

Gemellitheca gen. nov., a fertile pectopterid fern from the upper Permian of the Middle East

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Pectopterid fronds bearing typically bilocular synangia, *Gemellitheca saudica* gen. et sp. nov., are described from the Unayzah plant bed in Saudi Arabia and the Gomanimbrik Formation of the Hazro inlier in southeastern Turkey. The synangia are attached near the sharply incurved pinnule margin and extend across the whole or almost the whole half-width of the pinnules. Their apices lie near and in some cases over the midrib, and are curved abaxially away from it. The closest comparison is with *Dizeugotheca* Archangelsky & de la Sota, a Permian pectopterid with transversely placed fructifications which look very similar, but *Dizeugotheca* is described as having sori with sporangia consistently in groups of four, two of each group being largely overlapped by the other two. Synangia with three or four locules occur in *Gemellitheca saudica* but are rare.

The affinities of *Gemellitheca* are considered to lie with the marattialean ferns. A number of its characters are shared with species of *Scolecopteris* Zenker.

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Introduction	51
Systematic description	52
References	72

Introduction

Wagner (1962, pl. 28, figs. 22-23) described some vegetative pectopterid remains from the upper Permian of Hazro in southeastern Anatolia, Turkey, and named them *Pecopteris*

cf. *wongii* Halle p.p. Additional collecting from the Hazro inlier has since yielded rather more complete pinnae, some of which are fertile and which compare in general aspect with *Dizeugotheca* Archangelsky & de la Sota (1960) of the Gondwana Permian. The material was therefore named *Dizeugotheca?* sp. nov. by Archangelsky and Wagner (1983). Similar material also occurs in the Unayzah plant bed of central Saudi Arabia. Initially, a single fragment was figured as 'Fertile *Pecopteris*' by El-Khayal et al. (1980, fig. 2C). Later, a vegetative pinna from the same locality was correctly regarded as identical to the species from Turkey and recorded as *Pecopteris* cf. *wongii* Halle by Lemoigne (1981, p. 618, pl. 6, fig. 1).

Fieldwork at Unayzah in 1980 (see El-Khayal & Wagner, 1985) has shown this species to be the most common element of the plant fossil assemblage. Its burial in clayey shales, which became impregnated with iron minerals at some stage after compression of the plant remains, has preserved structural details of the epidermal cells and spores. At Hazro the species is also abundant, though not the most common one, and is preserved as coaly compressions and impressions. Unlike the Arabian specimens those from Hazro retain the organic substance, from which spores have been macerated. Although differently preserved, the material from these two Middle Eastern localities clearly belongs to the same species and the description that follows is therefore based on specimens from both localities.

Acknowledgements

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Systematic description

Gemellitheca gen. nov.

Type species — *Gemellitheca saudica* sp. nov.

Derivatio nominis — A compound of *gemellus* (Lat.), twin-born or paired, and *theca* (Gk.), case or container; referring to the bilocular construction of the synangia.

Diagnosis — Fronds at least bipinnate (known from fragments only), fragments either wholly vegetative or fertile, pinnules pecopterid. Fertile pinnules bearing elongate synangia on abaxial surface; synangia typically composed of two sporangial compartments (loculi) oriented at right angles to the pinnule midrib and margin and extending across the whole or almost the whole half-width of the pinnule, curving abaxially away from the lamina at their tips. Synangia borne at the distal ends of the lateral veins, laterally contiguous with neighbouring synangia to form an orderly row along the whole length of the pinnule half-width. Individual locules of each synangium large, exannulate, joined for most of their length to leave only their tips free. Spores initially shed into cavity between locules; spherical, alete to trilete, exospore ornamented with minute spines.

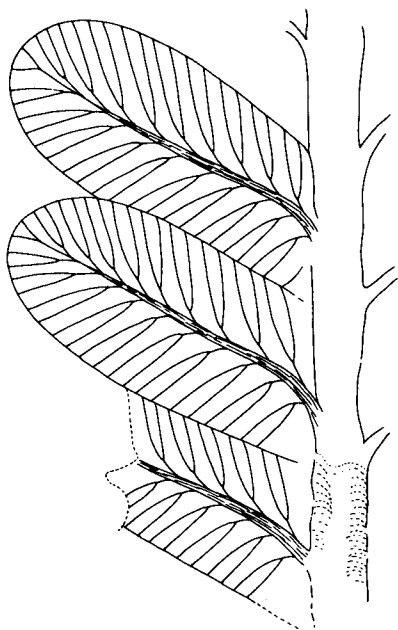


Fig. 1. Venation diagram of vegetative pinnules of *Gemellitheca saudica* gen. et sp. nov.; $\times 6$.

Fertile pinnules of same size, outline and venation as vegetative ones but with a laterally expanded marginal region. Marginal region scarious, without veins; strongly incurved abaxially to cover the basal regions of the synangia.

Gemellitheca saudica gen. et sp. nov.

Pls 1-9; Figs. 1-3.

- ? 1939 *Pecopteris densifolia* (Göppert), Stockmans & Mathieu, p. 78, pl. XVI, figs. 2-3, 3a.
- 1962 *Pecopteris* cf. *wongii* Halle p.p., Wagner, pp. 746-747, pl. 28, figs. 22-23.
- 1980 'Fertile *Pecopteris*', El-Khayal, Chaloner & Hill, p. 34, fig. 2c.
- 1981 *Pecopteris* cf. *wongii* Halle, Lemoigne, p. 618, pl. 6, fig. 1.
- 1983 '*Dizeugotheca*? sp. nov.', Archangelsky & Wagner, p. 87.

Derivatio nominis — The species is named after the Kingdom of Saudi Arabia.

Holotype — The fertile specimen in Pl. 1, fig. 1, RGM 382 643. All the paratypes are in the Rijksmuseum van Geologie en Mineralogie (National Museum of Geology and Mineralogy), Leiden, with duplicate specimens in the British Museum (Natural History), London.

Description — Fronds at least bipinnate (known from fragments of penultimate and ultimate orders of pinnae only), presumed to have been at least tripinnate and probably of large size. Rachis of pinnae of penultimate order flat, broad (20 mm wide), abaxial epidermis composed both of isodiametric polygonal and axially elongate cells about twice as long as broad; hemispherical multicellular emergences frequent (Pl. 1, fig. 1). Rachis of pinnae of final order up to 2 mm wide, abaxial epidermis composed of distinctly elongate cells; emergences frequent, smaller than on rachis of penultimate pinnae. [Adaxial surface of rachides unknown; free part of emergences, if any, also unknown.]

Pinnae of final order attached to rachis at 50-90° (characteristically 60-80°), slightly overlapping one another, up to 13 cm long; width gradually diminishing from 2 to 1.5 cm but narrowing fairly abruptly at the terminal which is a small, rounded and well individualised pinnule (Pl. 2, fig. 3).

Pinnules touching laterally or very slightly overlapping, characteristically attached at 60-80° (range 50-90°), parallel-sided with a broadly rounded apex; generally two to three times as long as broad (occasionally up to four times), with little variation in pinnule size and proportions except for the reduced terminal and immediately adjacent pinnules; length 6-12 mm, width 2.5-4 mm. Pinnule margins entire. Pinnules normally attached to rachis by their whole width but in region immediately adjacent to terminal their bases are narrowly confluent.

Lamina of pinnules flat or slightly vaulted; apparently thin. Midrib rather slender but strongly marked, straight, often slightly decurrent at the extreme base; cells of its abaxial epidermis elongated (Pl. 7, fig. 1; Pl. 8, figs. 3, 4). Lateral veins simple near apex of pinnule but otherwise consistently once-forked, forking at or near the midrib, arising at a rather wide angle and then curving more or less rapidly to adopt a course perpendicular (or almost perpendicular) to the pinnule margin; cells of abaxial epidermis of veins elongated (Pl. 8, fig. 1). Vein density at pinnule margin about 24 per cm. Abaxial epidermis of lamina between veins composed of more or less isodiametric polygonal to slightly elongate ordinary cells and numerous irregularly scattered stomata. Stomata small, anomocytic, mostly oriented in the direction of the veins.

Vegetative and fertile pinnules of identical size, venation and outline but in fertile pinnules the lamina has a laterally expanded marginal region. This is sharply incurved so as to cover the basal regions of the synangia. Extent of infolding $\frac{1}{3}$ to $\frac{1}{2}$ of the pinnule half-width (Fig. 2). Infolded region probably scarious; lacking veins and stomata and composed either of elongate cells with septa, to form polygonal sub-units, or elongate packets of polygonal cells (alternatives given since interpretation at present uncertain).

Fertile pinnules each with two orderly rows of laterally contiguous, elongate synangia, one row to each half-width of the pinnule. Synangia extending from well within infolded marginal region to (or slightly overlapping) the midrib; typically bilocular but with some variation: occasional synangia have three or four locules. Locules fused for most of their length but free at the tips, in proximal region their identity marked by a longitudinal groove between the locules. Synangia corresponding in density to lateral vein branches; presumably each synangium was attached over a vein branch near or at its end (details obscured by the infolded margin and strong degree of compression).

Synangia curving abaxially away from the pinnule lamina, particularly at their apices (Fig. 2); angles of curvature of 5-20° relative to plane of lamina, recorded in the compressed material, indicate that the angle was greater than this during life. Seen in plan view the synangia are almost uniformly oriented at right angles to the pinnule midrib and margin except for end ones nearest to rachis: synangium nearest to rachis on basiscopic half of pinnule often out of line with the rest, pointing towards the rachis rather than the pinnule midrib; occasionally the synangium nearest to the rachis on the acroscopic side also out of line, pointing either towards the rachis or (more rarely) towards the pinnule apex.

