

Qasimia gen. nov., an early *Marattia*-like fern from the Permian of Saudi Arabia

Hill, C.R., R.H. Wagner and A.A. El-Khayal

Hill, C.R., R.H. Wagner & A.A. El-Khayal. *Qasimia* gen. nov., an early *Marattia*-like fern from the Permian of Saudi Arabia. — Scripta Geol., 79: 1-50, 6 figs., 19 pls, Leiden, April 1986.

The marattialean fern *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov. is described from the Late Permian plant bed at Unayzah in central Saudi Arabia. Although no organic matter is preserved, impregnation of the compressions by iron minerals at an early stage of diagenesis has partly mineralised the synangia and spores. The impressions in a fine-grained shale preserve epidermal cell outlines, including those of the stomata.

Qasimia resembles *Marattia* closely in its bivalved synangia and in its monolaesurate spores with a warty or spiny ornament. It differs in the rounded rather than pointed apices of the pinnules and the greater density of veins, particularly in the vegetative pinnules. Unlike *Marattia*, its synangia characteristically extend across the full half-width of the pinnules, their sporangial compartments are longer, and the cells of the dorsal walls of the compartments are mainly elongate rather than rounded. Venuli recurrentes occur in the fertile pinnules only (which show less than half the vein density of the vegetative pinnules). They are interpreted as vestigial vein branches that were surplus to the number needed to supply the synangia of the fertile pinnules. Such fibre bundles are common in Mesozoic *Marattia* but are absent from extant species. *Marattia anglica* (Thomas) Harris, one of the better known Mesozoic species, is compared both with *Qasimia* and with extant *Marattia*, and is shown to have a synangial structure like that of the extant species.

Similar ferns occur in the Permian of China, the Soviet Far East and Southeast Asia and attention is drawn to *Lophotheca panxianensis* Zhao, from the Permian of Guizhou, which may be a preservational state of *Qasimia*. A new combination, *Q. tobaensis* comb. nov., is proposed for material previously assigned to *Taeniopteris tobaensis* by Li, Yao & Deng, 1982. Many ferns from the East Asian Cathaysian Province have been wrongly determined as *Taeniopteris* and *Neuropteridium*.

Qasimia is the earliest known *Marattia*-like fern having taeniopteroid foliage, and is linked by Mesozoic species of *Marattia* to the extant ones. Its origin is discussed with reference to the Carboniferous pectopterid *Danaeites saraepontanus* Stur. Fusion of the separate sporangia of *D. saraepontanus* would produce bivalved synangia of the *Qasimia* type, and condensation of a pectopterid frond would produce taeniopteroid pinnules with rounded apices.

C.R. Hill, Department of Palaeontology (Palaeobotany Section), British Museum (Natural History), Cromwell Road, London SW7 5BD, England, U.K.; R.H. Wagner, Department of Geology, The University, Beaumont Building, Brookhill, Sheffield S3 7HF, England, U.K. (now at Jardín Botánico de Córdoba, Apartado 3048, Córdoba, Spain); A.A. El-Khayal, Department of Geology, King Saud University, P.O.Box 2455, Riyadh 11451, Kingdom of Saudi Arabia.

Introduction	2
Systematic description	3
<i>Qasimia</i> gen. nov.	3
<i>Qasimia schyfsmae</i> (Lemoigne) comb. nov. et emend.	12
Phylogeny	44
Conclusions	48
References	48

Introduction

There are few reports of Palaeozoic plants from the Arabian Peninsula. Hemer (1965) summarised the Carboniferous and Permian microfloras but the first reference to plant megafossils was in Lemoigne's (1978) discussion of the limits of the Gondwana floral province. He referred to four specimens of presumed Permian age collected from the Khuff Formation at Unayzah in central Saudi Arabia, some 350 km northwest of Riyadh. A brief general description of megafossil plants from Unayzah was given by El-Khayal, Chaloner and Hill (1980), who compared them with Euramerian floras and regarded their age as 'not greater than Westphalian' and 'not younger than early Permian'. Lemoigne (1981a, b) disagreed with this age determination and emphasised the Cathaysian aspect of the flora. He compared with the late Permian flora of Hazro in southeastern Anatolia (Wagner, 1962), and assumed a middle to late Permian age. Apart from plant impressions and compressions, he also recorded some fossil wood (*Dadoxylon* spp.) from a locality 100 km north of Unayzah (Lemoigne, 1981b).

In December 1980, R.H. Wagner and A.A. El-Khayal jointly visited Unayzah, recorded a stratigraphic section (El-Khayal & Wagner, 1985), and began a more detailed description of the plant remains. Over a thousand specimens were available already at the Geology Department of King Saud University in Riyadh, and much additional material resulted from the joint collecting.

Lemoigne's comparisons with the late Permian flora of the Hazro District in Turkey have been largely substantiated by our work, and the Cathaysian aspect of the Permian flora at Unayzah is also undeniable. Two of the pectopterid ferns described from Hazro also occur at Unayzah: *Pecopteris pirae* Wagner (which incorporates *Pecopteris tenuidermis* Wagner) and *Pecopteris* cf. *wongii* Halle pro parte (named *Dizeugotheca?* sp. in Archangelsky & Wagner, 1983). The Hazro flora contains a third fern-like plant, *Fascipteris hallei* (Kawasaki) Gu & Zhi (see Archangelsky & Wagner, 1983) which has been recorded from Unayzah by Lemoigne (1981b). One of the less common remains at Unayzah is a gigantopterid of an evolutionary grade below that of *Bicoempletopteris hallei* Asama, which also occurs at Hazro (compare Asama, 1976). The '*Annularia stellata* (Von Schlotheim) Wood' recorded by El-Khayal et al. in 1980, is determined as a form of *Lobatannularia* of earlier Permian age than the very late Permian *Lobatannularia heianensis* (Kodaira) Kawasaki from Hazro. The middle to late Permian age assigned to the Unayzah flora by Lemoigne (1981b) thus appears eminently reasonable (see also the remarks to this effect in Hill & El Khayal, 1983).

The preservation at Unayzah is somewhat unusual, since the plants occur as impressions (and originally as compressions, although no organic matter now remains) in lacustrine shales which have been impregnated by iron-bearing minerals. These minerals are presently the hydrated iron oxides limonite and haematite (D.T. Moore, pers. comm.). Mineralisation is restricted to the upper part of the shale bed where it is overlain by a coarse, permeable sandstone. The lower part of the bed occurs as a heavily weathered, friable, grey shale, whereas the upper part is more resistant to weathering as a result of the impregnation by iron oxides. The whole bed is full of drifted plant fragments in thin parallel layers. The plants are often of large size and include predominantly the strap-like leaves of *Cordaites* (which improve the fissility of the rock) and often rather large pinna fragments of peccopterid ferns. The mineralisation has facilitated recovery of large sized frond fragments. Although the disposition of the plant remains makes it clear that the assemblage is transported, the large size of the fragments and the thinly laminate structure of the bed indicate a low energy environment of deposition and probably also a rather short distance of transport.

The mineralisation must have happened at an early stage of diagenesis, since fern sporangia stand out in strong relief from the frond laminae on which they are borne, and the cells of their walls are preserved almost in three dimensions. This indicates only limited compaction (and organic decay) at the time of impregnation with the iron compounds.

Acknowledgements

We are grateful to King Saud University in Riyadh for defraying field and travel expenses, including one visit to Riyadh and Unayzah by R.H. Wagner and two visits to Sheffield University by A.A. El-Khayal. Mr B.L.H. Pigott (Sheffield) produced most of the photographs at low magnification, the remainder being the work of Mr C.H. Shute (BM(NH)) and A.A. El-Khayal. The SEM pictures in Pls 12-19 were all taken by C.R. Hill. Dr Zhao Xiuhu (Academia Sinica, Nanjing) is thanked for photographs and translation of the description of *Lophotheca*; Dr Zhou Zhiyan (Academia Sinica, Nanjing) kindly provided a translation of '*Danaeites mirabilis* Gu & Zhi, and Dr Zhou Zhiyi (Academia Sinica, Nanjing) provided further translations. Mrs H. Sabo (BM(NH)) is thanked for translating passages from Burago (1977), Miss J.M. Camus for helpful discussion and criticism, and Professor Li Xingxue (Academia Sinica, Nanjing) for helpful correspondence on Cathaysian plants. Professor Y. Lemoigne kindly reviewed the manuscript. We are also indebted to Prof. Lemoigne for permission to refigure the holotype of *Qasimia schyfsmae*.

Systematic description

MARATTIALES

Qasimia gen. nov.

Type species — *Qasimia schyfsmae* (Lemoigne) comb. nov.

Derivatio nominis — Qasim Province in the Kingdom of Saudi Arabia.

Diagnosis — Fronds at least bipinnate. Pinnules mainly taeniopteroid but some small and neuropteroid, extremely variable in size, particularly in length; bases typically cordate but very narrowly confluent in terminal parts of pinnae with small pinnules; apices rounded, lamina vaulted. Midrib strongly marked, giving rise to lateral veins that initially curve away from the midrib at an acute angle but almost immediately adopt a course perpendicular to subperpendicular to the pinnule margin, particularly in the longer pinnules (which are the most common); lateral veins of smaller pinnules curve more gradually. In vegetative pinnules the lateral veins characteristically fork twice (occasionally additional vein dichotomies occur); the first bifurcation occurring almost invariably near the midrib. Vein density quite high (40-50 veins per cm at the pinnule margin). No venuli recurrentes in vegetative pinnules.

Fertile pinnules identical in size and shape to vegetative ones, but bearing closely-spaced pendant synangia on the undersurface; tilted sideways on or before their final compression, the synangia typically appear 'louvred'. Lateral veins characteristically branched only once near the midrib, with a relatively low vein density (less than half that of vegetative pinnules) and venuli recurrentes (where visible) occurring between and parallel to the veins. Bivalved synangia attached below lateral vein branches, one per branch, occupying characteristically the entire half-width of pinnule lamina. Each valve consists of a large number of laterally joined spore-bearing (sporangial compartments which are compressed in such a way that the shared walls (septa) stand out as ridges. Details of dehiscence slit unknown. Sporangial compartments long in relation to their width and cells of their dorsal wall also elongate except at the apex. Spores monolaeurate, warty or spiny.

General comparisons — Taeniopteroid species of *Marattia* are very similar but their pinnules have pointed apices; also the sporangial compartments and the cells of their dorsal walls are shorter, and the synangia do not generally occupy the entire half-width of lamina. The lateral veins of *Marattia* are less often forked and less densely spaced than those of vegetative pinnules of *Qasimia*.

The next most similar genus is *Lophotheca* Zhao. Although possibly congeneric with *Qasimia* (discussion on p.), the type specimens (which are the only presently known material) are fertile pinnules which lack the lamina. The elements for a full comparison are therefore lacking.

The name *Neuropteridium* has been applied to East Asian Permian vegetative remains similar to *Qasimia*. This usage, which goes back to Halle (1927), does not bear scrutiny if compared with the original diagnosis of *Neuropteridium* by Schimper (1869) and his illustrations of the European Triassic fronds on which the genus is based (discussion on p. 34). The large pinnules of typical *Neuropteridium* have broad bases, are partly fused to the rachis, and possess a decurrent midvein with oblique lateral veins. This gives this foliage a rather different aspect to the taeniopteroid pinnules with cordate bases and the perpendicular to subperpendicular veins that characterise *Qasimia*.

Gigantotheca Li & Yao, the reputed microsporangiate frond of *Gigantonoclea* (Li & Yao, 1983), shows an apparently similar synangial structure to *Qasimia* but is very different vegetatively. *Gigantotheca* synangia occur in the central region of coarsely denticulate pinna segments. These display a taeniopteroid vein pattern in direct association with the fructifications, but have reticulate veins in the surrounding lamina.

More remote comparisons involve the vegetative remains described as *Macralethopteris* (Jongmans & Gothan, 1935) and *Compsopteris* (Zalesky, 1934). The former shows large pinnules with constricted bases in the lower parts of the pinnae and confluent ones in the upper parts. Their venation differs from that of vegetative pinnules of

Plate 1



Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. The elongate (taeniopteroid) kind of vegetative pinnules attached to a wide rachis; note the cordate bases and the rounded apex; $\times 1$; RGM 382 433.

Fig. 2. The basal regions of elongate vegetative pinnules, showing their cordate bases; $\times 1$; RGM 382 450.

Fig. 3. Fertile pinna fragment showing the more elongate kind of pinnules; the apparent venation represents the basal margins of the synangia; $\times 1$; RGM 382 434.

Qasimia in that the lateral veins are described as only once bifurcate near the midvein. *Compsopteris* Zalesky refers to *Protoblechnum* sensu Halle (non Lesquereux) which shows quite variable pinnule attachments (including markedly decurrent forms) and oblique lateral veins; both of these characters set this genus clearly apart from *Qasimia*.

The generic identity of Qasimia vs Marattia and Marattiopsis — *Marattia* Swartz is a genus of primitive ferns, several species of which reach huge frond sizes up to 4 m long. It survives today in pantropical rain forests. Fossils with taeniopteroid foliage referable to the extant genus have long been known from the Mesozoic worldwide and have been discussed by many authors, e.g. Harris, 1961; Kilpper, 1964; van Konijnenburg-van Cittert, 1975. They have often, however, been referred to the fossil genus *Marattiopsis* Schimper, 1874. The main difference from extant *Marattia* discussed in the literature is the frequently observed occurrence of venuli recurrentes, i.e. of fibrous strands which run between and parallel to the lateral veins. These strands are lacking from all extant species. However, as Harris (1961) has pointed out, the closely related genus *Angiopteris* Hoffmann nomen cons. possesses many species with such strands and some that lack them. He therefore concluded that the presence or absence of venuli recurrentes is not a character of generic significance in Marattiales. We agree.

