsis malaiana*. Some female cones of *Conites spinulosus* are found attached to shoots of *F. malaiana* and are thus referable to this conifer species. Additionally, the single specimen of *Cupressinocladus acuminifolia* may well be a variant of *F. malaiana*, rather than representing a different cupressoid taxon. Needle-leaved conifers are rare and are represented only by a few leafy shoots in the Gagau composite flora. The common Gagau and lower Maran specimens of *?Pelourdea*, and the rare *?Nageiopsis*, may be relict members of primitive conifer lines or of otherwise extinct conifer taxa; but their affinities are not now clear, and they may belong to some different group of plants.

*Frenelopsis malaiana* Kon'no  
(Pl. 1, Figs. 8–10; Pl. 2, Figs. 1–5)

*Frenelopsis malaiana* Kon'no, Geology and Paleontology of Southeast Asia, 3, p. 156–159, Pl. 26, Fig. 1–5a, 1967; Geology and Paleontology of Southeast Asia, 4, p. 147–149, Pl. 26, Figs. 1–7, 1968.

*Frenelopsis malaiana* subsp. *parvifolia* Kon'no, Geology and Paleontology of Southeast Asia, 3, p. 159–160, Pl. 26, Figs. 6–8, 1967.

*Frenelopsis malaiana* subsp. *tenuis* Kon'no, Geology and Paleontology of Southeast Asia, 4, p. 149–150, Pl. 25, Figs. 1A–3, 1968.

This species of cupressoid conifer is represented by numerous branches and short shoots in the lower Maran locality. A few associated female cones, some of which are attached to shoots of *F. malaiana*, are indistinguishable from cones which Kon'no (1968) described as *Conites spinulosus*. The jointed stem with leafless internodes on older organs, and with overlapping and closely appressed scaly leaves on younger terminal shoots, are diagnostic characters. The abundant Maran specimens (about 70) show a wide range in internodal, nodal, and leaf characters, as one would expect to find in a suite of specimens containing foliage shoots from different parts of a branching system.

A few Gagau specimens representing one of the variants were described by Kon'no (1968) as the subspecies *tenuis* and a Panti specimen as the subspecies *parvifolia* (1967); but based on the larger collections from Maran they do not seem to warrant such formal designations. The more slender and spreading leaves of Kon'no's subspecies *tenuis* also seem to "bridge the gap" between more typical specimens of *Frenelopsis malaiana* and the cupressoid shoot he named *Cupressinocladus acuminifolia* (1968). In a large suite of variable specimens, therefore, it is difficult to distinguish three formal taxa of *Frenelopsis* and one of *Cupressinocladus*. The specimen of *C. acuminifolia*, however, shows a part of the branching system to have opposite penultimate shoots and alternate ultimate branches, rather than distinctly alternate throughout as is typical of *Frenelopsis*. Thus the two cupressoid conifers will not be placed in synonymy unless a clearer relationship can be shown by additional specimens.

Kon'no notes (1968, p. 154) that the female cone found attached to shoots of *Frenelopsis* cannot be referred to any existing conifer genus or with certainty to any existing family. *Frenelopsis* appears to be an extinct conifer with cupressoid foliage shoots but with cones that may have characters of both the Cupressaceae and the Taxodiaceae. The genus is exclusively Mesozoic in age, ranging from lower to upper Cretaceous, and was widely distributed in North America, Europe, and Asia. In Malaysia, *F. malaiana* occurs as a co-dominant with sun-ferns (Gleicheniaceae) at the Gagau, lower Maran, and Panti localities.

Hypotypes Nos: 6546, 6547, 6548, 6549, 6550, 6551.

Occurrence: Lower Maran locality (5201); Gagau composite flora; Panti locality.

Cones of *Frenelopsis*  
(*Conites spinulosus* Kon'no)

*Conites spinulosus* Kon'no, *Geology and Paleontology of Southeast Asia*, 4, p. 151-154, Pl. 27, Figs. 2-8, 1968.

The lower Maran collection contains nine female cones of the type referred by Kon'no to *Conites spinulosus*. Of these, four or five are attached to shoots of *Frenelopsis* and the remainder are isolated cones. The cones are about 7 mm. long and 4 mm. wide, with a slender stalk of attachment about 1 mm. Three of the specimens show attachment at nodes of mature stems by very short and slender stalks, and one specimen with two cones on the same stem shows the attachment to be apparently alternate. One small ovoid cone is attached to a leafy terminal branch by a scaly shoot 2 mm. long; another larger cone is near the end of a long side branch on the same shoot, but its organic connection is obscure. Where a distinct organic attachment of cones to shoots is evident, the forms *Conites spinulosus* and *Frenelopsis malai-ana* are known to represent the same plant species. But the biologic affinities of isolated cones, although resembling those that are attached, are not so certain. For this reason, the name *Conites spinulosus* is not synonymized.