Plate 1

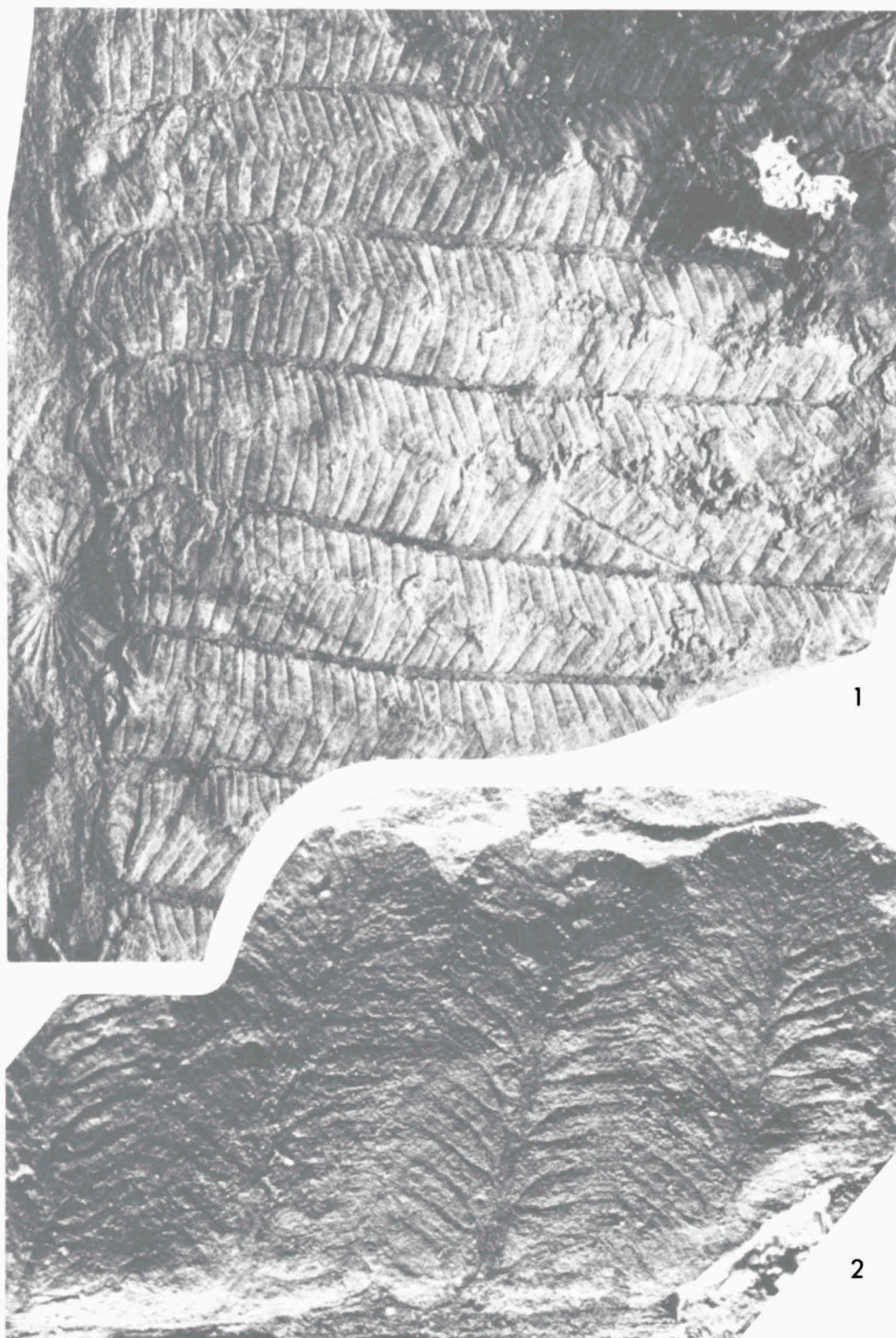
Gemellitheca saudica gen. et sp. nov.

Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

Fig. 1. Fragment of a vegetative pinna showing the partly overlapping pinnae and very closely spaced, rather elongate pinnules; $\times 1$; holotype RGM 382 643.

Fig. 2. Vegetative pinnules touching laterally and showing the venation: i.e. a slightly decurrent but otherwise straight and rather thin midrib, and regularly disposed once-bifurcate lateral veins forking at or near the midrib; $\times 12$; RGM 382 644.

Plate 1



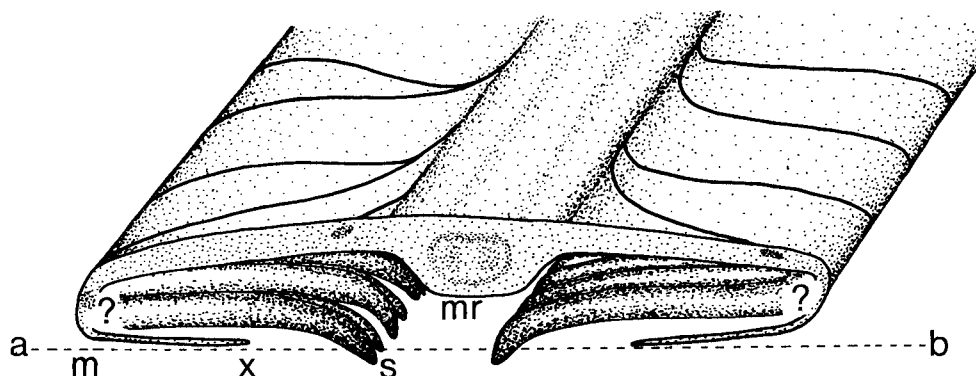


Fig. 2. Reconstruction of *Gemellitheca saudica* gen. et sp. nov., oblique view of 'half' pinnule, approx. $\times 75$; x, true margin; m, folded edge of pinnule (region between m and x is the infolded marginal region of the lamina); s, synangium; mr, midrib. ? indicates region of synangial attachment, details of which are unknown. The dashed line between points a and b indicates the plane of weakness of the specimen when split into part and counterpart, which (in this instance) would pass through the tips of the synangia. The truncated synangia on the part would therefore appear shorter than they in fact are.

Locules of synangia originally rounded in transverse section; outermost cell layer of wall composed of elongate, thick-walled cells which become shorter towards the apex of the locule, files of cells curving towards apex of synangium. Number of spores per locule probably several thousand. Spores very small (c. $15\ \mu\text{m}$ in diameter), initially shed into cavity between free tips of locules, amb circular; alete to trilete, exospore of mature spores ornamented sparsely with minute spiny granules.

Discussion — Although the most complete fragments with attached pinnae include rachides of penultimate pinnae, up to 2 cm in width, similar rachides without pinnae also occur separately. These are up to 5 cm broad, suggesting that the frond was much larger than the available fragments with attached pinnae indicate. It seems likely, therefore, that the frond was at least tripinnate. The denuded rachides show similar emergences to those having attached pinnae and are therefore determined with confidence. The emergences appear as pits in impressions of the rachides and may have been podia of scales or bases of spines (as occur in extant members of Marattiales). The free part however is not preserved and there may have been none originally.

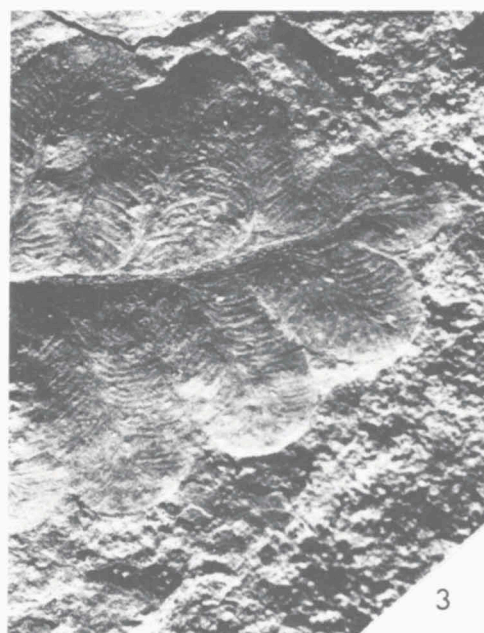
Plate 2

Gemellitheca saudica gen. et sp. nov.

Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

- Fig. 1. Fragment of a vegetative pinna of the penultimate order (together with a *Cordaites* leaf) from a slightly more terminal position in the frond than that of Pl. 1, fig. 1. The pinnules have a smaller length/breadth ratio than those of Pl. 1, fig. 1; $\times 1$; RGM 382 645.
- Fig. 2. Fragment of a vegetative pinna of the last order. Its pinnules show the rather thin, slightly decurrent midrib and the regularly once-bifurcate lateral veins; $\times 6$; RGM 382 646.
- Fig. 3. Terminal of a pinna of the last order showing the characteristically small and rounded apical pinnule. The lateral pinnules touch or partly overlap one another and are relatively short; the venation appears denser than it actually is since the synangia, each with two loculi per lateral vein, are faintly marked on the adaxial surface of the thin lamina as a result of compression; $\times 6$; RGM 382 647.

Plate 2



The expanded and sharply infolded marginal region of the fertile pinnules presumably protected the developing synangia from desiccation or from predatory animals, as suggested for some comparable species of *Scolecopteris* Zenker emend. Millay by Millay (1979). There is no direct evidence that the marginal region was scarious, though the thin substance, the lack of veins and stomata and the cellular structure suggest this interpretation. Although not an indusium as in Filicales the marginal region probably had a comparable function.