The other difference that might be used to distinguish *Marattiopsis* (and therefore justify continued use of this name, apart from spurious convenience as a purely fossil genus) is one that has been discussed rarely in the literature but which has caused some difficulty in delimiting Mesozoic species (see van Konijnenburg-van Cittert, 1975, vs Kilpper, 1964). This refers to the large variation in length of the synangia in relation to the half-width of pinnule lamina, i.e. relative to the distance between midrib and margin.*) The fronds of extant *Marattia* are divisible fairly neatly into two groups according to whether the foliage is taeniopteroid or sphenopteroid. In sphenopteroid species such as *Marattia alata* J. Smith, the synangium typically covers most of the half-width of the pinnules. It may also do so in certain species with abnormally narrow taeniopteroid pinnules, e.g. in *Marattia wernerii* Rosenstock, as in T.G. Walker, T 8482 (sheet 2 of 2), New Guinea, of the B.M.(N.H.) Herbarium Collection (BM). However,

*) Harris (1931) used a different ratio, that of the length of one synangium relative to the whole width of the pinnule. Although this has been followed by most authors, we believe the ratio in terms of 'half-width' of the pinnule to be more useful. Firstly, the synangia occur twice over the whole width, which makes Harris' ratio difficult to apply in practice, particularly when examining fragmentary specimens; secondly and more importantly, the use of half-width excludes the midrib whereas Harris' method includes it. Since the midrib varies considerably in width, this reduces the botanical significance of the ratio.

In relation to other genera of Marattiales it is botanically more important to appreciate that the synangia may extend over the full half-width of the pinnule lamina, as in *Danaeopsis* Heer, a condition that for *Marattia anglica* is not at all clear from Harris' (1961) percentages of 'Above 40%..., 41% and 44%'. Harris' method is a good example of Operationalism in biology at the expense of clear understanding (see Hull, 1968). Use of half-width is no less operational but is botanically more relevant.

Plate 2

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. The elongate kind of vegetative pinnules, enlarged $\times 3$ to show the taeniopteroid venation; right hand side of the specimen in Pl. 1, fig. 1, which shows the pinnule bases only; RGM 382 433.

Fig. 2. Pinna of the last order with smaller kind of (neuropteroid) pinnules and showing the small, rounded, apical pinnule; $\times 1$.



Plate 2

in all extant taeniopteroid species with a more expanded lamina, and which thus resemble most Mesozoic species, the synangia rarely extend even as far as half of the half-width, and are usually much shorter. In the fossils the synangia are often equally short, but in a few specimens of *Marattia anglica* (Thomas) Harris they extend over the entire half-width of the lamina (Pl. 19, fig. 1). In the Mesozoic material the synangia are also frequently longer in absolute terms than in any extant species, by up to three or more times (Pl. 19, figs. 1-5).

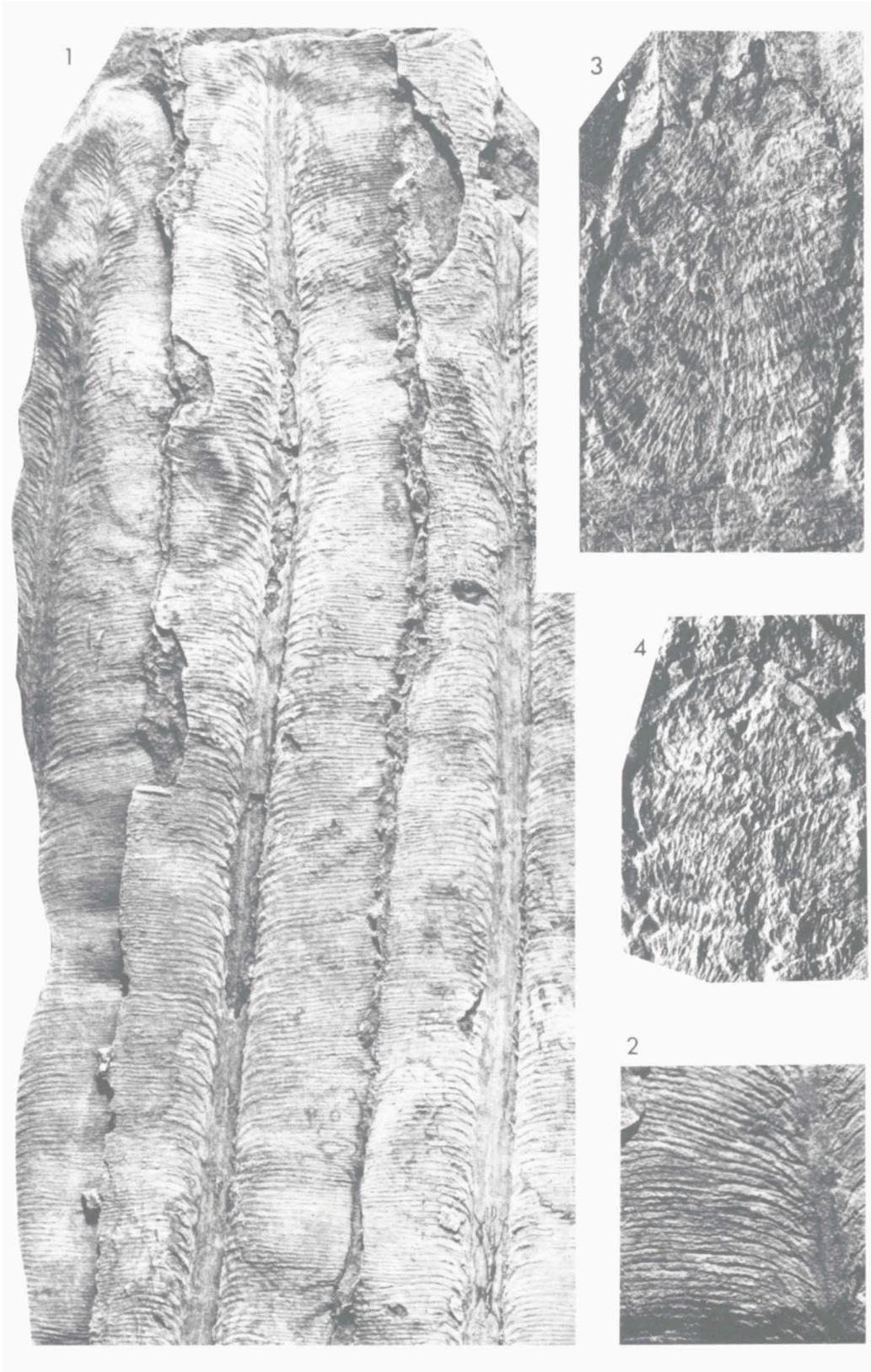
Thus the Mesozoic forms extend the range of variation of this character as typically observed in the living taeniopteroid species. The scope of the generic diagnosis of *Marattia* consequently requires some revision. Alternatively it might also be considered a basis for reviving *Marattiopsis*, but this view is rejected for a number of reasons. Firstly, the type illustrations of *Marattiopsis* (Schimper, 1869, pl. 38, figs. 1-6: as suggested by Andrews, 1970, p. 126) are of a species that does not extend the range of form as found in extant species. If the meaning of *Marattiopsis* were expanded, the various species would grade continuously into typical *Marattia*, requiring a purely arbitrary cutoff. Three facts emphasise this. Firstly, even the longest synangia of Mesozoic species are within the compass of extant *Marattia* as a whole in terms of the extent of half-width covered by them. Secondly, the only absolute difference would be quantitative, i.e. the synangia of some species of *Marattiopsis* are longer than those found in any of the extant species of *Marattia*. Thirdly, and most significantly, those specimens of *Marattia anglica* which possess extremely long synangia merely represent an extreme of variation and are not entirely characteristic of this species. (Even so, the typical synangia of *Marattia anglica* are longer than those of extant species.) It thus appears that Harris (1961) was right in regarding *Marattiopsis* as a redundant genus.

Despite the slight widening of the concept of *Marattia* by incorporating the Mesozoic species, it seems that the Permian material should definitely be assigned to a different genus. The main difference is in the shape of the pinnules, which have rounded apices in *Qasimia*, whereas they taper in *Marattia* (this is based on the type species, *Qasimia schyfsmae*, and excludes the vegetative pinnules ascribed to *Marattiopsis orientalis* by Burago (1977) discussed below). Furthermore, the dorsal wall of the synangium in *Qasimia* differs in structure from that of *Marattia*. Additionally, the lateral veins of the vegetative pinnules of *Qasimia* are more profusely branched than those of *Marattia*, with a vein density of 40-50 veins per cm in the type species. This is much higher than commonly found in *Marattia*, 8-10 per cm, though occasionally values of 14-20 are recorded (e.g. L. Humblot, 130, Comoro Islands, BM). Humblot's specimen shows exceptionally dense venation for an extant *Marattia*, though nearly all the lateral veins are bifurcate only, with about half the number of veins forking near the midrib whilst the other half fork further away. Only a very small proportion fork twice, as occurs typically in *Qasimia*. These branch in a similar manner to *Qasimia*, with a basal fork followed by another nearer to the pinnule margin. None were seen that branched more than twice,

Plate 3

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

- Fig. 1. Vegetative pinnules enlarged $\times 3$ to show the repeatedly forked lateral veins; RGM 382 440.
 Fig. 2. Near-apical region of a pinnule of specimen in Pl.1, fig. 1 and Pl. 2, fig. 1, enlarged $\times 6$ to show the repeated vein bifurcations; RGM 382 433.
 Figs. 3, 4. Abaxial surface of the smaller (neuropteroid) kind of fertile pinnules, showing the sideways compressed and largely overlapping ('louvred') synangia which extend across the entire half-width of the pinnules; $\times 6$. The pinnule insertion is shown in fig. 3; both pinnules show the typically rounded apex.



whereas this occasionally occurs in *Qasimia*. Mesozoic species of *Marattia* show a similar range to the living ones, c. 10-20 veins per cm, for instance *Marattia anglica* has 10-12 per cm (misprinted as per mm in Harris, 1961). The only exception appears to be *Marattia curvinervis* Lorch, from the Jurassic of Israel (Lorch, 1967). In this species the veins have been described as occurring at 26-34 per cm, though with no suggestion that they forked more than once. Lorch's holotype (V. 42 679), has been re-examined. Its venation is too poorly preserved to allow accurate observation of the number of vein bifurcations. However, we agree that there is an appearance of denser than usual venation. On the other hand, there is a hint from this specimen and also from the figures published by Lorch (1967) that the greater concentration of veins may partly result from including venuli recurrentes. Better material is required to solve this question. The synangia of *Marattia curvinervis* are well preserved and extend across a little less than half the half-width of the pinnule lamina. There is some comparison with *Qasimia* in that the veins of *Marattia curvinervis* are more broadly arched than is commonly the case. Interestingly, there is also a hint that the pinnule apices were rounded rather than pointed, but no actual apices have been seen. Although *Marattia curvinervis* is much younger than *Qasimia schyfsmae*, its Middle Eastern location is geographically close.

Another difference of *Qasimia* from *Marattia* is its greater length of the spore-bearing compartments; they are 1.5 times longer than those of *Marattia*, both living and fossil.

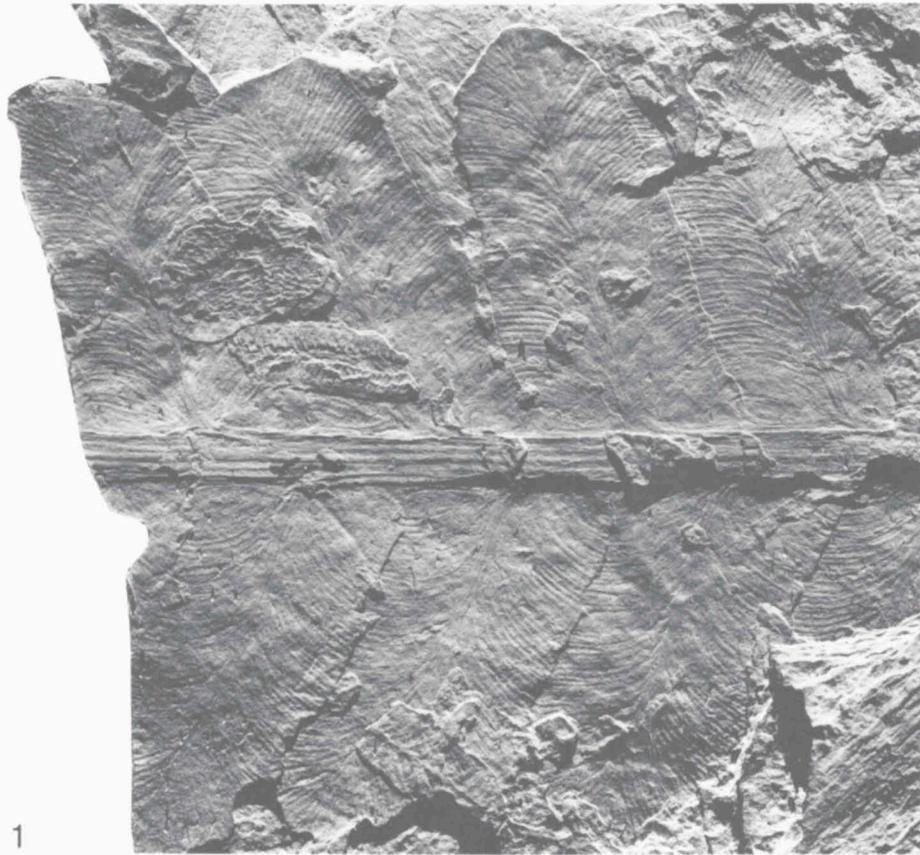
Clear perception that *Marattia*-like ferns occur in the Permian is only recent, although comparable material had been figured under various names for several decades. Burago (1977) was the first to recognise such material, *Marattiopsis orientalis* Burago. It seems likely that the fertile remains of *M. orientalis* (and possibly also some of the associated vegetative specimens described under the same name) should be referred to *Qasimia*. Burago discussed the possibility that a new genus might be involved. Subsequently, the present material from Unayzah was tentatively identified as *Marattiopsis* sp. by El-Khayal et al. (1980), an identification provisionally accepted by Lemoigne, 1981b). It has been explained above why the continued use of the name *Marattiopsis* is now regarded as inappropriate. The position was complicated to some extent by Lemoigne's separate identification of the vegetative remains as *Neuropteridium schyfsmae* Lemoigne, although he did suggest that the *Marattiopsis* specimens might represent fertile remains of the same species.