Hypotypes Nos: 6552, 6553, 6554.

Occurrence: Lower Maran locality (5201); Gagau composite flora.

?CONIFERAE

?*Pelourdea* cf. *megaphylla* (Phillips) Seward  
(Pl. 2, Figs. 10, 11)

*Pelourdea megaphylla* (Phillips) Seward, *Fossil Plants*, 3, p. 281, 1917.

*Pelourdea* cf. *megaphylla* (Phillips) Seward. Kon'no, *Geology and Paleontology of Southeast Asia*, 4, p. 143-144, Pl. 24, Figs. 1-3 only, 1968.

Large strap-like leaves with numerous fine parallel veins are common at the lower Maran locality, but they are difficult to obtain except as fragments. They are very similar in size, shape, and venation to plants in the Gagau composite flora identified by Kon'no as representatives of the genus *Pelourdea*. Other authors have referred fossils of this type to the genus *Yuccites*, but Seward (1917) considered them to represent probably a relict line of the Cordaiteae. The preservation of the Malaysian specimens is incomplete, and many different kinds of plants produce foliage of this general type. Thus it would appear to be fruitless to speculate at this time as to their affinities, and they are referred here to ?*Pelourdea* as a form-genus. However, neither the Maran nor the Gagau specimens are adequate to show the broad basal attachment and spiral phyllotaxy necessary to refer them definitely to this genus, and their assignment to *Pelourdea* must therefore remain provisional.

In the Maran section this species is restricted to the lower locality. The specimens are about the size and shape of two of Kon'no's figured specimens (1968, Pl. 24, Fig. 1 and 3); no specimens of the extremely large size of his Fig. 2 have been found at the Maran locality. Leaves resembling his Fig. 4 are not present in the lower Maran collection, but they are common at the upper locality where they

have been identified as a species of *Zamites*. None of the larger specimens of *?Pelourdea* has been found with *Zamites* in the Maran section, and none of the *Zamites* leaf forms has been found with *?Pelourdea* at the lower locality. Leaves of the *Pelourdea* (*Yuccites*) type have been described in Triassic to lower Cretaceous floras of Europe and North America.

Hypotypes Nos: 6556, 6557.

Occurrence: Lower Maran locality (5201); Gagau composite flora.

*?Nageiopsis* cf. *longifolia* Fontaine  
(Pl. 2, Fig. 9)

*Nageiopsis longifolia* Fontaine, Proc. U.S. Nat. Mus., 16, p. 261, 1893.

*Nageiopsis?* spp. Kon'no, Geology and Paleontology of Southeast Asia, 3, p. 162–163, Pl. 27, Figs. 13–15, 1967.

Five fragmentary specimens that appear to have the size, the lanceolate shape, and the venation of specimens identified by Kon'no as *Nageiopsis?* are present in the lower Maran collection. The Maran specimens show the veins to be about 9 in number and widely spaced; their size appears to be a little larger than the Gagau specimens but they appear otherwise to represent this species. Their few and uncrowded veins distinguish them from the somewhat similar specimens of *Zamites* at the upper Maran locality, and the fact that the two leaf forms have not been found together but are stratigraphically separated supports the view that they are distinct taxonomic entities. The incomplete Maran specimens are not adequate to refer definitely to the genus *Nageiopsis* and their assignment is thus provisional. Both the Maran and Gagau specimens resemble the lower Cretaceous form *N. longifolia* from North America.

Hypotype No: 6555.

Occurrence: Lower Maran locality (5201); Gagau composite flora.

#### INCERTAE SEDIS

*Carpolithes* Schlotheim

*?Carpolithes maranensis* n.sp.  
(Pl. 5, Fig. 5)

Description: Shape ovoid, about 2.7 cm. diameter, with abruptly acute apex and obtuse base; palmate lineation (?venation) pattern of two distinct ranks; coarser veins few near base, tending to divide once or twice by dichotomy as they diverge across surface of lamina, subparallel, becoming slightly recurved and converging toward apex, spaced at intervals of 1–2 mm. in widest portion of specimen; weaker veins very fine, parallel, numbering about 6–7 between adjacent coarser ones; texture coraceous.