The gaps between the inner edges of the infolded region (i.e. the true pinnule margin) and the midrib are not very large. The curve of the apical regions of the synangia away from the lamina may therefore have served to provide optimal exploitation of these gaps for shedding of the spores. The initial shedding of the spores into the cavity between the tips of the locules is of interest in this regard and also because of its similarity to *Scolecopteris* (Millay, 1979). This initial shedding is quite clear from the Saudi specimens (Pl. 9, figs. 1-3) and provides direct evidence for assuming that the spores of these specimens were mature or almost mature. Using cellulose acetate replicas the ornamentation of their exospores with minute, sparsely distributed spines is clearly evident (Pl. 9, figs. 4, 5). In contrast all spores macerated so far from the Hazro specimens have entirely smooth exospores. (This was confirmed from direct view with SEM of untreated spore-masses in situ.) The occurrence of the spores solely as strongly coherent spore-masses in these Hazro specimens, however, suggests that they were all immature, thus explaining their lack of spines. A similar coherent spore-mass in an Arabian specimen also proved to have spores with smooth walls (other than an irregular pitting produced by crystals). There is therefore no evidence from the spores to suggest that the Hazro specimens represent a different species from the Saudi material.

The number of spores produced per locule is crudely estimated as several thousand. This estimate is based on spore-masses macerated from the Hazro specimens and on the number of spores (319) counted on a single layer exposed on longitudinal fracture of a spore-mass in an Arabian specimen. This spore-mass is about $\frac{2}{3}$ complete, permitting an estimate of c. 500 spores in that layer for the whole locule. Several such (two dimensional) layers are needed to constitute a three dimensional spore-mass. We assume a factor of 10 and thereby very approximately estimate that the spore production was about 5000 per locule.¹⁾ This is comparable with spore production in extant Marattiales.

The orderly arrangement of the synangia transverse to the long axis of the pinnules is at a different angle to that of the veins, which become transverse only as they approach the edge of the pinnule. To this extent the orientation of the synangia conflicts with the course of the veins except in the region near the pinnule edge. This indicates clearly that

1) It would be of more genuine interest to use a mathematical formula based on an ellipsoid, for calculating more rigorously the assumed spore production per locule in such instances.

Plate 3

Gemellitheca saudica gen. et sp. nov.

Gomaniimbrik Formation near Dadas Köy, Hazro Inlier, Diyarbakir Province, Turkey (Wagner loc. 3111).

Fig. 1. Fragment of a fertile pinna of the penultimate order, showing its similarity in pinna and pinnule size, outline and spacing of the pinnules to the vegetative material of Pl. 1, fig. 1 and Pl. 2, fig. 2. The pinnules are densely covered by transversely arranged, elongate synangia which occupy the whole half-width of the pinnules; $\times 3$; RGM 382 648.

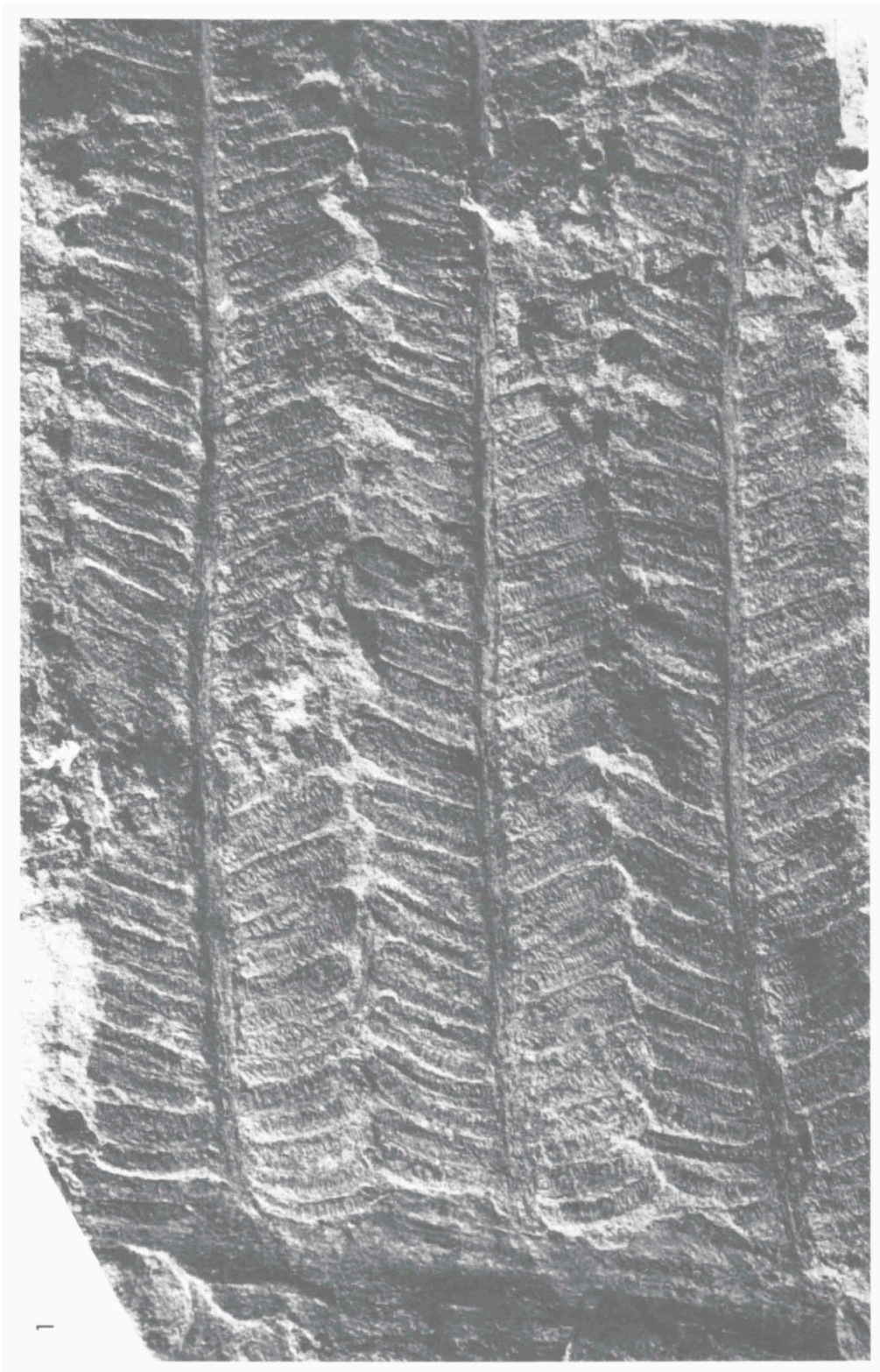


Plate 3

the synangia were attached to the lamina near their bases, rather than along the greater part of their length. The exact details of attachment, however, are unknown.

The curvature of the apical regions of the synangia away from the lamina varies with the degree of compression of the specimens. In general the Arabian specimens are more strongly compressed than those from Hazro and the curvature is correspondingly less strongly marked. Splitting of the rock into part and counterpart often passes through the apical regions because of this curvature (Fig. 2). Particularly in the Hazro specimens the apices are therefore rarely preserved in the compressions, and this gives the superficial appearance of synangia shorter than they in fact are. In general, the more compressed a specimen is, the longer the length of the synangia retained on the parts. The specimen in Pl. 6, figs. 6, 7, is unusual for a Hazro specimen in showing the synangial apices clearly, owing to oblique compression as a result of abnormally strong inrolling of the pinnule half-width on the acroscopic side of the pinnules in this specimen.

The shape of the locules in section was determined from material embedded in resin and ground so as to give a tranverse section of the synangia. In occasional synangia infilled with rock matrix their shape proved to be circular. Grinding in this way was used also to attempt to determine whether the synangia were consistently bilocular or have a greater number of locules. Most of the specimens proved to be too strongly compressed to reveal their structure clearly, and where fairly clear the synangia appeared mostly to be bilocular. A few were found to be apparently tri- or tetralocular (as seen in surface view in Pl. 8, figs. 3, 4). The results of grinding were not entirely clear, however, and possibly the proportion of synangia with three or four locules is greater. The evidence overall indicates that *P. saudica* had typically bilocular synangia but with some variation (as is to be expected in biological material) to result in some synangia with three or four locules. This is of particular interest in relation to comparison with *Dizeugotheca* Archangelsky & de la Sota (p. 62).

Affinity — The pectopterid pinnules with laminae of thin substance, the synangiate sori, and fecund production of spores of *Pecopteris saudica* all indicate affinity with the marattialean ferns. Without further knowledge of the attachment region of the synangia, exact relationships are difficult to specify, but attribution to Psaroniaceae sensu lato seems appropriate. As mentioned above, there are several similarities to *Scolecopteris*. The apparent reduction of the number of locules to typically two rather than three or more, however, distinguishes the genus clearly from those such as *Scolecopteris* and *Asterotheca* Presl which are more characteristic of Palaeozoic Marattiales. We hope that permineralised material may become available to test this hypothesis of synangial construction and affinity in more detail.