Plate 4

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

- Fig. 1. Holotype, $\times 3$ (figured as *Neuropteridium schyfsmae* by Lemoigne, 1981b, pl. 3, fig. 8); Laboratoire de Paléobotanique, Univ. Lyon No. Ar/U.5. Shorter neuropteroid kind of pinnules with curved lateral veins. The confluent pinnule bases are more apparent than real.
- Fig. 2. Smaller (shorter), neuropteroid kind of pinnules with broadly rounded apices and curved lateral veins; $\times 2$; RGM 382 613.
- Fig. 3. Basal region of more elongate pinnule, showing the attachment of the midrib and cordate pinnule base; $\times 6$; RGM 382 450.

Plate 4



Qasimia schyfsmae (Lemoigne) comb. nov. et emend.
Pls 1-10; 11, fig. 3; 12-15; 17; 18, figs. 3-4; Figs. 1-5.

- ? 1932 *Gigantopteris antiqua* Kawasaki & Konno, pp. 34-36, pl. C, figs. 2-3.
? 1932 *Gigantopteris* sp. cf. *G. antiqua* Kawasaki & Konno, pp. 36-37, pl. CIV, figs. 18, 18a.
1980 cf. *Marattiopsis* sp. El-Khayal, Chaloner & Hill, pp. 33, 34, figs. d-e.
cf. 1980 *Taeniopteris crassinervis* Mo, in Zhao et al., p. 84, pl. XVIII, figs. 6-7.
1981b *Neuropteridium schyfsmae* Lemoigne, pp. 618-619, textfig. 4, pl. 3, fig. 8, pl. 4, fig. 1.
1981b ?*Marattiopsis* sp. Lemoigne, p. 620, pl. 5, figs. 1-3.

Diagnosis — Fronds large, at least bipinnate. Pinnules showing considerable size variation, particularly in length (11-110 mm × 4-15 mm); bases mainly cordate, margins parallel, apex broadly rounded. Midrib strong, straight, giving rise to densely arranged lateral veins (40-50 per cm), perpendicular or subperpendicular to the pinnule margin. Lateral veins of vegetative pinnules characteristically bifurcating twice, once at the midrib and subsequently at variable distances from the pinnule margin: occasionally with a third bifurcation. Fructification composed of bivalved synangia formed from fully joined, relatively large sporangia; synangia pendant from the abaxial surface of fertile pinnules and placed lengthwise beneath lateral vein branches issued by a single bifurcation near the midrib. Vein density of fertile pinnules less than half that of vegetative ones, 12-14 per cm at the pinnule margin; venuli recurrentes poorly visible between lateral veins. Synangia occupying the whole, or almost the whole half-width of the pinnule lamina, characteristically 'louvred' after sedimentation and compression. Sporangial compartments long, cells of their dorsal walls mostly elongate. Spores monolaesurate, exine ornamentation warty or spiny.

Holotype — Lemoigne, 1981b, pl. 3, fig. 8 (shown enlarged in Pl. 4, fig. 1), from the plant bed at Unayzah, Qasim Province, Saudi Arabia. Repository: Lab. Paléobot. Univ. Lyon, Specimen No Ar/U.5. Age: probably early Late Permian.

Topotypes (which are essential to the emended diagnosis) — All specimens figured in the present paper. Repository of figured topotypes: Rijksmuseum van Geologie en Mineralogie, Leiden (RGM 382 433-382 450). Additional topotypes stored in the Geology Department, King Saud University, Riyadh, and in the Department of Palaeontology, British Museum (Natural History), V. 62 120 62 137.

Description — Fronds large, at least bipinnate, with pinnae of the last order overlapping. Presumed terminals abruptly tapering, with a small, rounded, poorly individualised apical pinnule. Rachises up to 10 mm wide, flat, with faint, irregular, longitudinal striations. Pinnules closely spaced, inserted at 45° to 75° (depending on position in the frond), mainly cordate at base, with parallel margins and broadly rounded apices; entire (there are no lobed frond fragments amongst the numerous specimens collected). Pinnule size, particularly their length, extremely variable, depending probably on the position in what appears to have been a large frond. Taeniopteroid pinnules in the lower

Plate 5

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Fertile pinna in Pl. 1, fig. 3 enlarged × 3, showing the lateral veins below which the sideways compressed synangia are attached; venuli recurrentes are faintly visible between some of the vein pairs; RGM 382 434.



Plate 5

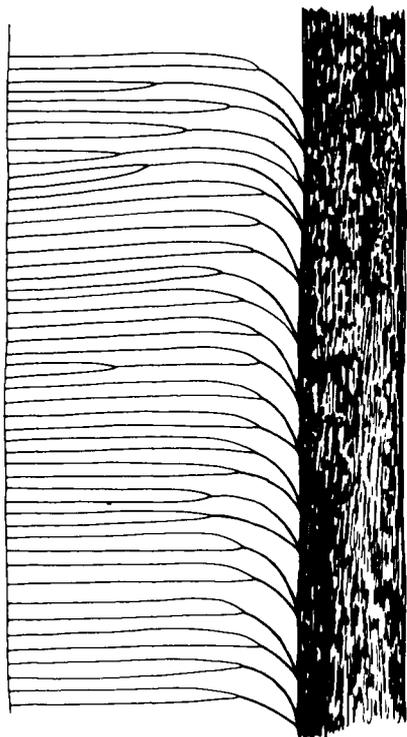


Fig. 1. *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov. Venation diagram ($\times 4$) of one of the more elongate, taeniopteroid pinnules (based on the specimen figured in Pl. 10, fig. 4); RGM 382 440.

part of the frond are up to at least 110 mm \times 12-15 mm, whilst the smaller (neuropteroid) pinnules (which correspond, most probably, to the upper part of the frond) are typically 11 mm \times 6 mm. Pinnule bases remaining cordate regardless of size, with the exception of the near-terminal neuropteroid ones which are partially fused to the broadly rounded apical pinnule. Apices broadly rounded in most sizes of pinnules, but some tapering of the apical part occurs in the longer ones. Pinnule lamina vaulted.

Midrib very strongly marked in the more elongate pinnules, particularly on their undersurface; straight even in the smaller pinnules. Characteristically it persists almost to the very apex. Lateral veins arching at source but turning almost immediately to a course perpendicular or subperpendicular to the pinnule margin. They dichotomise once near the midrib, then again a short distance from the midrib and sometimes once again nearer the pinnule margin. The effect of two successive vein bifurcations quite near the midrib is to produce a regular, parallel venation pattern over most of the half-width of the pinnules. Lateral veins often most strongly marked near the midrib (i.e. before the second bifurcation). Vein density high and fairly constant, c. 40-50 veins per cm at the pinnule margin (Figs. 1, 2).

Fertile pinnules the same size and shape as the vegetative ones, lamina unmodified; the only difference in venation is that the lateral veins are only once bifurcate and hence are less densely spaced than those of the vegetative pinnules.

Synangia pendant from the abaxial surface of the lamina, each located below and in the same orientation as single branches of the lateral veins. They are closely spaced and largely overlap owing to presumed sideways tilting at or before deposition, thus producing the characteristic 'louvred' aspect. Synangia bivalved, composed of two long strips of laterally joined, elongate, fairly large sporangial loculi 1.5-2.0 mm long; the

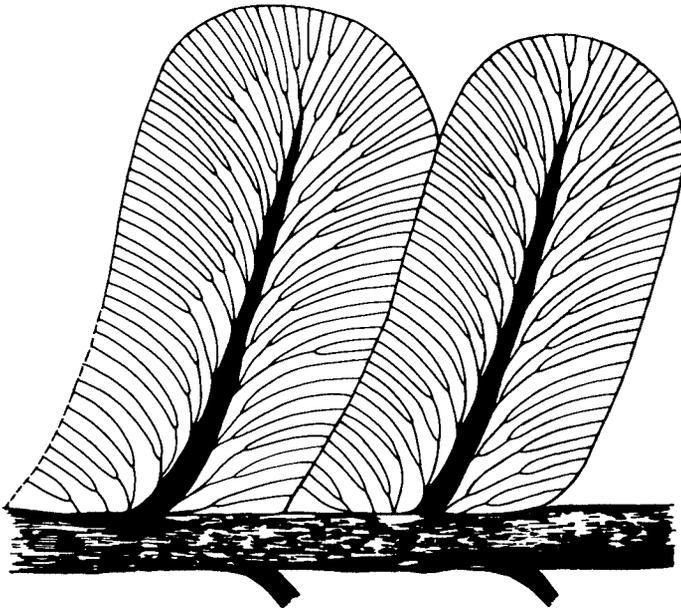


Fig. 2. *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov. Venation diagram ($\times 4$) of one of the shorter, more neuropteroid pinnules (based on the specimen figured in Pl. 10, fig. 5).

great length of the sporangial loculi contributes to the large overlap of the louvred synangia, which exceeds that seen in Mesozoic *Marattia*. Synangia extending characteristically across the entire half-width of fertile pinnules, but in rare cases (Pl. 10, fig. 1) the extreme margin and region bordering the midrib not covered by synangia. The number of loculi varies with the half-width of pinnules, with up to 40 in each valve of the longest synangia (Pl. 9, fig. 3). The length of the loculi diminishes towards both ends of the synangium, which are rounded. The bivalved structure of the synangium, though most clearly apparent in the few synangia that have been compressed in a spread-out condition (Pl. 8; Pl. 10, figs. 3, 3a; Pl. 12, fig. 2), is also visible with the SEM in specimens compressed sideways (Pl. 12, fig. 1). The individual loculi (sporangial compartments) are separated by septa which stand out as ridges as a result of compression and are composed of very elongate cells. Elongate cells are also visible over most of the dorsal walls of the loculi, becoming somewhat shorter near the base; at the apex (free margin of the valve) they become very short to isodiametric (Pls. 13; 14; 15, figs. 1, 2). Files of cells towards apex increasingly diverging away from mid-line of the locule, arching towards neighbouring locules on either side (Pls. 13; 14).

Synangial locules (sporangial compartments) with large number of spores; spores monolaeurate, cast of exine punctate, cast of possible 'perine' also punctate (Pl. 15, figs. 3-6); exine and ?perine presumably warty or spiny in life.

Lower epidermis of vegetative pinnules (Pl. 17, figs. 1-3; Figs. 3, 4) displays elongate cell outlines over lateral veins, without stomata. Broad strips between veins crowded with oval stomata oriented more or less in the same direction as the veins; guard cells of stomatal apparatus sometimes surrounded by a narrow ring of cells likely to be elongate subsidiary cells but with scarcely marked end walls. Their general appearance is

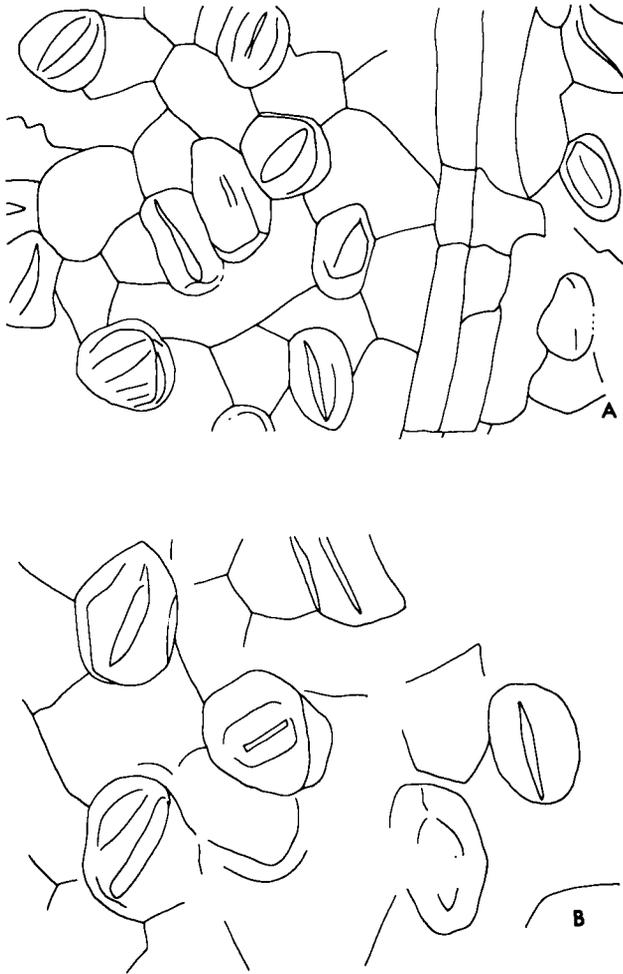


Fig. 3. *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov. Tracing of SEM photographs showing apparently cyclocytic and anomocytic stomata on imprints of the abaxial epidermis; A: $\times 350$ (same as in Pl. 17, fig. 1); B: $\times 525$ (same as figured in Pl. 17, fig. 2).

that of a monocyclic, cyclocytic arrangement as occurs in living *Marattia* (Pl. 18, figs. 1, 2), though may be polocytic. The ordinary epidermal cells are isodiametric polygonal to somewhat elongate and pear-shaped, characteristically twice as long as broad. The undersurface of fertile pinnules shows a confused pattern of cell outlines representing more than one cell layer, probably hypodermal (Pl. 18, figs. 3, 4).

Material — *Qasimia schyfsmae* is known from over a hundred fragments. Some of these are quite large, consisting of up to three parallel pinnae of the last order which clearly constitute part of a pinna of the penultimate order (Pl. 6, fig. 1). One of these fragments measures 25 cm across the width of three parallel pinnae. In view of the relatively small variation in pinnule size within this fragment (and others like it), and taking into account the considerable size variation of pinnules in the total collection from the Unayzah plant bed, it is clear that the frond must have been quite large, well over one metre long and probably even longer.