Discussion: A single specimen with counterpart is provisionally assigned to *Carpolithes*, a form-genus for fossil seeds or fruits that cannot otherwise be identified. The affinities of the specimen are at present not known, and it is not clear whether it represents a fruiting body rather than some other plant organ. Small seed-like

bodies described by Kon'no (1967) in the Gagau and Panti collections are quite unlike the Maran specimen, and no other fossil *Carpolithes* has been found in other Mesozoic floras that is similar to the Maran *C. maranensis*.

Holotype No: 6588 (counterpart 6589).

Occurrence: Upper Maran locality (5202).

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#### SMILEY: PLATE I

##### Lower Maran (5201)

(all Figs. natural size, unretouched)

Figs. 1, 2, 3. *Gleichenoides pantiensis* Kon'no. Hypotypes 6538, 6539, 6540.

Fig. 4. *Gleichenoides* cf. *stenopinnula* Kon'no. Hypotype 6541.

Figs. 5, 6, 7. *Gleichenoides serratus?* Kon'no. Fig. 5 shows open frond system, with pinnae in widely separated clusters. Fig. 6 shows pinnal clusters with closely spaced penultimate pinnae. Fig. 7 shows more open clusters, and pinnules resembling *G. serratus* Kon'no. Hypotypes 6542, 6543, 6544.

Figs. 8, 9, 10. *Frenelopsis malaiana* Kon'no. Figs. 8 and 9 are counterparts. Fig. 10 shows closely appressed leaves, perhaps of a young terminal shoot. Hypotypes 6545, 6546.





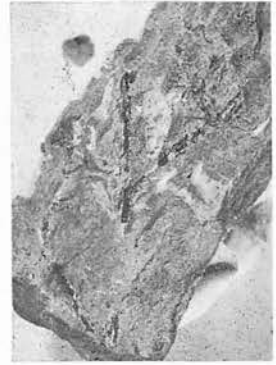
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PLATE 1

Lower Maran (5201)

(all Figs. natural size, unretouched)

## SMILEY: PLATE 2

Lower Maran (5201)

(all Figs. natural size, unretouched)

Figs. 1, 2, 3, 4, 5. *Frenelopsis malaiana* Kon'no. These specimens, in addition to Figs. 8-10 on Pl. 1, show the range of forms of *F. malaiana* in the Maran collections. Fig. 1 shows a cone (*Conites spinulosus* Kon'no) in center of photograph to left of main shoot, and an attached immature cone about 1 cm. above. Hypotypes 6547, 6548, 6549, 6550, 6551.

Figs. 6, 7, 8. *Conites spinulosus* Kon'no. Fig. 6 is a mature isolated cone. Fig. 7 shows three cones attached to nodes on stem of *F. malaiana*. Fig. 8 shows a mature cone in close proximity to jointed shoots of *F. malaiana*. Hypotypes 6552, 6553, 6554.

Fig. 9. ?*Nageiopsis* cf. *longifolia* Fontaine. Two leaf fragments showing lanceolate shape and widely spaced veins. May be parts of the same leaf offset by a small fault. Hypotype 6555.

Figs. 10, 11. ?*Pelourdea* cf. *megaphylla* (Phillips) Seward. Two fragments of longer leaves with fine and numerous parallel veins. Complete specimens not obtained because of jointing in matrix. Hypotypes 6556, 6557.



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PLATE 2

Lower Maran (5201)  
(all Figs. natural size, unretouched)