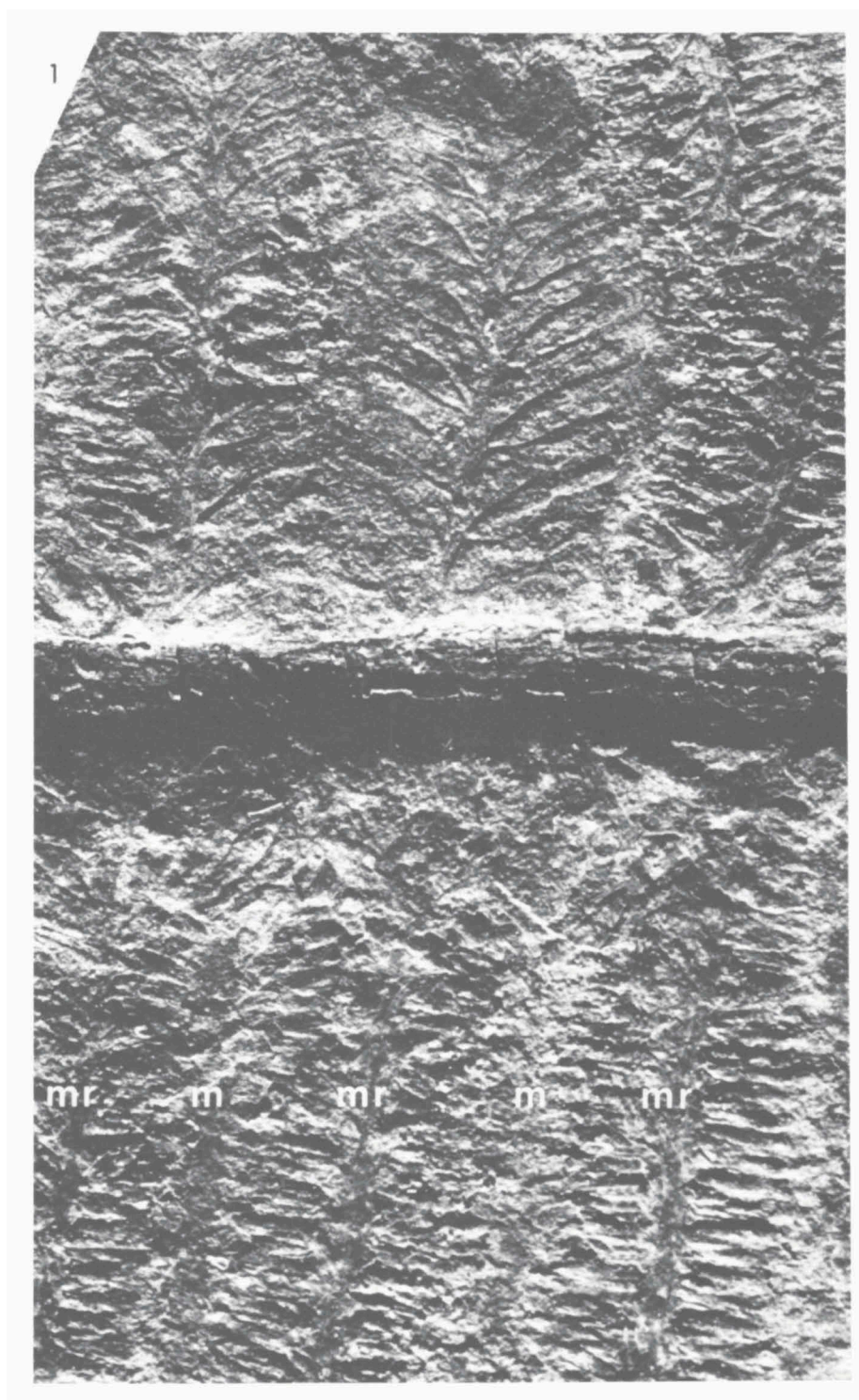
Plate 4

Gemellitheca saudica gen. et sp. nov.

Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

Fig. 1. Fertile specimen which has split at different levels so as to show the pinnule lamina in the upper part of the photograph (especially the middle pinnule) and the underlying synangia elsewhere. The lateral vein pattern is oblique at the midrib and more perpendicular near the pinnule margin, whereas the synangia are perpendicular to both; they occur in orderly rows and are composed of two loculi. The synangia are attached near the pinnule margin, presumably beneath the ends of the lateral veins; they extend horizontally across the pinnule half-width and their free tips virtually touch the midrib. Margin, m; midrib, mr; $\times 12$; RGM 382 649.

Plate 4



Comparison — *Dizeugotheca* Archangelsky & de la Sota (1960) is another Permian pecopterid with elongate synangia or sori lying transversely across the pinnule lamina in an orderly fashion. The fructifications have been described definitely as sori rather than synangia and as composed of groups of four sporangia, though overlapping so as to give the appearance of paired sporangia. Their insertion has been described as probably near the midrib and their transverse orientation has been supposed to result from flattening. Vegetative pinnules of *Dizeugotheca* were originally described as having simple veins but Arrondo (1972) has since reported pinnules with bifurcate veins.

Unfortunately the Argentinian type material of *Dizeugotheca*, from Patagonia, is not well known. The photographs of these and additional remains from Bolivia and Patagonia illustrated by Arrondo (1967, 1972) are at too low a magnification to depict the structure of the sori (or synangia?) adequately. The drawings made by Archangelsky and de la Sota (1960) and Arrondo (1967) are interpretative and the material is poorly preserved (Archangelsky, pers. comm.). Perhaps its most evident character is the transverse position of the sori. The attachment of the fructifications is largely debated by the South American authors, and although Archangelsky and de la Sota (1960) opted for probable attachment near the midrib, this is regarded as unproven by Arrondo (1972, pp. 46-47) who stated that the free tips of the sporangia faced either the midvein or the pinnule margin, the state of preservation being such as to leave both possibilities open. Archangelsky (pers. comm.) agrees. Arrondo's (1967, p. 59) drawing is of interest in apparently showing the sporangia of each fructification fused in the area facing the margin and free in the area near the midrib, as in *Gemellitheca*. Re-examination of the South American material may throw further light on this. Archangelsky and de la Sota (1960) and Arrondo (1967, 1972) all concur however in interpreting the sporangial units as sori constituted of four free sporangia. If so, there appears to be a clear difference from *Gemellitheca*, which typically has only two sporangial compartments per clearly synangial unit. Although Arrondo's (1967) drawing also shows two sporangia per unit, these are supposed to cover another pair belonging to the same sorus or synangium.

Cazzulo-Klepzig (1978) recorded another species of *Dizeugotheca* from the state of Santa Catarina in Brazil. She also mentioned doubts about the attachment of the sori and described the sporangia as occurring in groups of four, the lower two of which were not visible.

Despite its poor preservation and the difficulties therefore of interpretation, the *Dizeugotheca* as described from South America appears to be very similar to *Gemellithe-*

Plate 5

Gemellitheca saudica gen. et sp. nov.

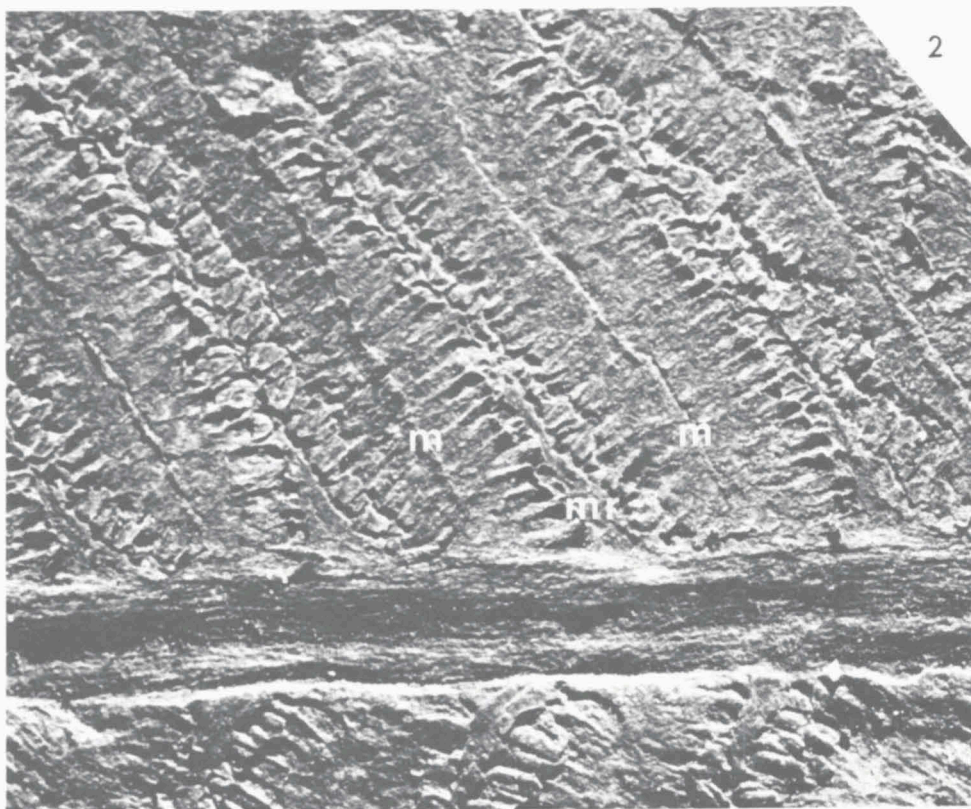
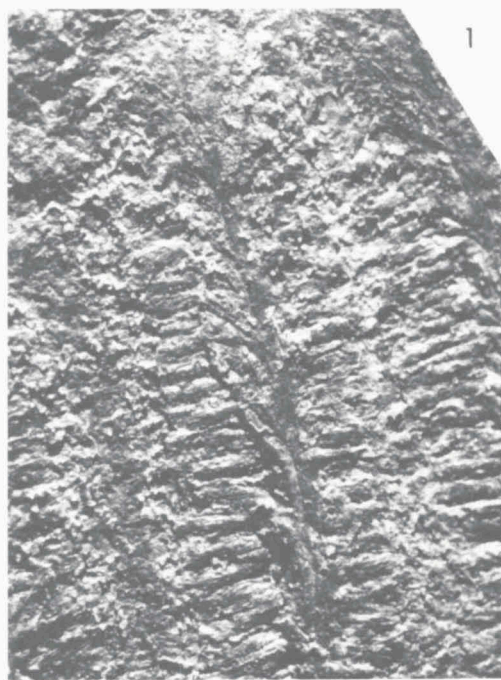
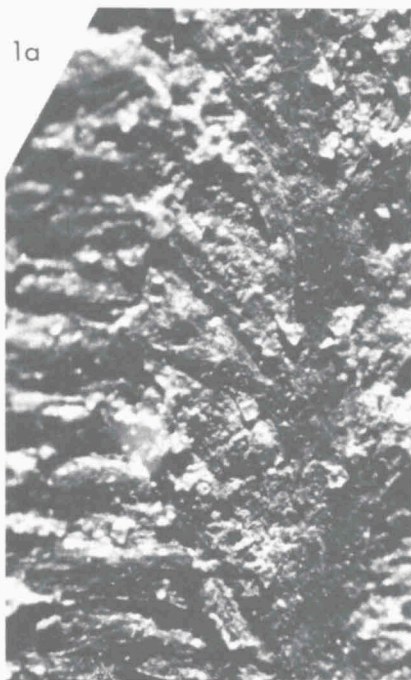
Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