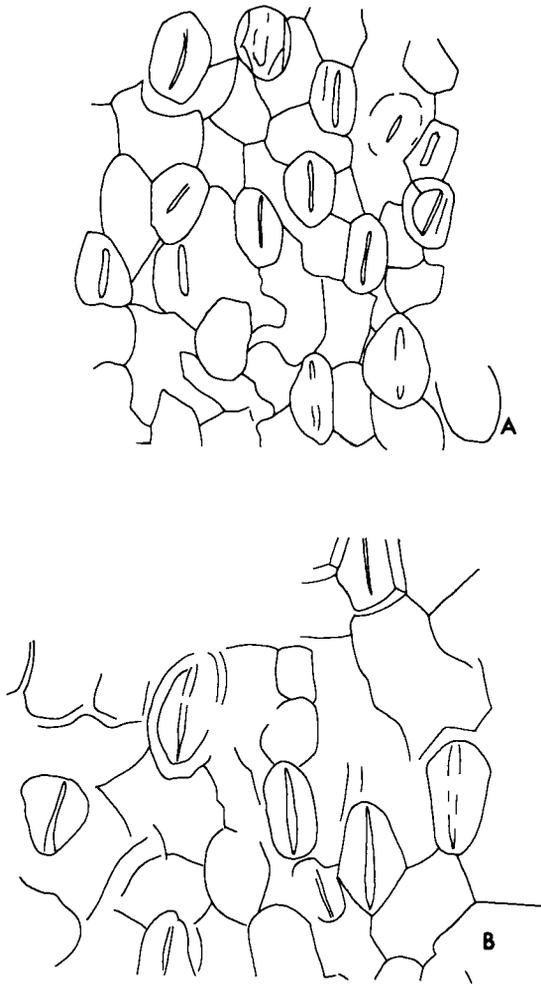


Fig. 4. *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov. Tracing of SEM photographs of abaxial epidermis; A: mainly anomocytic stomata, $\times 300$; B: a mixture of anomocytic and cyclocytic stomata, $\times 375$.

Notes on the figured specimens — Plate 1, figs. 1, 2, Pl. 2, fig. 1 and Pl. 3, Fig. 1, all show the more elongate kind of vegetative pinnule which predominates in the assemblages at Unayzah. These are markedly taeniopteroid. Their rounded apices show clearly in the specimens of Pl. 1, fig. 1; Pl. 2, fig. 1; and Pl. 3. The cordate bases are evident in Pl. 1, figs. 1-2, and in Pl. 4, fig. 3 (which is a partial enlargement of Pl. 1, fig. 2). Pl. 1, fig. 3 shows the abaxial surface of a fertile monopinnate element comparable in size to the vegetative specimen of Pl. 1, fig. 1. The thinner rachis suggests that this pinna occupied a more distal position in the frond. The broad midrib is apparent on both the vegetative and fertile pinnae (figs. 1 and 3 of Pl. 1).

The detail of the venation of the elongate vegetative pinnules is displayed by Pl. 2, fig. 1; Pl. 3, figs. 1-2; Pl. 9, fig. 1; and Pl. 10, figs. 4-5. The enlargement ($\times 6$) in Pl. 3, fig. 2 shows the repeated vein bifurcations. The general pattern of the lateral veins comes out most clearly in Pl. 3, figs. 1-2, and Pl. 10, figs. 4-5. These illustrations show that the lateral veins arise rather steeply from the midrib and curve sharply to a position perpendicular to

the pinnule margin over most of the width of the pinnules (see also Fig. 1). This makes these elongate pinnules look very taeniopteroid. Pl. 3, fig. 2 represents the near-apical part of an elongate pinnule.

The smaller (approximately neuropteroid) pinnules and the apical parts of larger, more elongate ones, show a slightly different vein pattern, i.e. the lateral veins are more broadly arched and are not as immediately perpendicular to the pinnule margins (Pl. 4, fig. 1; Pl. 10, fig. 5; Pl. 11, fig. 3; Fig. 2). The apical pinnule of a monopinnate frond fragment showing the smaller (neuropteroid) kind of pinnules is displayed in Pl. 11, fig. 3. Although the photograph does not depict the complete outline of the apical pinnule, it is clear that it represents a short, partially fused terminal with the same rounded apex and lateral veins that characterise the adjacent pinnules. This pinna is depicted at natural size in Pl. 2, fig. 2. A comparison with Pl. 1, fig. 1, displaying the more elongate kind of pinnules (also at natural size), shows the extreme variation in pinnule sizes.

Fertile frond fragments are illustrated at various different magnifications. Pl. 5 shows an enlargement ($\times 3$) of the monopinnate fragment shown at natural size in Pl. 1, fig. 3. It is the imprint of the abaxial surface of a fertile pinna, and displays the sideways compressed, overlapping synangia with their constituent sporangial compartments. These are preserved at right angles to the straight lateral veins which occur in pairs as a result of a single vein bifurcation taking place almost at the midrib. An enlargement at $\times 6$ (Pl. 10, fig. 2) shows the paired lateral veins and the position of the synangia at right angles to them. Venuli recurrentes are visible between some of the veins. Each lateral vein branch corresponds to a bivalved synangium which is placed immediately below it.

More highly enlarged photographs of the synangia as they occur in the larger, more elongate pinnules, i.e. with a large number of sporangial compartments, are shown in Pl. 8 ($\times 12$); Pl. 9, fig. 3 ($\times 24$); and Pl. 10, figs. 3-4 ($\times 12$, and $\times 36$, respectively). Pls 12-14 give SEM pictures. With the exception of Pl. 10, figs. 3, 3a, and Pl. 12, fig. 2, which depict the two valves of a synangium in a spread-out condition, all the figures show the synangia in sideways compression. Pl. 8 shows both. The compression combined perhaps with some organic decay has made the septa joining neighbouring sporangial compartments stand out in relief, thus appearing as grooves in the latex replicas of Pls 12-14 and Pl. 15, figs. 1, 2. The illustrations also show the gradually diminishing length of sporangial compartments at both ends of the synangia (e.g. Pl. 9, fig. 3; Pl. 12, fig. 2), though their width remains the same.

The generally overlapping condition of the synangia is explained, by analogy with extant *Marattia*, as resulting from sideways compression of structures that were originally pendant from the abaxial surface of the fertile pinnules. The bivalved organisation is evident from the specimens in Pl. 10, figs. 3-4, and Pl. 12, fig. 2, which show the two valves spread out and apparently connected at a lateral vein (in fact, the vein would have been slightly above the midline of the bivalved synangium, but compression would condense the placental area and other intervening soft tissue). The bivalved structure is also seen in the SEM view of sideways compressed synangia in Pl. 12, fig. 1. Comparison with extant *Marattia* suggests that the two valves became spread apart somewhat from one another at maturity, to facilitate spore dispersal (Fig. 5). However, the synangia are too concentrated on the pinnule for the valves to have come apart in life to the extent of the fully spread-out examples discussed above.

Pl. 6 shows a bipinnate fragment with fertile pinnae at natural size. Although not quite the largest pinnules found, they represent the elongate pinnule shape that is most common at Unayzah. This specimen is important in that it provides a fair hint of the large size of the complete frond.



Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Portion of a completely fertile penultimate pinna with the elongate (taeniopteroid) kind of pinnules; $\times 1$; RGM 382 435.

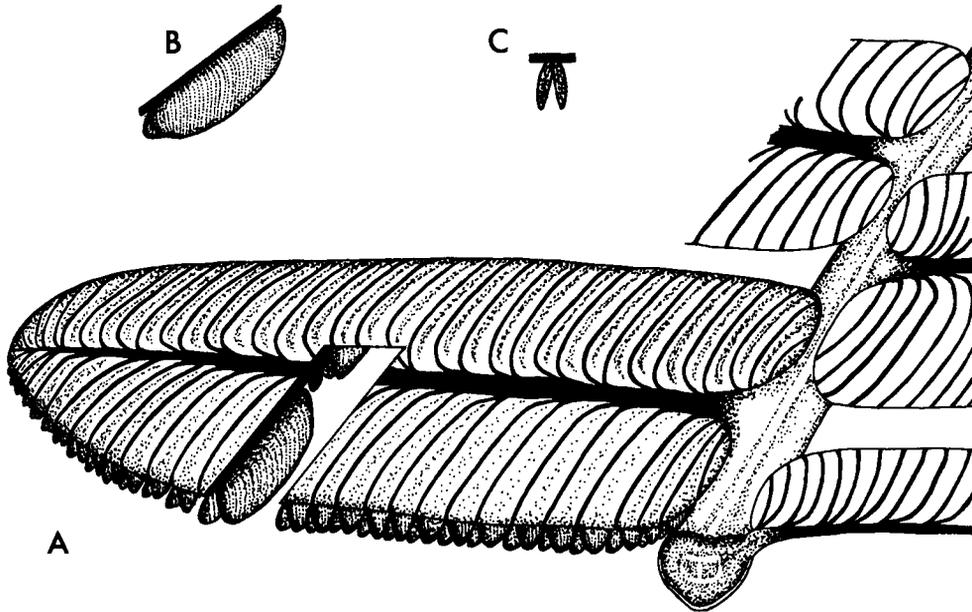
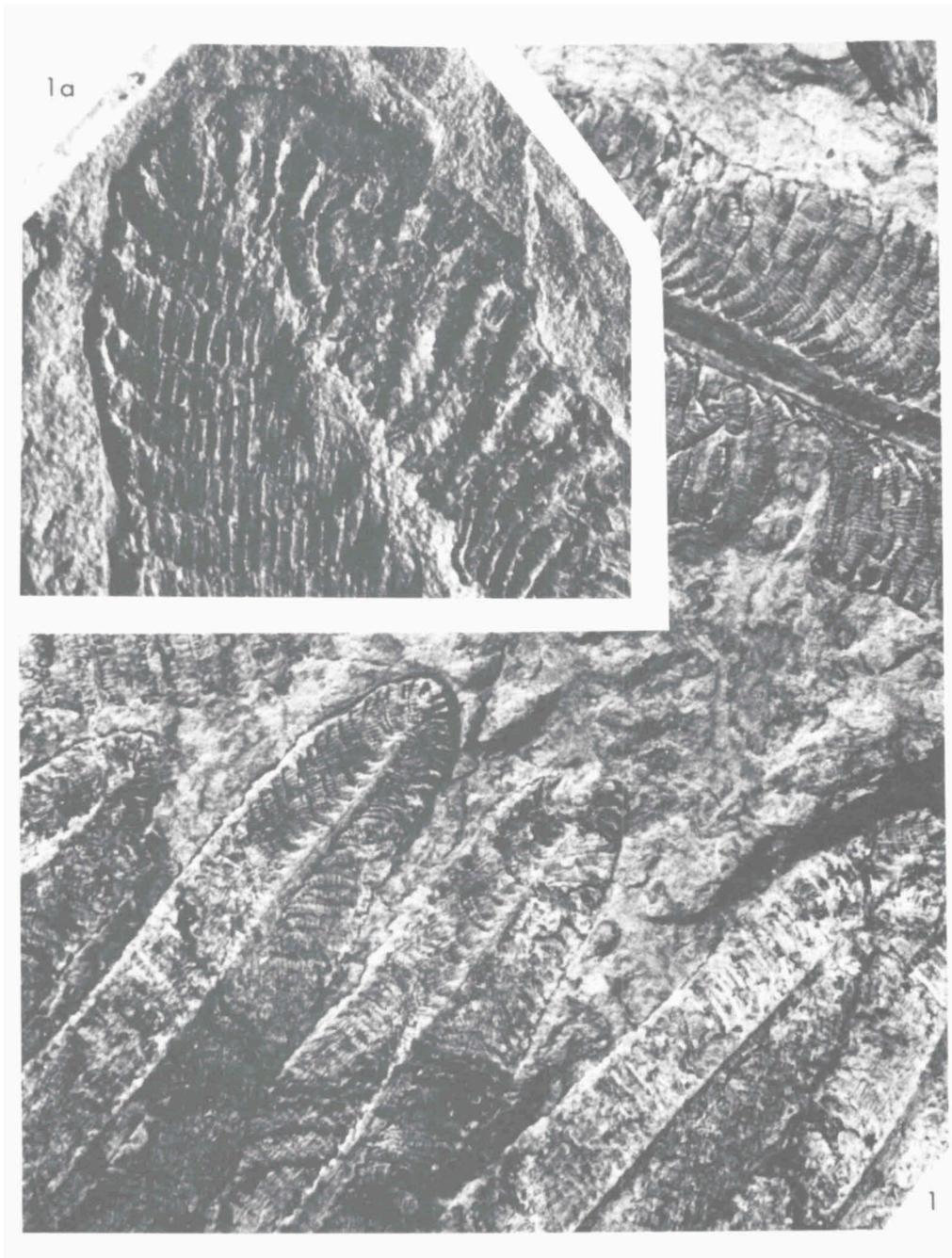


Fig. 5. *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov. Restoration ($\times 5$); A: portion of an ultimate pinna fragment, with a fertile pinnule shown in detail on the left; the two valves of the synangia are shown opened as they would have been at maturity (closed valves are envisaged for immature synangia); B: a single synangium: the dotted lines show the location of septa between the sporangial loculi; C: diagrammatic transverse section of a synangium: all the details of the ventral wall and curvature of dorsal wall entirely imaginary.

A portion of a pinna showing a smaller, intermediate size of fertile pinnules is illustrated in Pl. 7, fig. 1 (which also shows a larger fertile pinnule in the top right hand corner). The inset (fig. 2) is an enlargement ($\times 12$) of the apical region of one of the pinnules of fig. 1. The smaller width of these intermediate size pinnules is matched by the smaller number of sporangial loculi forming a synangium. (The structure of the synangia is the same as in the other material). Pl. 3, figs. 3-4, show small fertile pinnules at $\times 6$. These are of the same size and shape as the vegetative ones in Pl. 2, fig. 2, Pl. 4, fig. 1 and Pl. 10, fig. 5, and display a dense covering of synangia on the abaxial surface. They provide particularly critical evidence for linking fragments having small (almost neuropteroid) pinnules with the more typical taeniopteroid ones of larger size.