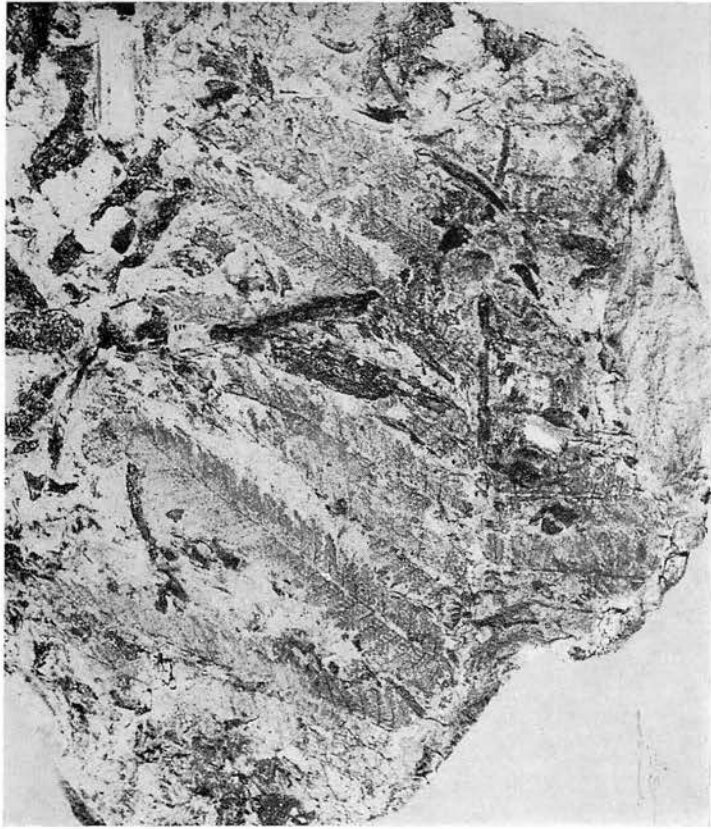
## SMILEY: PLATE 3

Upper Maran (5202)

(all Figs. natural size, unretouched)

Figs. 1, 5. *Gleichenoides maranensis*. n. sp. Black specimens on matrix are carbonized wood chips. Fig. 1 Holotype 6558. Fig. 5 is counterpart 6562 of basal portion of Fig. 1.

Figs. 2, 3, 4. *Gleichenoides gagauensis* Kon'no. Hypotypes 6559 6560, 6561.



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PLATE 3  
Upper Maran (5202)  
(all Figs. natural size, unretouched)

## SMILEY: PLATE 4

Upper Maran (5202)

(all Figs. natural size, unretouched)

Figs. 1a, 4. *Otozamites malayana* n. sp. Fig. 1a, Holotype 6563. Fig. 4, Paratype 6564.

Figs. 1b, 1c, 2, 10. *Otozamites gagauensis* Kon'no. Fig. 1b shows medial part of frond. Fig. 1c shows part of frond near base. Fig. 2 is counterpart of Fig. 1b. Hypotypes 6564A, 6565, 6566, 6567.

Fig. 1d. *Zamites* cf. *buchianus* (Ettingshausen) Seward. Lamina twisted near base, bending downward into matrix near apex. Hypotype 6568.

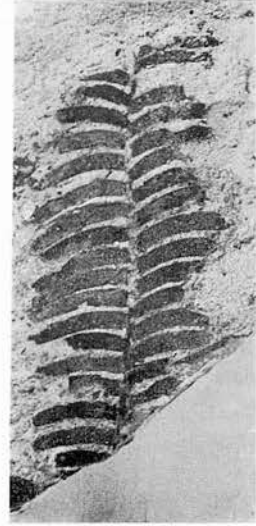
Fig. 3. *Ptilophyllum ayobanum* n. sp. Holotype 6569.

Figs. 5, 6, 7. Small, immature fronds of *Otozamites* sp. Paratypes 6570, 6571, 6572.

Figs. 8, 9. Small, immature fronds of *Ptilophyllum ayobanum* n. sp. Paratypes 6573, 6574.



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PLATE 4  
Upper Maran (5202)  
(all Figs. natural size, unretouched)

## SMILEY: PLATE 5

Upper Maran (5202)

(all Figs. natural size, unretouched)

Figs. 1a, 2, 10b, 11c. *Zamites* cf. *buchianus* (Ettingshausen) Seward. Hypotypes 6575, 6576, 6577, 6578.

Figs. 1b, 11a, 12-15. *Otozamites malayana* n. sp. Paratypes 6579, 6580, 6581, 6582, 6583, 6584.

Fig. 3. *Ptilophyllum ayobanum* n. sp., from same piece of matrix as Fig. 1. Paratype 6585.

Figs. 4, 7. *Equiserites* sp. Fig. 4 shows nodes spaced at intervals of about 2 cm. Fig. 7 shows oblique section across stem. Hypotypes 6586, 6587.

Fig. 5. *?Carpolithes maranensis* n. sp. Holotype 6588.

Figs. 6, 8, 9, 10a, 11b. *?Zamites microphylla* n. sp. Fig. 10a is Holotype 6592; others are Paratypes 6589, 6590, 6591, 6593.

(Undesignated black fragments on matrix are carbonized wood chips).





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PLATE 5  
Upper Maran (5202)  
(all Figs. natural size, unretouched)