Fig. 1. Pinnule split so as to show the apical and median regions of the lamina, as well as the underlying synangia; $\times 12$; RGM 382 650.

1a: Portion of the same specimen enlarged $\times 24$ to show the lateral veins arising obliquely from the midrib and following a different course to the synangia (at left) which have their long axes perpendicular to the midrib.

Fig. 2. Fertile pinna fragment showing the rachis with obliquely attached pinnules which are laterally touching or even partly overlapping; the abaxial surface (uppermost) shows the imprints of synangial bases near the pinnule margins (m) and preservation of their compressed tips in the region of the midrib (mr); $\times 12$; RGM 382 651. A similarly preserved specimen was figured by El-Khayal, Chaloner & Hill (1980, fig. 2c) as fertile *Pecopteris*.

Plate 5



ca. If the sporangial units of *Dizeugotheca* had not been described as sori composed consistently of four sporangia, we might well have attributed the Middle Eastern specimens to that genus.

The Indian Gondwana fern *Pecopteris phegopteroides* (Feismantel) Arber was attributed to *Dizeugotheca* by Maithy (1975) and Lele et al. (1981). This appears to be a misidentification since the fructification of *P. phegopteroides* consists of small, but mature, tetralocular synangia, placed along the extreme margins of the pinnules (Pant & Misra, 1976). Lele et al. (1981, p. 134) appear to have misread the description of *Dizeugotheca neuburgiae* Archangelsky & de la Sota when they state that the sori of *D. neuburgiae* occur at the margins of the pinnules. In fact, the South American authors mention that the very prominent capsules (their wording) occupy the whole half-width of the pinnule (Archangelsky & de la Sota, 1960, p. 104). Herbst (1978, p. 126) also mentions that Maithy's usage of *Dizeugotheca* does not correspond to the original definition of that genus.

Pant and Misra (1976) made a detailed study of the fructification of *Pecopteris phegopteroides* and critically described the small, marginal fructifications as synangiate. They introduced the new generic name *Asansolia* for this species. As for *Dizeugotheca* (and *Gemellitheca*), the attachment of the synangia was not clear (op. cit., p. 137), but the small size of the synangia composed of four loculi, and their marginal position, constitute obvious differences both from the South American genus and from *Gemellitheca*. Pant and Misra (1976, p. 130) transferred *Dizeugotheca neuburgiae* to *Asansolia* on the assumption that this species was also characterised by marginal synangia, but this is not borne out by the description of *D. neuburgiae* (see Archangelsky & de la Sota, 1960).

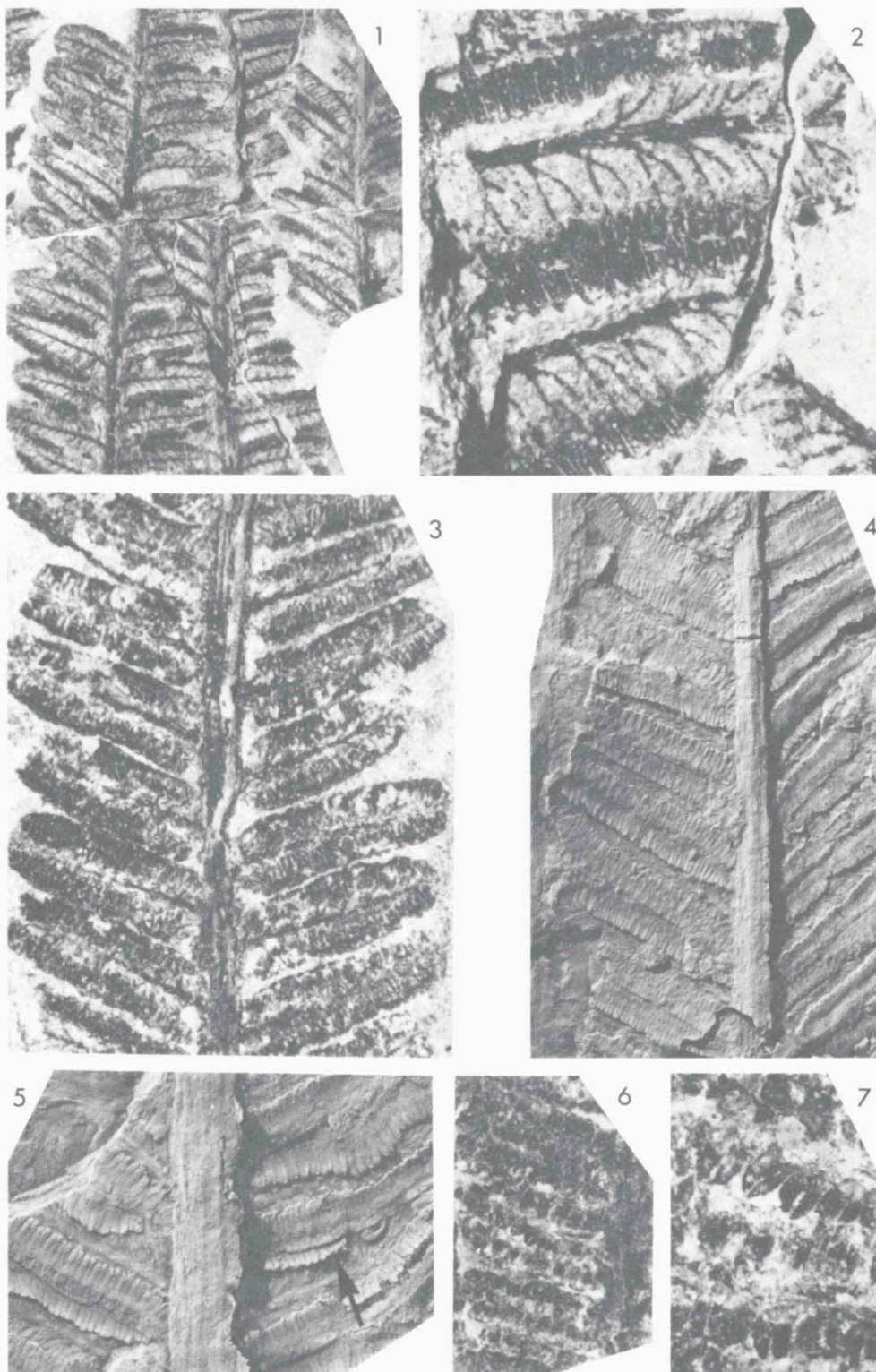
Plate 6

Gemellitheca saudica gen. et sp. nov.

Specimens in figs. 1-3, 6, 7 are from the Gomanimbrik Formation, near Dadaş Köy, Hazro Inlier, Diyarbakır Province, Turkey (Wagner loc. 3111). Specimens in figs. 4-5 from the Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

- Fig. 1. Three neighbouring pinnae of the last order showing false appearance of short synangia as a result of splitting of the rock through the tips of the synangia; $\times 2$; RGM 382 652.
- Fig. 2. Two pinnules from the same specimen (top right of fig. 1), enlarged $\times 10$ to show venation as in the Saudi Arabian specimens and the truncation of the synangia as a result of splitting of the rock through the tips of the synangia. The tips are buried in the matrix of the counterpart, in the region where the venation is shown on the part (i.e. the specimen figured). The synangia thus appear much shorter than they in fact are (for other examples of such splitting, at varying levels, see the Saudi Arabian specimens on Pl. 4, fig. 1 (top) and Pl. 5, figs. 1, 1a).
- Fig. 3. Pinna of the last order in which the highly compressed specimen has split to reveal the synangia covering more or less the whole half-width of the pinnule lamina, as in the Saudi Arabian specimens of Pl. 4, fig. 1 and Pl. 5, fig. 2; $\times 5$; RGM 382 653.
- Figs. 4, 5. Latex replica coated with ammonium chloride (NH_4Cl) sublimate to enhance the relief for light photography. Specimen with long pinnules in which the synangia, which have particularly well preserved apices, do not quite extend to the midrib. Note their highly orderly arrangement. At these low magnifications it is difficult to see whether the spore-producing members are synangiate or composed of separate sporangia. Fig. 5, at arrow, shows strongly upturned synangial apices accentuated by oblique compression, indicating that they were not fused with the lamina. 4: $\times 3$; 5: $\times 5$; RGM 382 654.
- Figs. 6, 7. Specimen showing the individual synangia unusually clearly at low magnification. Although the synangia extend across the whole half-width of the pinnules, they are shorter than usual. In fig. 6 the rachis is at right, with fertile pinnules to the left. 6: $\times 4$; 7: $\times 10$; BM(NH) V. 60 794.