Even though there is no single specimen with fertile and vegetative pinnules in organic connection, their close field association in the Unayzah plant bed and the identical shape and size variation of the different kinds of pinnule indicate that they are parts of the same plant. Their venation pattern is also very similar, with the sole difference that the vein density is markedly lower in the fertile pinnules and that the fertile pinnules alone have venuli recurrentes. The fertile pinnules show consistently once veins, the vein bifurcation being situated at or very near the midrib. There is a clear association with the synangia, which occur one to each branch of a bifurcate lateral vein. In the vegetative pinnules the lateral veins characteristically branch twice, and this suggests a correlation of the two branches of the second dichotomy with the bivalved synangia. Although this appears to be a reasonable assumption, there is in fact no simple ratio of 2:1 between the vein density of vegetative and fertile pinnules, since the lateral veins in the vegetative pinnules occasionally dichotomise three times. The vein density of



Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Several fertile pinnules of intermediate size together with a fragment of one of the larger, more elongate fertile pinnules; all show the sideways tilted synangia; $\times 3$; RGM 382 441. 1a: Detail of the apical region of one of the pinnules shown in fig. 1. The synangia cover the whole pinnule lamina on the abaxial surface, extending right up to the pinnule margin; $\times 12$; RGM 382 441.

vegetative pinnules is therefore well over twice that of the fertile ones. (Millay, 1979, p. 53) draws attention to comparable dimorphism in *Scolecopteris* Zenker.

In this regard, a very few 'intermediate' specimens as figured in Pl. 10, fig. 1, are of great interest. They show shorter than usual synangia, with sterile regions of lamina next to the midrib and margin. The region next to the midrib is vaulted, as is usual in the vegetative pinnules, whilst the synangiate region is flat, as is usual over the whole half-width of normal fertile pinnules. These specimens thus appear to be preserved at two different planes. To the extent that the plane of splitting of the matrix passes over the weakness of the undersurface, both of the vegetative and synangial regions, this appearance is correct, and it confirms that the synangia were borne on the abaxial surface. Corresponding with the exceptionally short synangia, some of the veins show secondary bifurcation, as is usual in entirely vegetative pinnules, thus providing direct evidence for linking the normally very different branching patterns of vegetative versus fertile pinnules of *Qasimia*.

The SEM photographs in Pls 13-14 and Pl. 15, figs. 1, 2, illustrate the detailed structure of the synangium, including in situ spores. In so far as the cells of the septa may be seen between the loculi (sporangial compartments), as in Pl. 13, fig. 1 left and fig. 3 right, they appear to be very elongate, ranging from two to many times as long as broad. Elongate cells are also visible over most of the dorsal walls of the sporangial compartments (Pls 13, 14). Towards the base (Pl. 14) they tend to become shorter, and at the apex (free margin of the valve) they become very short to isodiametric (Pls 13, 14). Towards the apex the otherwise entirely longitudinal files of cells diverge increasingly away from the midline of the loculus, and run towards those of neighbouring loculi (Pls 13, 14). At the left of Pl. 13, fig. 2, where the loculi are somewhat damaged, may be seen the extent to which the mineralised cells are preserved in three dimensions, with but little compaction. As in extant *Marattiales* it seems likely that these isodiametric cells at the apex were exceptionally thick-walled. Pl. 15, fig. 1 left, shows the thickness of the wall of a sporangial compartment, whilst fig. 2 reveals the very elongate cells of the inner (as opposed to outer) surface of the dorsal wall.

Details of wall securely identifiable as ventral, including the form of the dehiscence slit, have not yet been observed, since the louvred synangia generally expose little, if anything of their ventral wall (Pl. 12, fig. 1, Pl. 15, figs. 1, 2) whilst the spread-out synangia referred to earlier lack the diagnostic features as to whether the surface seen is ventral or dorsal. Further work is needed. It should be noted that the slits of extant *Marattia* shown for comparison (Pl. 16, figs. 1, 2) are dehiscence slits, and that the septa are hidden from view. The slits are therefore not to be confused with the grooves in Pls 12-14 (replicas), which represent the compressed septa of *Qasimia*. It may also be noted that the cells of the dorsal wall in extant *Marattia* (Pl. 16, fig. 3) are unlike those of *Qasimia* in being typically isodiametric (and usually thin-walled), as also appears to be the case in *Marattia anglica* from the Jurassic of Yorkshire (Pl. 19, figs. 7, 9).

Plate 15, figs. 1, 2, show spore-masses in situ that were first observed during a routine survey of latex replicas with the SEM rather than by optical examination of the

Plate 8

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Detail of a fertile pinnule showing the partly overlapping, sideways compressed ('louvred') synangia on one side of the midrib and a spread-out synangium beneath a lateral vein on the other side. The length of the elongate sporangial compartments gradually decreases towards both ends of a synangium; $\times 12$; RGM 382 439.



Plate 8

hand specimens. As to be expected in Marattiales the number of spores per locule is large, and like *Marattia* the spores are monolaesurate (Pl. 15, figs. 3-6). Their preservation is entirely as moulds, with no remaining organic matter. Mineralising solutions presumably impregnated the sporangium after compression but prior to organic decay of the spore walls, and this replicated the spore surfaces with great clarity of detail. The moulds of the apparent exine (Pl. 15, figs. 3-6) are finely punctate, the punctae presumably representing spines or warts on the surface of the original exine. In some cases the apparent exine is surrounded by a second wall (marked p in Pl. 15, fig. 6). This shows similar punctae and is interpreted tentatively as representing a perispore. Replicas of the spore moulds in latex, even when applied under vacuum, proved to have insufficient resolution of detail to reconstruct the original form of the sculptural elements. The replicas show merely the outlines of the spores and, faintly, the monolaesurate mark, with the wall otherwise reproduced as more or less smooth and featureless. Further work with other replicating substances is in progress.

Although the sporangial compartments are joined laterally over their whole length, there is an occasional hint that their extreme tips may have been somewhat free from one another, as in Pl. 9, fig. 3, and Pl. 12, fig. 1, giving the appearance of a crenulate free margin to the synangial valves. The detailed SEM photographs in Pl. 13 appear to resolve this. In Pl. 13, fig. 2, the sporangial compartments at left appear somewhat crenulate at their tips, but the two at right are not crenulate. The crenulation at left is clearly the result of damage and this is borne out by figs. 1 and 3, in which there is no evidence of crenulation but very clear evidence of structural continuity of adjacent loculi to the extreme margin of the valve. If, as suggested earlier, the apical cells were very thick-walled, the different degree to which crenulation is apparent in some sporangial loculi may be a result of water-wear or else decay to a different extent in specimens suffering from different degrees of natural maceration.

All of the specimens examined in this study appear to show a more or less well preserved lower epidermis but not the upper. Plate 17, figs. 1-3 (see also Figs. 3-4), show the lower epidermis as seen in direct view of uncoated material (using the 'Environmental Chamber' facility of an ISI 60A scanning electron microscope). Elongate cells are visible over the veins, as is to be expected, and stomata can also be seen, though not with great clarity. An extensive search was made for better areas of preservation but failed to yield better results than the initial ones shown in Pl. 17.

These results suggest that some of the stomata of *Qasimia* were possibly cyclocytic, like those of modern Marattiales. These are the only extant ferns that possess strongly cyclocytic stomata (van Cotthem, 1970). Pl. 18, figs. 1, 2, show comparable stomata from a herbarium specimen of living *Marattia*. In these it can be seen that the subsidiary cells form a narrow, well marked ring around the stoma, depressed owing to shrinkage of their periclinal walls. The end walls of the individual cells are visible in the living example whereas these have not been seen clearly in *Qasimia*, probably because of the limitations

Plate 9

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Vegetative pinnule of intermediate size, showing the venation; $\times 3$.

Fig. 2. Portion of a fertile pinnule from the specimen in Pl. 6, showing the largely overlapping, sideways tilted synangia; $\times 3$; RGM 382 435.

Fig. 3. Two successive synangia of the specimen in Pl. 8, enlarged $\times 24$ to show the laterally joined sporangia, their relation to a lateral vein, and the faint crenulation of the free margin of the synangium; RGM 382 439.

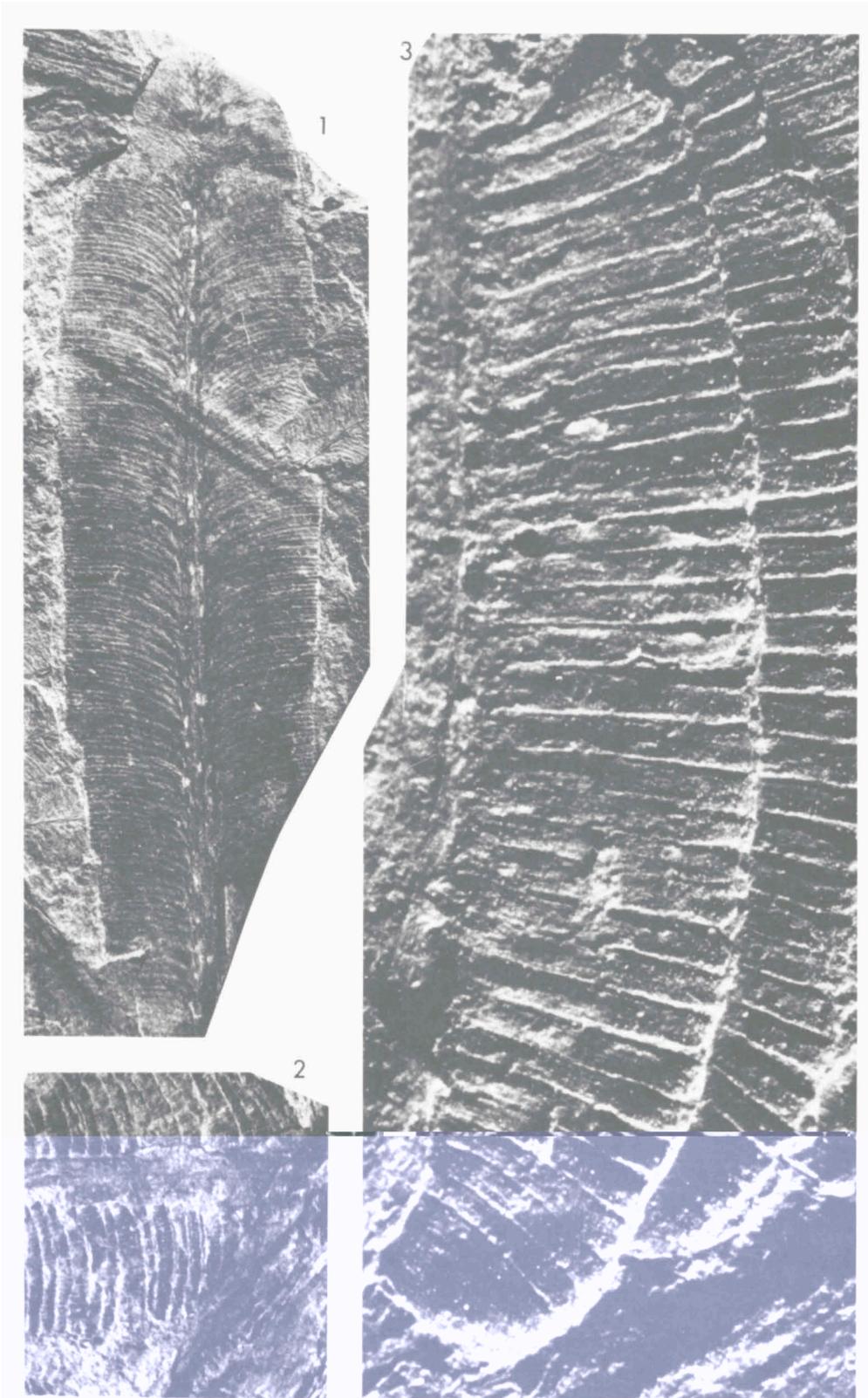


Plate 9

imposed by fossil preservation but possibly because *Qasimia* stomata were polocytic.

SEM study of fertile pinnules has not so far provided additional information for the attribution of these pinnules to the associated vegetative foliage. Pl. 18, figs. 3, 4, show the confused cell pattern visible on the surface of the specimen in Pl. 1, fig. 3 and Pl. 6. It shows the outlines of more than one layer of cells. In view of the absence of stomata, these must be hypodermal layers. This shows evidence of decay prior to the impression on mud and impregnation by iron minerals.

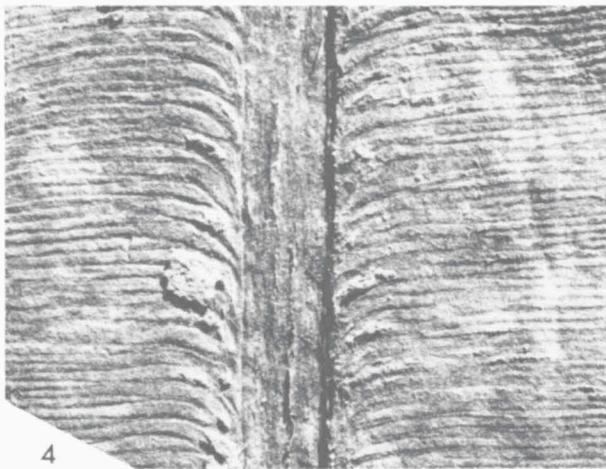
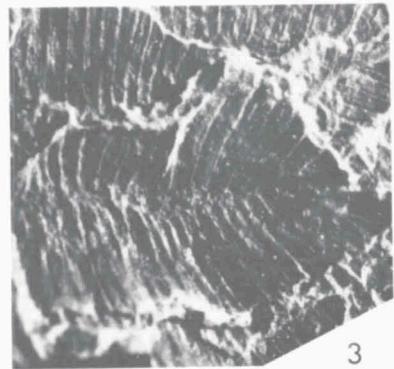
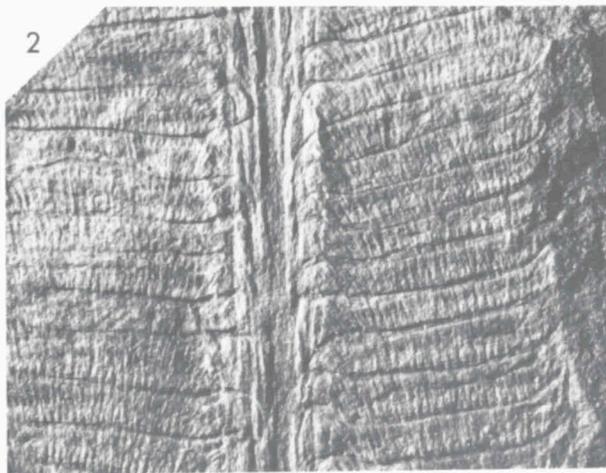
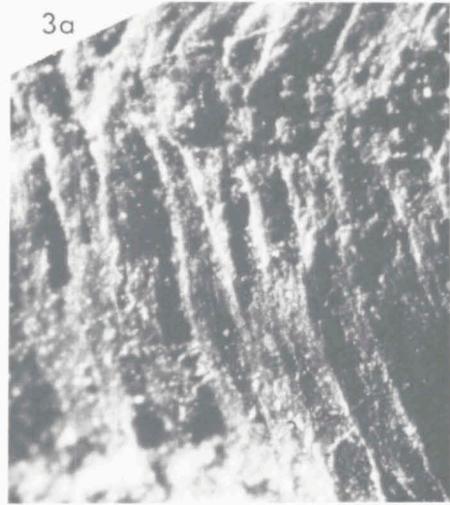
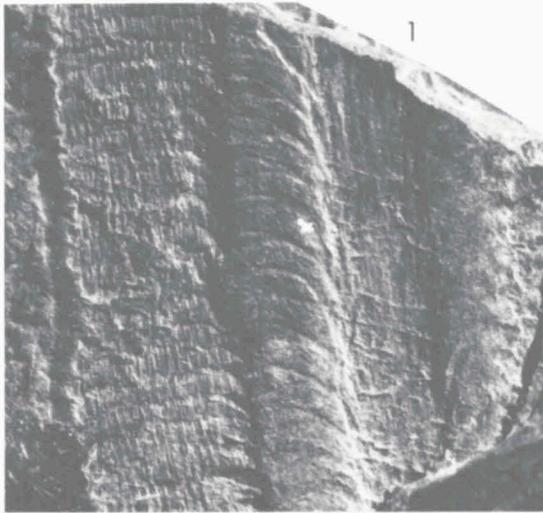
Remarks on synonymy — Judging from the illustrations rather than the description, it is possible that Kawasaki and Kon'no (1932) had specimens of *Qasimia schyfsmae* in the Permian rocks of Korea. These were recorded as *Gigantopteris antiqua* Kawasaki & Kon'no. The specimens figured as *Gigantopteris* sp. cf. *G. antiqua* (loc. cit., pl. CIV, figs. 18, 18a) and as *G. antiqua* (Pl. C, figs. 2-3) are particularly suggestive of fertile specimens of the Arabian species. The shape, size and venation all seem to coincide with the characters shown by *Qasimia schyfsmae*, and so do the markings which appear to represent the loculi of synangia extending across the entire half-width of the pinnule. It appears that these loculi (sporangial compartments) were mistaken for reticulate vein meshes. Stockmans and Mathieu (1939, p. 83) commented upon the likelihood that the plant figured by Kawasaki and Kon'no was a fertile fern. Although a specific identity is strongly suspected, it would appear inadvisable at present to attach the epithet '*antiqua*' to the Arabian species, in view of the totally different description given by the authors of the Korean species. We note that Asama (1959, p. 70) listed *Gigantopteris antiqua* as one of the lesser known gigantopterids.

There must be a suspicion that the large pinnule or leaf fragments figured as *Taeniopteris crassinervis* Mo (Zhao et al., 1980, pl. XVIII, figs. 6-7) belong to the same plant as *Qasimia schyfsmae*. The apparent size and shape of the incomplete leaflets and their vein pattern are comparable with the more elongate pinnules of *Q. schyfsmae* as figured in Pl. 1, fig. 2 and Pl. 4, fig. 2, of the present paper. However, the tips of these leaves (pinnules?) are apparently not preserved and the bases show a constriction on the acroscopic side and a possible decurrence on the basisopic side. These remains are simply too fragmentary for a proper identification and it is also possible that the attribution to *Taeniopteris* is correct. Alternatively, *Macralethopteris* may be considered for them.

Plate 10

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

- Fig. 1. Portion of a fertile pinnule, previously figured by El-Khayal, Chaloner & Hill (1980, fig. 2d) as *Marattiopsis* sp.; from the reverse side of the block with the specimen in Pl. 8 and Pl. 9, fig. 3. The synangia, exceptionally, do not occupy the full half-width of the pinnule lamina and the lateral veins are correspondingly more densely branched than is usual in the fertile pinnules; $\times 6$; RGM 382 439.
- Fig. 2. Fertile pinnule showing sideways tilted synangia, attached beneath the lateral veins which fork only once at the midrib and afterwards remain single; faintly marked venuli recurrentes may be seen between some of the pairs of lateral veins; $\times 6$; RGM 382 436.
- Fig. 3. Synangium spread-out flat, with the axial element (placental region beneath lateral vein) in the middle and the two synangial valves spreading outwards; same block as in Pl. 8 and Pl. 9, fig. 3; $\times 12$; RGM 382 439. 3a: Detail of fig. 3 enlarged $\times 36$.
- Fig. 4. Portion of a vegetative pinnule showing the broad midrib and twice-forked lateral veins. Compare with the fertile pinnule in fig. 2, which shows the lateral veins forked only once near the midrib; $\times 6$; RGM 382 440.
- Fig. 5. Smaller (neuropteroid) kind of vegetative pinnules, showing gently curved (non-taeniopteroid) venation: $\times 6$.



Lemoigne (1981b) suggested that his ?*Marattiopsis* sp. and his *Neuropteridium schyfsmae* might belong to the same plant. Alternatively, he supposed that the fertile remains might belong to *Fasciapteris hallei* (Kawasaki) Lec. His doubts probably stemmed from the fragmentary nature of the vegetative remains available to him. In fact, he only figured a single fragment (holotype) of '*Neuropteridium*' *schyfsmae* and this represents the less common shorter kind of pinnule (Pl. 4, fig. 1).

Comparison with fertile remains from other regions — Apart from the material either firmly or tentatively brought into synonymy with *Qasimia schyfsmae*, a number of similar fertile remains from the East Asian Cathaysia Province need to be compared.

Specimens recorded as *Danaeites* from China (Gu & Zhi, 1974, pls. 66-67), particularly *Danaeites mirabilis* Gu & Zhi (1974, p. 98, pl. 66, figs. 8-10), appear close. This species has recently been transferred to *Rajahia* by Li et al. (1982, pl. VII, figs. 1-4a), an attribution which seems unlikely (see below). Dr Zhou Zhiyan has kindly provided a translation of the description of *D. mirabilis*.

'At least bipinnate, ultimate pinnae linear to lanceolate. Pinna rachis robust. Pinnules attached to upper margins of rachis, always perpendicular to rachis; separate or slightly touching laterally. Pinnules linear, up to 30 mm long, 8 mm wide, contracted at base, with obtuse apex. Midrib about 1 mm wide, showing a thin strand of vascular tissue, secondary veins sparse, arising at an acute angle, curving quickly to a position perpendicular to the pinnule margin. Fertile pinnules same shape as vegetative ones, but with wider spaced lateral veins. Lateral veins forking 2-3 times in sterile pinnules. In fertile pinnules the lateral veins fork twice near the base of the pinnule, once in the middle region and they are simple in the apical region. Synangia linear, attached to lateral veins on the undersurface of the pinnules; composed of 16-20 contiguous sporangia. Sporangia oval and arranged in two rows along lateral veins.'

This description apparently fits *Qasimia*, as do the illustrations although these are not very clear for the fertile material. It does not seem to apply to *Rajahia*, as described by Kon'no (see Kon'no et al., 1970, p. 522), which possesses pectopterid pinnules with small, globular synangia arranged in two rows along the lateral veins. The name *Danaeites* does not apply either since this refers to pectopterid foliage with sori composed of double rows of elongate single sporangia, which are not fused into synangia (Laveine, 1969).

There seems therefore to be a closer similarity with *Qasimia*, including the considerable range in pinnule sizes (particularly with regard to length), and the venation pattern. Unfortunately, since the fructification is not figured in detail, a final decision on its attribution to *Qasimia* must await re-examination of the Chinese material. If it should prove to be referable to *Qasimia*, it is certainly a different species to *Q. schyfsmae*; its lateral veins, though similarly disposed and branched 2-3 times, are more widely spaced.

Plate 11

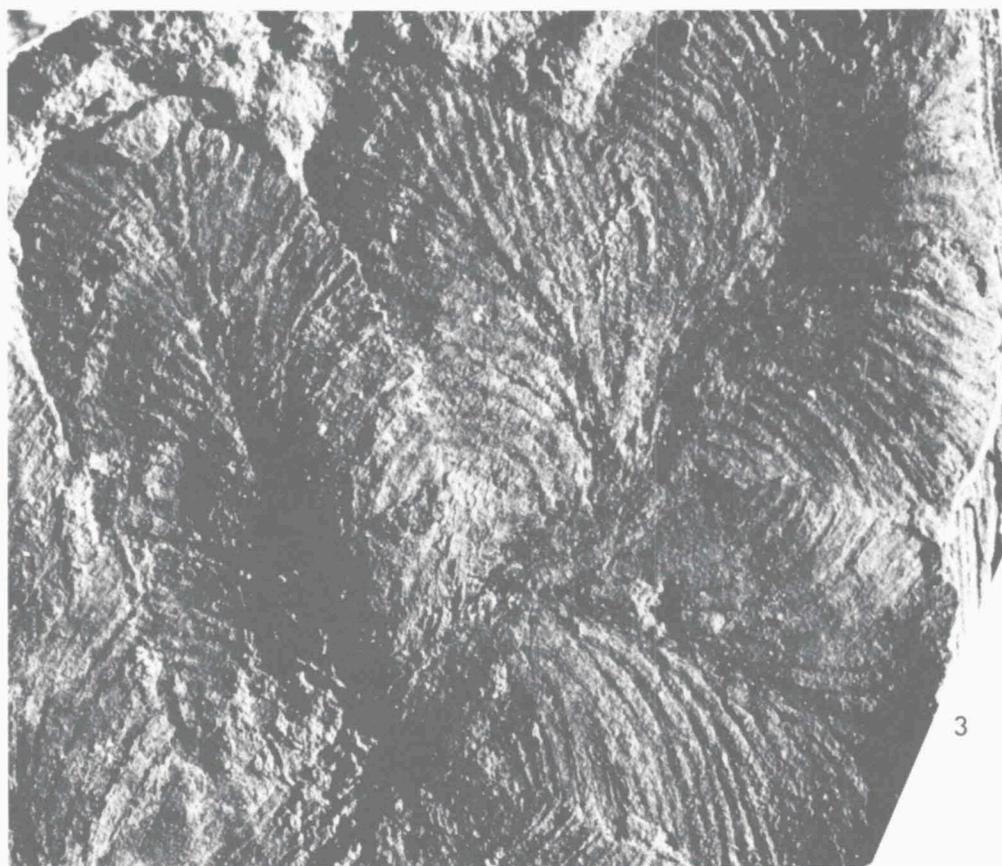
Figs. 1, 2. *Lophotheca panxianensis* Zhao

The two type specimens figured by Zhao et al. (1980, pl. XXIII, figs. 5a, 6), here refigured with permission of Dr Zhao Xiuhu from the original photographs. The specimens show apparently synangiate structures similar to those of *Qasimia*, but with no indication of a pinnule lamina; 1: $\times 3$; 2: $\times 1$.

Fig. 3. *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov.

Terminal region of an ultimate pinna with the smaller kind of vegetative pinnules and a short, rounded apical pinnule; same specimen as in Pl. 10, fig. 5; $\times 12$.

Plate 11



The pinnules shown at $\times 3$ on Gu and Zhi's pl. 66, fig. 10, appear to have a vein density of c. 30 per cm on the margin in the basal parts of pinnules, but only about 12 per cm in the middle and upper parts. The lower figure corresponds approximately to that characteristic of fertile pinnules of *Qasimia schyfsmae*, but not to that of its vegetative pinnules. The latter show characteristically c. 40 veins per cm.

Another very similar, and possibly also congeneric fern from the Upper Permian of China is *Lophotheca panxianensis* Zhao (in Zhao et al., 1980, p. 89, pl. XXIII, figs. 5-8, 5a). The type material, which is all fertile, is refigured here with permission on Pl. 11, figs. 1-2. Dr Zhao has kindly provided the following translation of the diagnosis of *Lophotheca*.

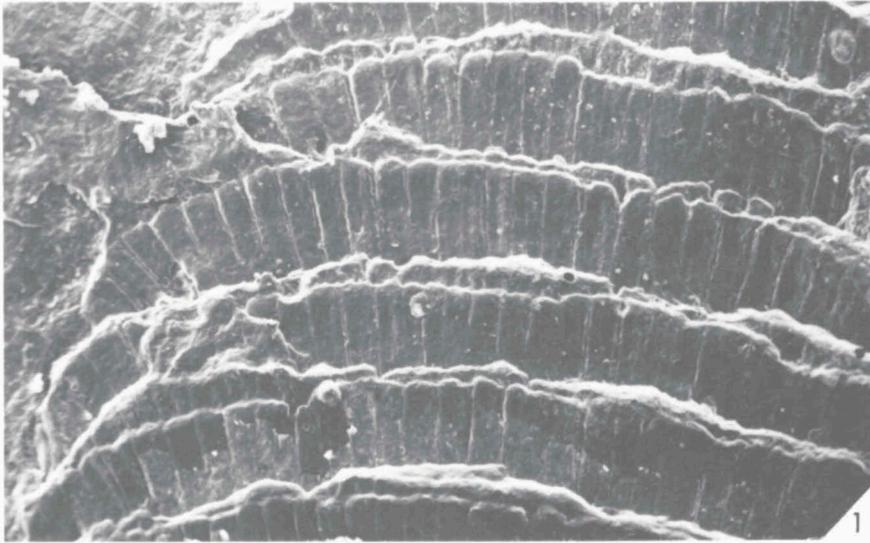
'The branches to which sporangia are attached (i.e. the fertile pinnae) are bipinnate; sporophylls, attached to the two sides of lateral branches, broadly linear in shape; sporangia linear to cuneiform in shape, hanging down closely from the undersurface of the sporophyll lamina and falling into a single file; spores circular in outline and about 30-47 μm in diameter; trilete mark thin, surface of spores covered with tapered granules.'