Plate 6



Asansolia differs from *Gemellitheca* in its short, four-locular synangia placed at the pinnule margin, occupying only $\frac{1}{5}$ to $\frac{2}{5}$ of the pinnule half-width, and in its monolet spores. It also differs in the relatively large ordinary cells of the abaxial epidermis, which have strongly sinuous anticlinal walls.

Elongate sporangia in pairs, extending across the half-width of pectopterid pinnules with dichotomous lateral veins, have been described under the name *Danaeites* by Göppert (1836, p. 380), who referred to 'Sporangia linearia, parallela, nervis frondis secundariis dichotomis insidentia. Indusii geminati vestigium'. In the description of the type species, *Danaeites asplenioides* Göppert, from the coal-measures of Charlottenbrunn in Silesia (Poland), Göppert mentioned that the sporangia are united horizontally to the lateral veins and that each sporangial unit is split into two by a sunken line which reminded him of an 'indusium geminatum'.

Göppert's illustrations unfortunately are too diagrammatic for adequate recognition of this fern and the type species has not been reported subsequently. The genus was further discussed by Stur (1883, pp. 146-150; 1885, pp. 221-222) with particular reference to *Danaeites saraeoptanus* Stur. He described the fructification of this species as composed of closely spaced, elongate, paired sporangia extending across the whole half-width of the pinnule lamina and corresponding in position to the lateral veins. This description and his diagrammatic representation of the *Danaeites* fructification would apparently fit *Gemellitheca* quite well. However, later interpretations of *Danaeites saraeoptanus* are quite different. Corsin (1951) described the fructifications as elongate sori composed of numerous small sporangia borne perpendicular to the lateral veins (*Orthotheca* Corsin). Laveine (1969) returned to the name *Danaeites* and reconstructed the sori as elongate, rather dense groupings of about ten pendant sporangia forming 'epaulets', which are attached over the lateral veins (for a reconstruction see Hill, Wagner & El-Khayal, 1985, fig. 6). Thus, although Göppert's original description suggests a *Gemellitheca* type of organisation, and may have been correct, that of *Danaeites* as typified by *D. saraeoptanus* is entirely different. It should be added that

Plate 7

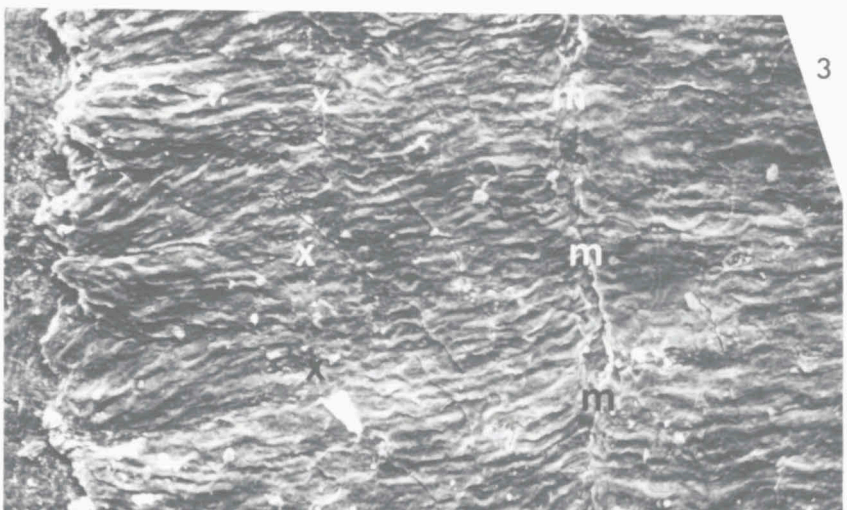
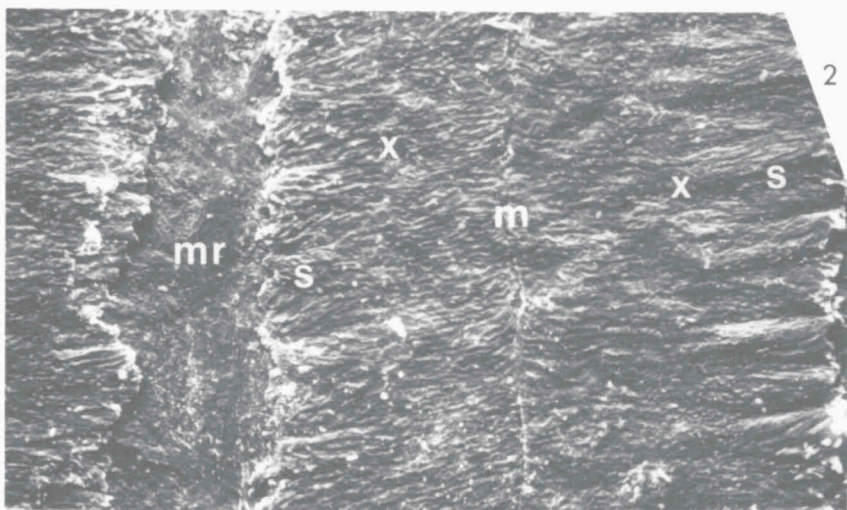
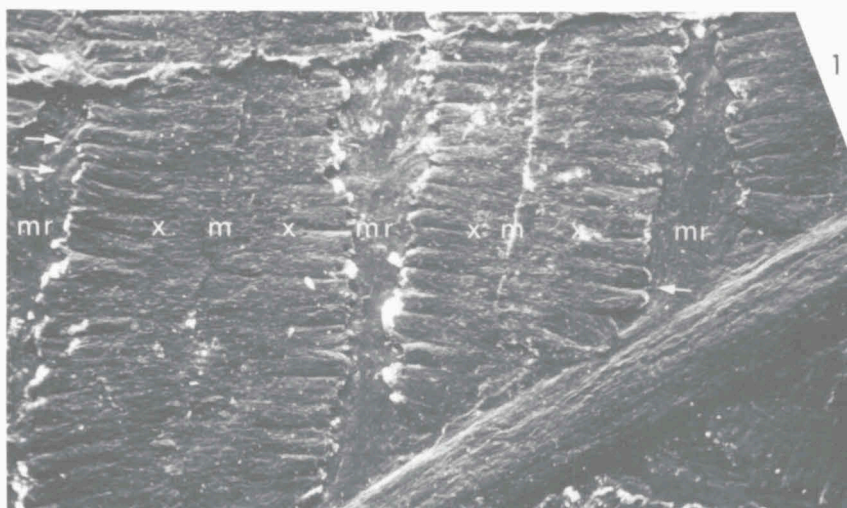
Gemellitheca saudica gen. et sp. nov.

Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

Latex replica of RGM 382 654 illustrated at low magnification in Pl. 6, figs. 4, 5; examined uncoated, using the Environmental Chamber facility of an ISI 60A scanning electron microscope. Bright spots represent adherent matrix, illustrating the usefulness of this backscatter facility for discriminating siliceous matter from organic material owing to crude detection of atomic number differences.

- Fig. 1. Pinna rachis with elongate cells and the basal regions of three pinnules (mr = midrib). Note the entire 'margin' (m) which, in fact, marks the angle of incurving of the marginal region of the lamina. The true margin is at 'x'. The expanded, incurved marginal region (between 'm' and 'x') overlies and thus obscures the basal regions and details of attachment of the synangia. The more completely preserved of the synangia (arrowed) show their typically bilocular (bisporangiate) construction. C. $\times 15$.
- Fig. 2. Enlargement of two neighbouring pinnules to show the junction at which the lamina is incurved (m) and the position of the true margin of the expanded lamina (x); midrib (mr), synangia (s). The synangia here are rather poorly preserved but the surface of their walls shows elongate, thick-walled cells. C. $\times 35$.
- Fig. 3. Further enlargement of the same two pinnules. Note the apparently elongate, thick-walled cells of the incurved marginal region, which lacks veins (region between 'm' and 'x'). At still higher magnifications the apparent cells are seen to be subdivided by relatively delicate cross-walls into more or less polygonal units or cells. C. $\times 75$.

Plate 7



this species is now generally regarded as the type since the original type specimen of *Danaeites asplenoides* cannot, apparently, be located and the species cannot be recognised adequately from his description.

Another Permian fern showing synangial clusters which extend in double rows across the pinnule is *Rajahia* Kon'no et al. (1970). Only very poorly preserved specimens might be confused with *Gemellitheca*.