Comparison was made with *Crossotheca*, but although there is a superficial resemblance, there is no real similarity with its fructification which consists of synangial groupings each composed of four sporangia attached to a lateral vein. Also the lamina of *Crossotheca* formed laterally enveloping flaps (compare Brousmiche, 1982), whereas *Lophotheca* shows apparently unprotected sporangial units.

If the description of *Lophotheca* is taken literally, there is no apparent identity with *Qasimia*, since the Chinese fructification seems to be separate from any pinnule lamina. However, a comparison with variously preserved material of *Marattia anglica* from the Yorkshire Jurassic shows that the absence of a lamina from the *Lophotheca* fructification may be a preservational feature. A common preservational condition of *M. anglica* displays pinnules with the synangia tilted sideways as in *Qasimia* and *Lophotheca*, but without preserved lamina between the veins. Examples are shown in Pl. 19, figs. 2-4; these show a strong resemblance to *Lophotheca*. As in the Chinese material, the synangia of such specimens of *Marattia anglica* are often well preserved, and some yield spores in situ. The more robust tissue of the lateral veins and the midrib is quite often well preserved in such specimens which have merely lost the more perishable tissue of the lamina between the veins. In the Yorkshire Jurassic material such specimens are intimately associated with forms showing a range of better preservation of the lamina. These link specimens with a fully preserved lamina, as in *Qasimia*, to the *Lophotheca* type of condition where the soft tissue between the veins is absent. It thus seems likely that *Lophotheca* represents merely a preservational condition of *Qasimia*, and that the two genera are in fact synonymous, in which case *Lophotheca* would have priority. However, the spores found in the type specimens of *Lophotheca panxianensis* are apparently trilete and it seems premature to take a decision on possible generic identity until the occurrence of *Qasimia*-like material with a fully preserved lamina can be demonstrated for the locality in which *Lophotheca* occurs. We note in this regard that both *Lophotheca* and '*Rajahia*' (*Danaeites*) *mirabilis* originate from Panxian County, Guizhou Province.

A third species that may, in part, be congeneric with *Qasimia*, has been referred to briefly in the generic discussion on *Qasimia* (p. 10). This refers to the fertile specimens of *Marattiopsis orientalis* Burago (1977, pp. 46-48, pl. XXIV, figs. 1-2), from the Permian of South Primorye in the Soviet Far East. (The vegetative material seems mostly quite different, as discussed below.) A translation (provided by the late Mrs H. Sabo) of the relevant part of Burago's diagnosis of *M. orientalis* (based on three fertile specimens), is as follows:

Plate 12



Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Louvred synangia showing their bivalved structure and evidently more or less crenulate free margins of the valves; SEM of latex replica, $\times 20$; RGM 382 439.

Fig. 2. Single detached synangium that has become spread out on compression to reveal the two valves; SEM of latex replica; $\times 12$; RGM 382 437.

'The fertile pinnules agree with the vegetative ones in shape, size and venation.' (sic) 'The synangia are of oblong-silicular shape, placed along the lateral veins; tilted so as to lean in a regular manner, one on another, each 4-6 mm long and composed of 17-23 sporangial compartments in each valve of the synangium.'

The specimens illustrated do not, in fact, show the lateral veins clearly, but we would be surprised if they were found to branch three to four times, as they do characteristically in the vegetative remains ascribed to *Marattiopsis orientalis* (see discussion on p. 38). Otherwise, even though preservation appears to be poor, the description and illustrations suggest that the fertile remains belong to a fern similar to *Qasimia*, perhaps sufficiently so to be regarded as congeneric. (Again, we are forced to refrain from formal synonymy in the absence of direct observation.) Since the holotype of Burago's species is a vegetative pinnule which is quite clearly different from those of *Qasimia*, it would be unwarranted to transfer his species to *Qasimia* (despite the obvious resemblance of the fertile material he figures in pl. XXIV).

Other comparable material from the Permian of East Asia is either too indifferently preserved for adequate consideration (e.g. Halle, 1927, p. 129, pl. 27, fig. 15: fertile fragment of *Neuropteridium polymorphum* Halle, showing 'linear sori parallel to the veins'); or else shows a clearly more distant relationship. *Rajahia* Kon'no falls into this category. It shows double rows of small synangia aligned along the lateral veins of pecoterid pinnules (Kon'no et al., 1970). These almost globular synangial structures placed in a row but not laterally adjoining, show a very different arrangement from the bivalved synangia with laterally joined sporangial compartments of *Qasimia*. Kon'no (1968) described identical sori for his *Neuropteridium kaishanense*, a form which he regarded as generically distinct from *Rajahia* on the basis of its more completely fused frond segments (see Kon'no et al., 1970, p. 524).

A general comparison of fertile *Qasimia* with *Marattia* (Triassic to Recent) is given on p. 8. Recently collected material of *Marattia anglica* (Thomas) Harris, from the Yorkshire Jurassic, has been examined. In the vast majority of specimens (see Harris, 1961), the synangia are tilted sideways as in *Qasimia*. However, unlike *Qasimia*, they are preserved as coaly compressions and do not show quite as clearly the bivalved structure. Favourably preserved pinnules, compressed without tilting (Pl. 19, figs. 5, 6, 9), show unequivocally that *M. anglica* synangia are bivalved. They also show (Pl. 19) that its sporangial compartments, as in the extant species, are shorter than those of *Qasimia schyfsmae*.

Well preserved specimens of *Marattia anglica*, mainly from the Roseberry Topping plant bed, have been examined directly (i.e. without replication) with the SEM. The object was to record the details of the surface cells of the synangial wall. As with *Qasimia*, the photographic evidence so obtained is not entirely clear as it is at the limits of preservational detail for such compression fossils. Nevertheless, Pl. 19, fig. 8, shows

Plate 13

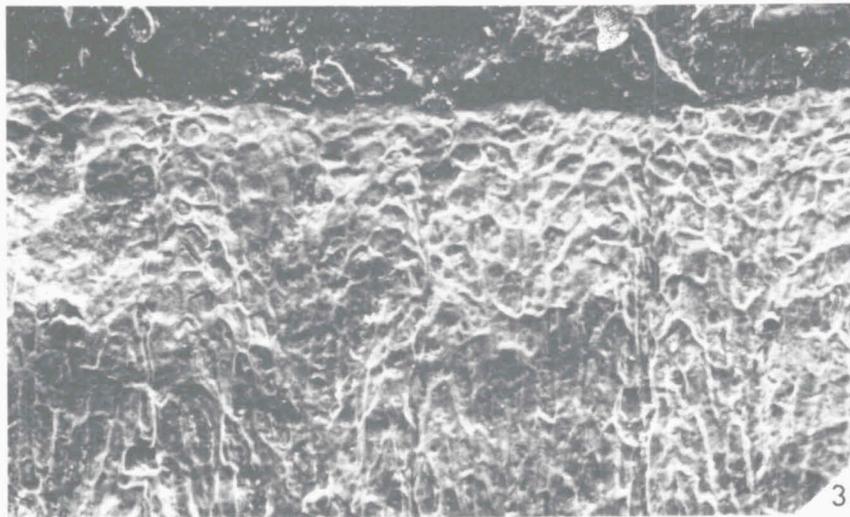
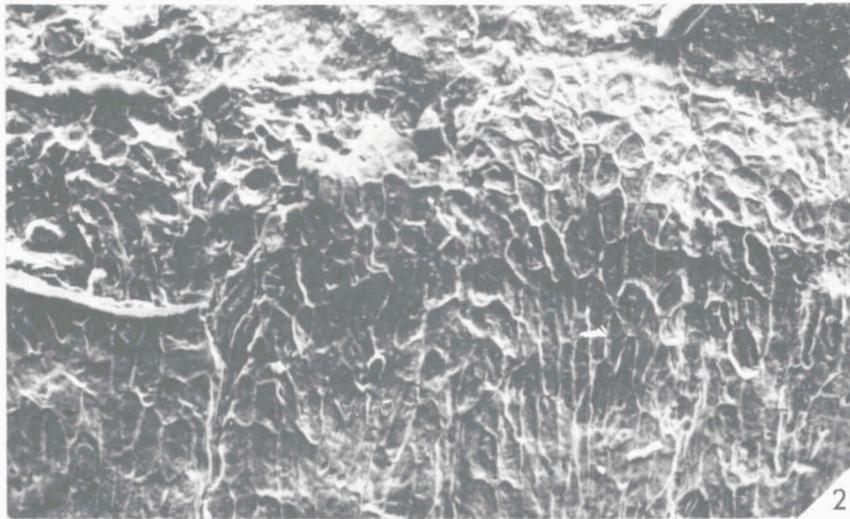
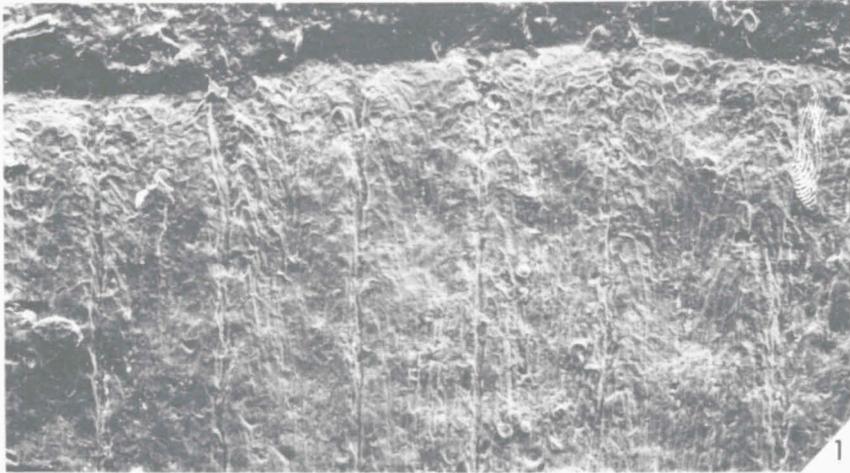
Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Detail of a synangial valve showing free margin and outlines of cells of the dorsal walls of the sporangial compartments; the free margin is not crenulate; SEM, latex replica; $\times 100$; RGM 382 441.

Fig. 2. Details of cells as in fig. 1; the sporangial compartments at left appear rounded and somewhat separate (crenulate) at their tips, whilst the two at right are not crenulate. The crenulation at left is clearly the result of damage; SEM of latex replica; $\times 200$; RGM 382 441.

Fig. 3. Detail as in fig. 2, showing continuity of cells of the adjacent sporangial compartments right up to their tips, without crenulation; SEM of latex replica, $\times 200$; RGM 382 441.

Plate 13



that the cell outlines of the ventral wall are more or less elongate, whilst those of the dorsal wall appear to be uniformly polygonal (Pl. 19, figs. 7, 9). This resembles closely the condition found in extant species of *Marattia*, such as *Marattia brassii*, figured in Pl. 16, figs. 1-3. Unlike *Qasimia*, the dehiscence slits of *Marattia anglica* sporangial loculi are well marked.

Taylor (1967) described a *Marattia*-like fructification on sphenopteroid foliage of late Carboniferous age from the Mazon Creek area of Illinois. He called it *Radstockia kidstonii*, a generic attribution that proves inappropriate after Brousmiche's (1983) reinterpretation of the type species, *Radstockia sphenopteroides* Kidston. The latter has been shown to possess a fructification consisting of sporangia in groups of four arranged in a double row at the end of pinna segments with virtually no lamina; this is very different from the bivalved synangia of Taylor's species. Taylor compared with extant *Marattia alata* and *M. excavata*, which are certainly remarkably similar. The synangia resemble those of *Qasimia* (and *Marattia*) in their bivalved structure, but they are shorter and more oval than in *Qasimia*. They are quite different from the synangia of both *Qasimia* and *Marattia* in that they appear to be sunken in the lamina, as in living *Danaea* and in the late Carboniferous and early Permian fern *Millaya* Mapes & Schabillion (1979). The usually large, taeniopteroid to occasionally small and approximately neuropteroid pinnules of *Qasimia schyfsmae* are very different from the sphenopteroid foliage of '*Radstockia kidstonii*'.

Comparison with vegetative remains from other areas — Vegetative remains of *Qasimia schyfsmae* are similar to several species recorded generically as *Neuropteridium* from the East Asian Cathaysia flora. Halle (1927, p. 126) was the first to apply this name to East Asian Permian plants. He compared them with Triassic species described as *Neuropteridium* by Schimper (1869) and with the Gondwana species first attributed to *Neuropteridium* by Feistmantel and later transferred to *Gondwanidium* by Gothan (1927, 1941). The latter are currently assigned to *Botrychiopsis* Kurtz (Archangelsky & Arrondo, 1971). *Botrychiopsis* fronds, which show extremely variable pinnule characteristics, are so clearly different from the European *Neuropteridium* of the Triassic, and the Cathaysian forms as well, that no comparison is required.

The validity of Halle's identification of the East Asian Cathaysian forms with Schimper's *Neuropteridium* has been discussed briefly on p. 4. A more detailed discussion follows here.