The late Carboniferous to Permian fructification *Scoleopteris* Zenker emend. Millay (Millay, 1979; see also Stubblefield, 1984) consists of synangia borne on more or less pedicellate placenta, composed of three or more (often four to six) loculi. These are characteristically elongate, generally pointed (though not invariably so), and fused at the base. They are free at their tips, at least at maturity. Although compressed material attributable to *Scoleopteris* might show the appearance of transversely elongate synangia, the positioning, and number of loculi in each synangium are different in *Gemellitheca*.

The Permian fern *Pecopteris densifolia* (Göppert) Weiss has the same shape and size of pinnules as *Gemellitheca* and its terminals appear to be identical. The venation is also very similar, with a very slightly decurrent, rather thin midvein, and once-bifurcate laterals in an apparently regular pattern. The vein density is about 20 veins per cm, as measured from Göppert's 1865, Taf. XVII, Fig. 2. This species has been figured from the type area most recently by Reichel & Barthel (1964) and Barthel (1976). Their photographs show the lateral veins bifurcating at some distance from the midrib, whereas in *Gemellitheca saudica* the bifurcation takes place nearer the midrib. Barthel (1976, p. 45) has referred the fructification to *Scoleopteris* (see Millay, 1979, for discussion).

Jongmans and Gothan (1935, pp. 106-107, Taf. 32, Fig. 4-6) referred three pinna fragments without terminals to *P. densifolia*. These specimens, from the Lower Permian flora of Djambi, Sumatra, are too fragmentary to be identified reliably. This applies also to those identified as *P. densifolia* from the Upper Permian Hung Ho Formation in the Kaiping Coalfield of eastern China by Stockmans and Mathieu (1957, pl. XI, figs. 3, 3a). However a more complete pinna fragment from the Chao Ko Chwang Formation in the same coalfield shows a fairly close resemblance to *Gemellitheca saudica* (Stockmans & Mathieu, 1939, pl. XVI, figs. 2-3).

Plate 8

Gemellitheca saudica gen. et sp. nov.

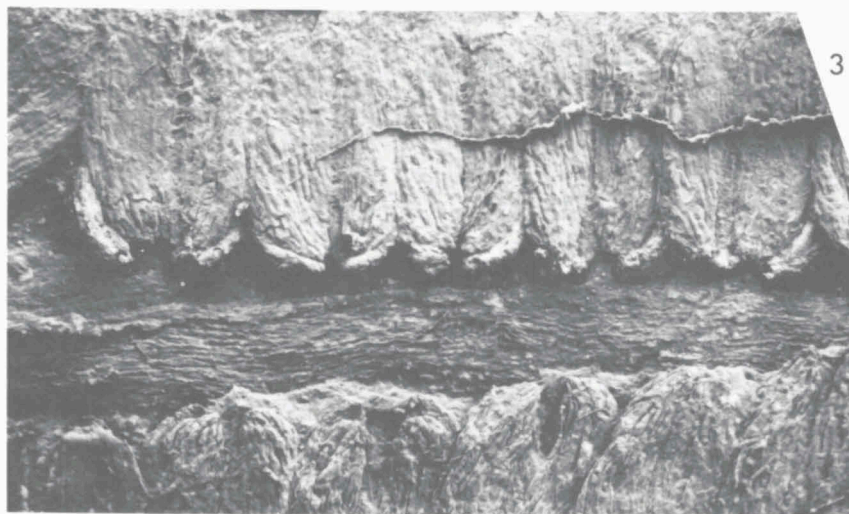
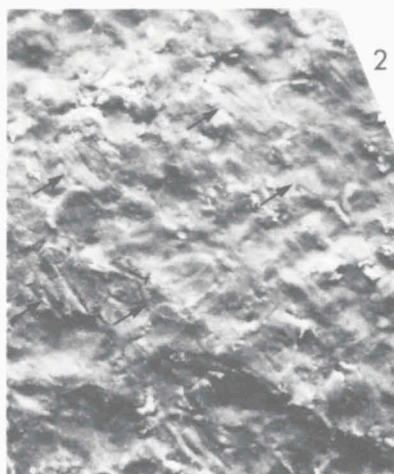
Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

SEM views of coated latex replicas of fertile specimens, using an ISI 60A microscope with Environmental Chamber.

Figs. 1, 2. Details of abaxial epidermis of RGM 382 643; 1: showing elongate cells over lateral vein at bottom right, with ill-defined ordinary epidermal cells and stomata in intervenal region (see also Fig. 3B); C. \times 350; 2: intervenal area showing the anomocytic stomata (arrowed) (see also Fig. 3A); C. \times 350.

Figs. 3, 4. Details of apical regions of selected synangia in specimen RGM 382 655. Individual locules show the files of elongate cells of their walls, the files curving towards the extreme tip where the cells become shorter. The loculi are fully separate only at their tips, and lower down a groove marks their identity. The synangia themselves may appear laterally adnate, though they are clearly seen to be separate where compressed obliquely as in the lower row of figs. 3 and 4. The lower row in each figure shows apparently bilocular synangia; the upper rows show at least some that are clearly trilocular or tetralocular. In general in *Gemellitheca* the synangia appear to be bilocular; c. \times 40.

Plate 8



The comparison with *Pecopteris wongii* Halle (1927, pls 21-22) suggested by Wagner (1962) for the Turkish material is no longer applicable. Unlike *Gemellitheca saudica*, *Pecopteris wongii* has twice-forked veins.

Palaeogeography — The foregoing comparison indicates that *Gemellitheca saudica* closely resembles certain ferns such as *Dizeugotheca* from the Permian of South America. This adds to the evidence provided by the occurrence of *Glossopteris* and *Botrychiopsis* at Hazro for a palaeobiogeographic link with Southern Hemisphere (Gondwana) floras (Archangelsky & Wagner, 1983). Together with the East Asian aspect of several other species, such as *Qasimia schyfsmae* and *Lobatannularia lingulata* (Halle) Kawasaki, at Unayzah, this underscores and extends the mixed composition of these Middle Eastern Permian floras, as has been emphasised by Lemoigne (1981). In consequence a reappraisal is needed of the floristic boundaries currently recognised for Permian floras worldwide. Continued assessment of Middle Eastern floras in the context of plate movements in the region is also necessary (El-Khayal & Wagner, 1985).

Remarks on figured specimens — Plates 1 and 2 show vegetative regions of the frond with their partially overlapping pinnae of the last order and the laterally touching, strap-shaped pinnules which have broadly rounded apices. Pl. 1, fig. 1 represents a somewhat lower region of a pinna of the penultimate order than Pl. 2, fig. 1 (which shows rather less elongate pinnules). The regularly once-bifurcate lateral veins which fork near the midrib are shown in Pl. 1, fig. 2, Pl. 2, fig. 2, Pl. 5, fig. 1, and Pl. 6, fig. 2. The small, rounded apical pinnule of a pinna of the last order is depicted on Pl. 2, fig. 3. This specimen has apparently denser venation than is characteristic, because the underlying synangia on the abaxial surface of the pinnules show after compression as faint markings on the adaxial surface.

Pl. 3 illustrates a fertile region of the frond at $\times 3$, showing its general similarity to the vegetative regions (illustrated at natural size on Pl. 1, fig. 1 and Pl. 2, fig. 1) except for the dense covering of elongate synangia over the whole half-width of the pinnules.

The pinna fragment enlarged in Pl. 4 shows fertile pinnules which have split on collecting at various levels, to illustrate the venation of the pinnule lamina and revealing also the synangia occurring beneath the lamina. The synangia run straight across the half-width of the pinnules, at right angles to the midrib and margin, and are seen most clearly in the lower part of the photograph. In the upper part of the photograph (seen particularly in the middle pinnule), the veins are at an angle of c. 60° to the midrib and only become more or less perpendicular to the pinnule margin after the bifurcation. This

Plate 9

Gemellitheca saudica gen. et sp. nov.

Unayzah plant bed, Unayzah, Qasim Province, Saudi Arabia.

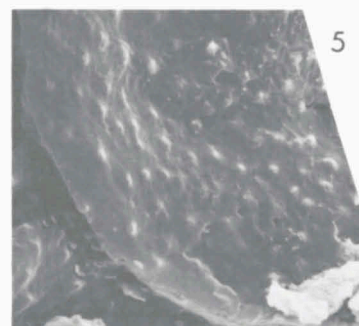
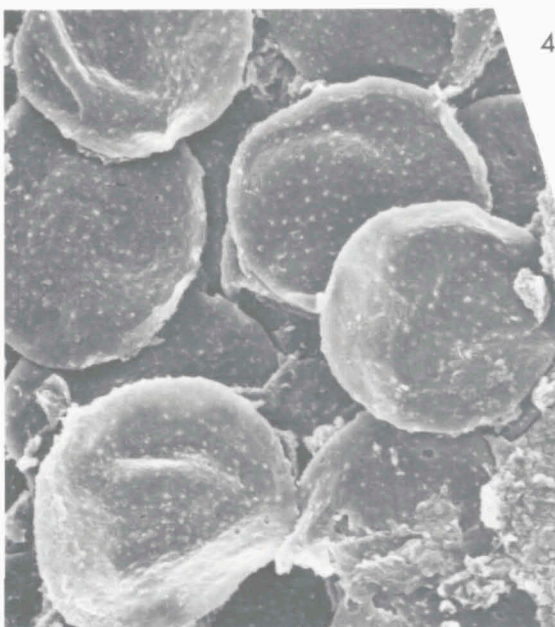
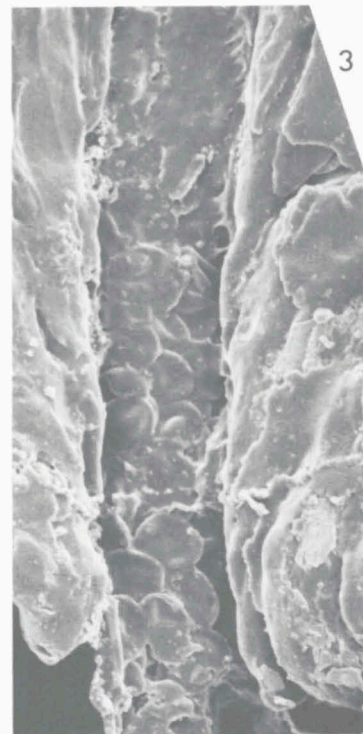
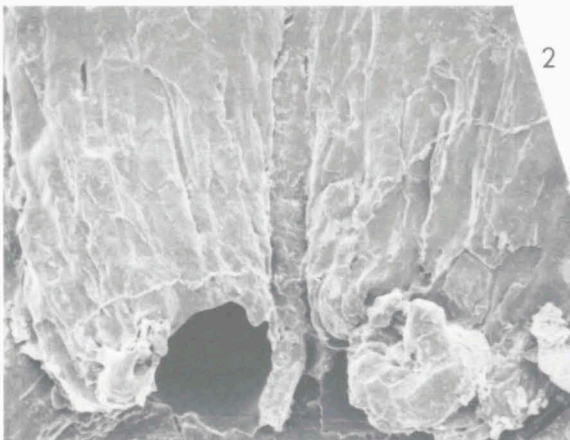
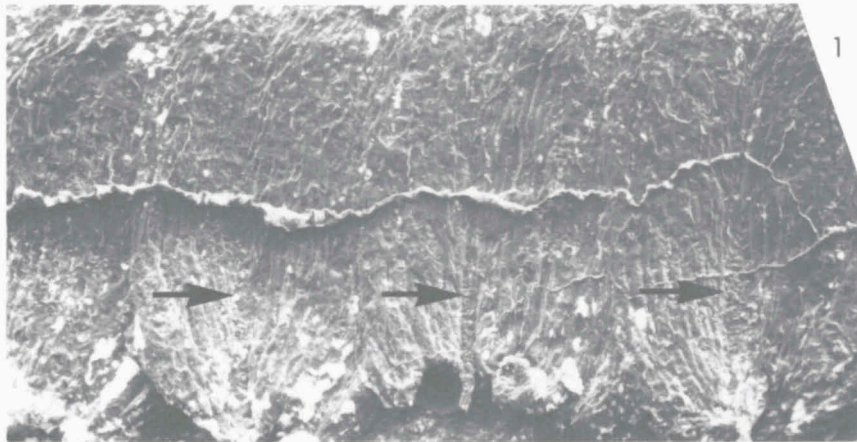
In situ spores as seen in replicas; fig. 1 uncoated, ISI 60A with Environmental Chamber; figs. 2-5, coated, Hitachi S 800 field emission scanning electron microscope; RGM 382 655. Figs. 1-3, latex replicas; figs. 4, 5, cellulose acetate replicas.

Fig. 1. Four neighbouring synangia. Three of them show spores in the split between the loculi (arrowed); $\times 65$.

Figs. 2, 3. Views of spores at progressively higher magnifications; 2: $\times 150$; 3: $\times 500$. The spores are rounded and their walls (replicated in latex) appear to be smooth and featureless, but the fact that they have been partly shed suggests that they were mature.

Figs. 4-5. Spores showing spiny granules on their walls when replicated in cellulose acetate; 4: $\times 2000$; 5: $\times 5000$.

Plate 9



partly different course of lateral veins vs sporangial units is shown more clearly by Pl. 5, figs. 1, 1a, which show the pinnule lamina partly broken away to uncover the underlying synangia. Pl. 5, fig. 2 shows the abaxial surface of pinnules with the imprints of the basal regions of the synangia towards the incurved margin and their free tips (preserved bodily as compressions) at the midrib.

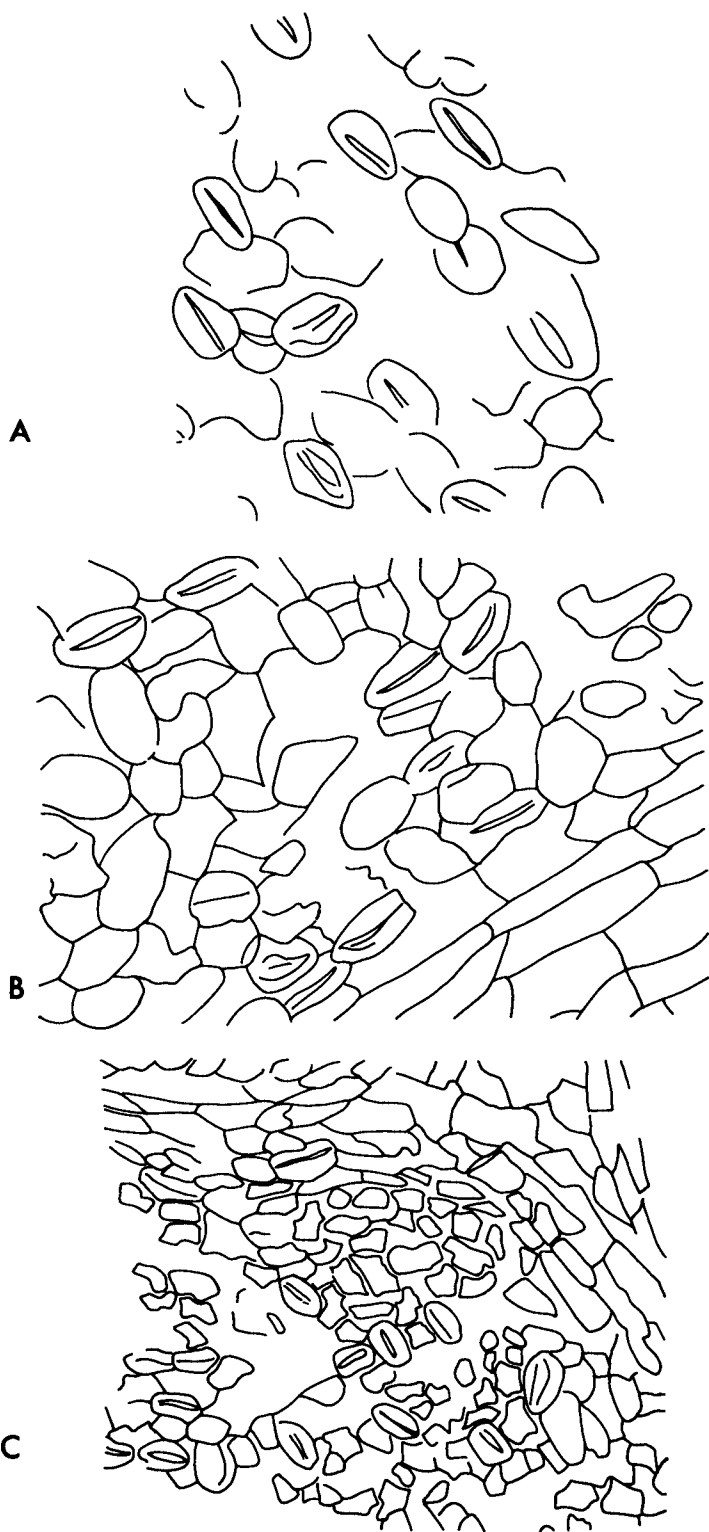
Pl. 6 shows the effect of different degrees of compression on the apparent length of the abaxially curved synangia as revealed after splitting of the rock matrix. Pl. 6, figs. 4, 5 are latex replicas of a highly compressed Arabian specimen, showing the whole length of the synangia and their curvature, which is accentuated where arrowed owing to oblique compression. All the other figures are of Hazro specimens, ranging from Pl. 6, fig. 3, which is as highly compressed as the Arabian specimens, to Pl. 6, figs. 1, 2 which are less compressed and therefore give the superficial appearance of short synangia. Pl. 6, figs. 6, 7, illustrate an unusual Hazro specimen in which the acroscopic half-width of each pinnule is strongly inrolled so as to clearly display (effectively by strongly oblique compression) the synangial apices.

Pl. 7 illustrates latex replicas of a Saudi specimen photographed with scanning electron microscopy, showing cellular details of the rachis and lamina. The incurved marginal region, between m and x, is clearly displayed. Details of well-preserved synangia are shown in Pl. 8, figs. 3, 4, and Pl. 9, fig. 1, indicating that some of the synangia (Pl. 8, figs. 3, 4, upper rows) may have more than two loculi. Pl. 8, figs. 1, 2, illustrate details of the abaxial epidermis of the lamina, with the irregularly scattered anomocytic stomata (see also Fig. 3). The in situ spores are shown in replicas at various magnifications in Pl. 9, illustrating their spiny ornamentation and the initial shedding into a cavity between the locules as in *Scoleopteris*.

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Fig. 3. Abaxial epidermis of *Gemellitheca saudica* pinnule, drawings on SEM photographs to show outlines of ordinary cells and the anomocytic stomata (RGM 382 643); A, B: drawings of photographs in Pl. 8, figs. 1, 2; c. $\times 250$; in B a lateral vein crosses the figure at bottom right. C: region of epidermis near fork of a lateral vein showing orientation of the stomata in parallel with the course of the vein, c. $\times 150$.



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