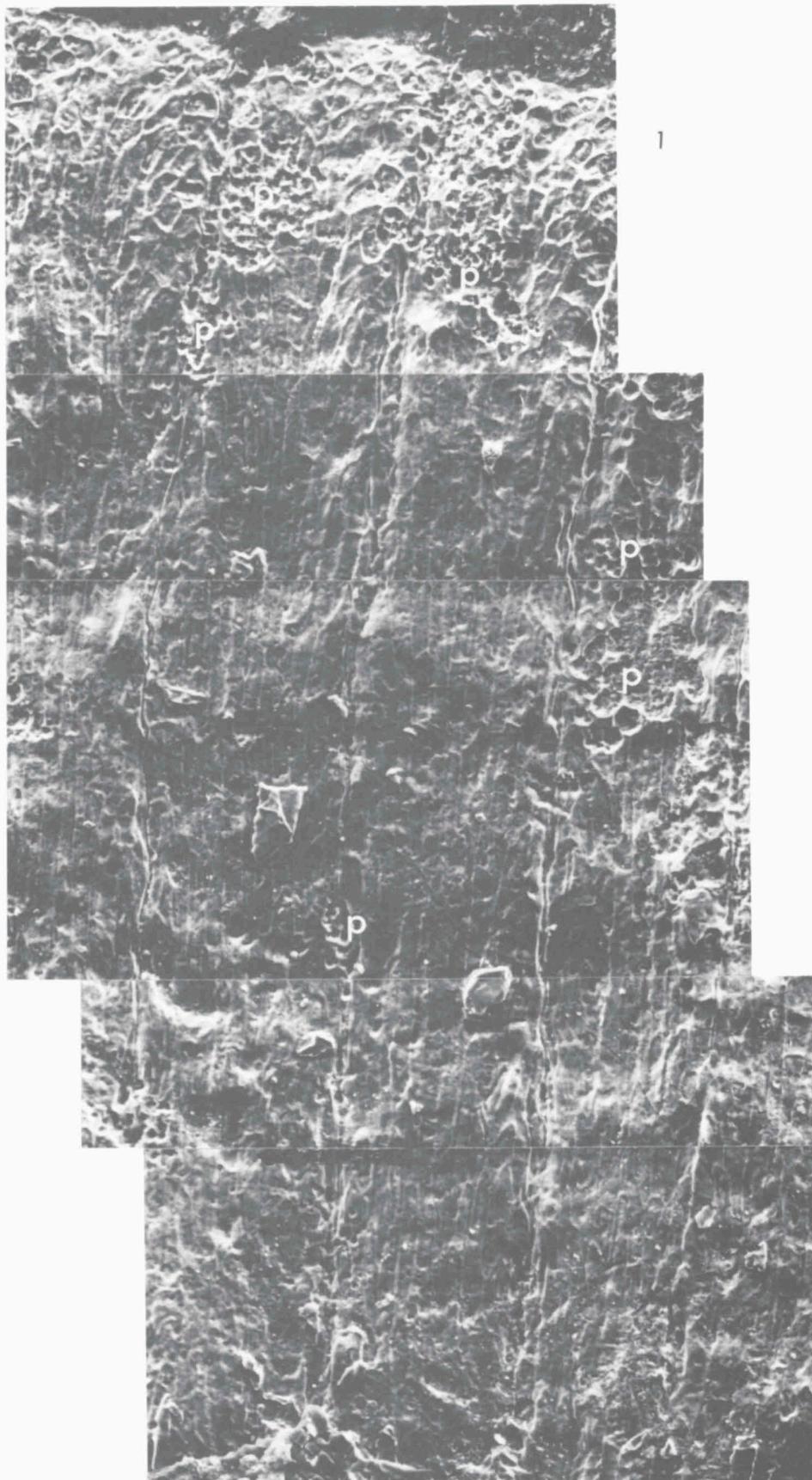
The original diagnosis of *Neuropteridium*, regarded by Schimper as a subgenus of *Neopteris* Brongniart, is as follows (Schimper, 1869, p. 447): 'Frons simpliciter pinnata, pinnis integerrimis basi coarctatis, infra mediam basin insertis; nervo medio plus minusve distincto.' The type species, *Neopteris (Neuropteridium) grandifolia* Schimper, is a form with large pinnules (up to 5 cm long) which are broadly based, to a large extent fused to the rachis, with an oblique, decurrent midvein and oblique lateral veins (Schimper & Mougeot, 1844, p. 77, pl. XXXVI). There is thus no real comparison with the larger pinnules of *Qasimia*, which show a more strongly marked, non-decurrent

Plate 14

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Fig. 1. Cell outlines of dorsal wall of a synangial valve, from base to apex of two adjacent sporangial compartments. The cells are mostly elongate, becoming isodiametric at the apex and also somewhat shorter at the base, next to the placenta. Mineral pitting (p) should not be confused with cell outlines. SEM of latex replica, $\times 200$; RGM 382 441.

Plate 14



midvein, and lateral veins that are mainly perpendicular to the pinnule margin. The smaller pinnules of *Qasimia* are a little more comparable since the lateral veins are more curved and hence less persistently perpendicular to the pinnule margin; they also show a slightly decurrent midvein. However, the bases of the pinnules of *Qasimia* are typically cordate and not largely fused to the rachis as in *Neuropteridium grandifolium*, and the lateral veins are never as oblique on reaching the pinnule margin as is the case in the latter. It should also be noted that Schimper's genus is regarded as monopinnate, whereas *Qasimia* is at least bipinnate.

Gothan (1941) observed that the other Triassic species included in *Neuropteridium* by Schimper, viz. *N. voltzii* Brongniart, *N. intermedia* Schimper, *N. elegans* Brongniart, and *N. gaillardotii* Brongniart, are also quite different from *Neuropteridium grandifolium*. He suggested that these species should be recorded under the name *Crematopteris*, a fructification genus.

The Permian remains attributed to *Neuropteridium* by Halle (1927) and by subsequent authors, are all too fragmentary to show the organisation of the frond. However, their pinnules of varied size, with cordate bases, parallel margins, a well developed midrib and densely arranged, slightly oblique to subperpendicular laterals, differ from *Neuropteridium grandifolium* Schimper. Three of these species from Cathaysia are relatively well known and constitute a more or less homogeneous group of vegetative remains: *Neuropteridium polymorphum* Halle, *Neuropteridium kaishanense* Kon'no, and *Neuropteridium yokoyamae* Kon'no & Asama (compare Halle, 1927; Konno, 1968; Kon'no & Asama, 1970). *N. polymorphum* and *N. yokoyamae*, in particular, are comparable to the vegetative remains of *Qasimia schyfsmae* (which Lemoigne, 1981b, described as *Neuropteridium schyfsmae*). Their morphological similarity is such as to admit attribution to a single form-genus for vegetative material similar to that of *Qasimia*. Since more than one natural genus may be involved, however, we refrain from attributing the East Asian species of '*Neuropteridium*' sensu Halle to *Qasimia* which has a well defined systematic position.

This point is underscored by *Neuropteridium kaishanense* Kon'no which has a *Rajahia*-like fructification and which, though showing a general morphological similarity to *Qasimia*, does not apparently possess the same pinnule size and length-breadth variation of the species mentioned above.

It follows that the East Asian *Neuropteridium* of the Cathaysian Province does not belong to this genus as typified by *Neuropteridium grandifolium* of the European Triassic, and that the various species recorded as *Neuropteridium* from the Permian of East Asia may not all belong to a single group of plants. This latter point is made even more forcibly if some of the other species described under this name are examined. For instance, *Neuropteridium? yongwolense* Kawasaki (1931-1934) should probably be trans-

Plate 15

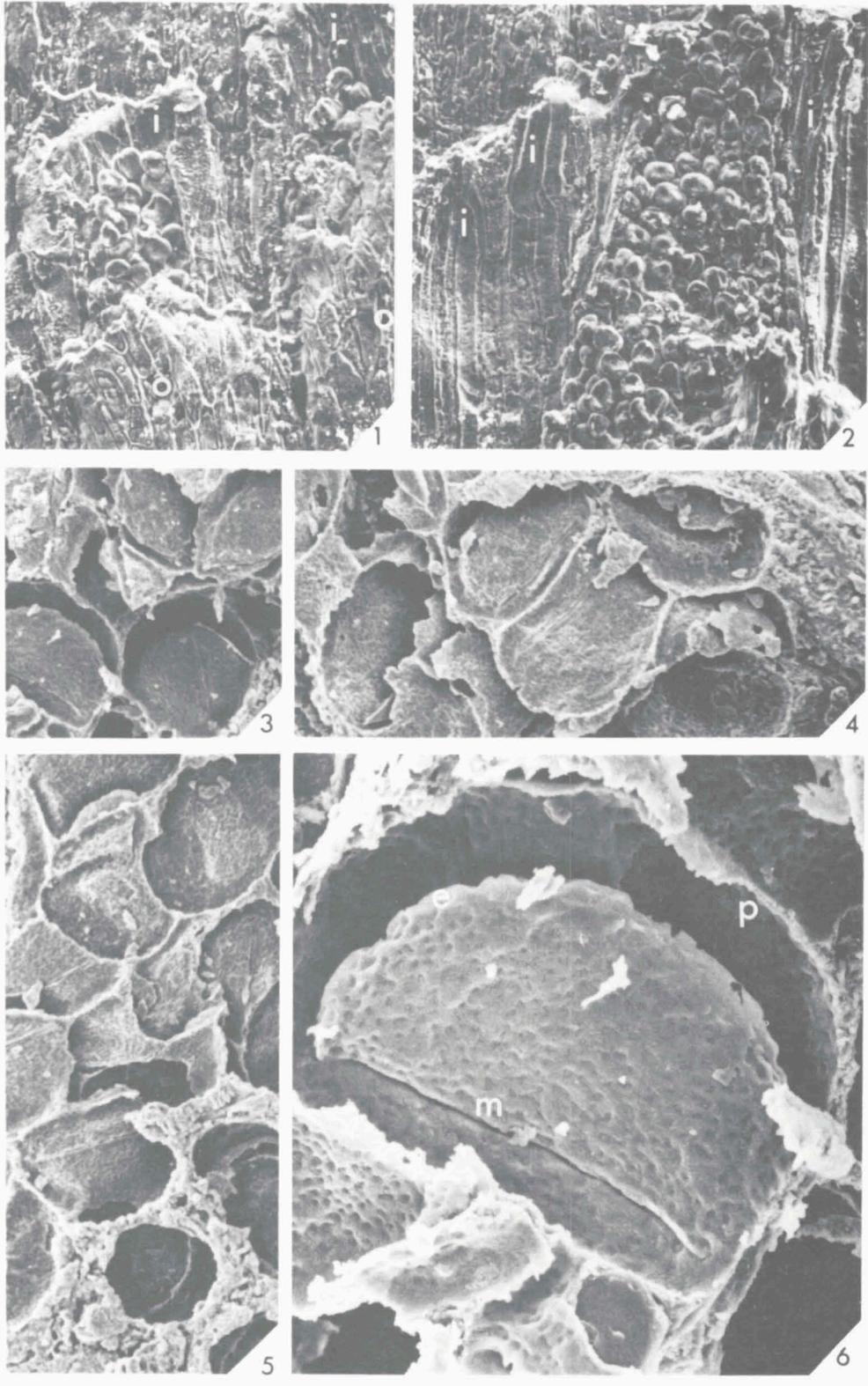
Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Figs. 1, 2. Somewhat damaged synangia, revealing in situ spore-masses and cell outlines on inner surface of dorsal wall (i) as well as on outer surface (o). Uncoated latex replica examined in an ISI 60A SEM fitted with 'environmental chamber' backscatter facility; $\times 200$; RGM 382 439.

Figs. 3-5. Detail of in situ spores showing monolaesurate tetrad mark; direct SEM views of stub-mounted spore-masses, coated and examined in a field emission SEM, Hitachi S.800: $\times 1000$; RGM 382 441.

Fig. 6. Single spore showing ornamentation of exine (e), ? perine (p) and monolaesurate tetrad mark (m); technique and specimen as for figs. 3-5 but $\times 3500$.

Plate 15



ferred to *Pseudomariopteris* (it is noted that Stockmans & Mathieu, 1939, p. 84, took it out of *Neuropteridium* but assigned it to *Cladophlebis*). Use of the name *Neuropteridium* in the Permian of Cathaysia has been quite unsatisfactory.

The smaller vegetative pinnules of *Qasimia schyfsmae* (Fig. 2) might be confused with those of *Neuropteridium polymorphum* Halle (1927, pp. 127-130, pl. 27, figs. 1-12, ?13-15). However, the longer pinnules of *N. polymorphum* show more broadly arching veins reaching the pinnule margin at c. 60°; these veins also appear more clearly grouped together, making up vein bundles as a result of the larger number of vein dichotomies (2-4 according to Halle, 1927). Its affinities are not clear, but attribution to *Neuropteridium* is certainly inappropriate.

Neuropteridium yokoyamae Kon'no & Asama (in Kon'no et al., 1970, pp. 515-517, text-fig. 10, pl. 6, figs. 1-7) shows pinnules of rather similar shape and size to those of *Qasimia schyfsmae*. The diagram given by these authors also shows a dense venation pattern (30 veins per cm), although not quite as dense as in *Q. schyfsmae* (c. 40-50 veins per cm). Moreover, the pinnule bases of the Malayan species are described as 'often considerably expanded into large auricle' and this differs from the cordate bases of *Q. schyfsmae* pinnules. The veins of *Neuropteridium yokoyamae* are depicted as forking more repeatedly than seems to happen in the Saudi Arabian material, and they are more oblique. The photographs of Kon'no et al. are poor and the specimens are very fragmentary. This makes it impossible to observe all details and does not allow gauging the range of variation of the foliage. Additional specimens of *Neuropteridium yokoyamae* were recorded by Kon'no and Asama (1970). These show a higher vein density (37-50 per cm) and appear quite similar to the vegetative foliage of *Qasimia schyfsmae*. However, these remains are even more fragmentary and a positive identification does not seem to be warranted.

The vegetative pinnae described by Burago (1977, pp. 46-48, pl. XXIII, figs. 1-4; pl. XXIV, figs. 3-4; pl. XXV, figs. 2, 4-5; pl. XXVI, figs. 2-3), and which were attributed to his *Marattiopsis orientalis*, apparently belong to one or more different species, perhaps close in part to *Neuropteridium yokoyamae*. Burago's diagnosis for the vegetative remains is as follows (translation by Mrs H. Sabo):

'The frond is compound-pinnate, with a more or less well marked, grooved rachis, 4-9 mm wide. The pinnules are large, elongate-oblong, linguiform, with entire or sometimes irregularly crenate margins; they have a gradually narrowing, rounded apex, a somewhat cordate or irregular base, and a short petiole. The pinnules are attached alternately to the rachis, at angles of 40-65°. The venation is catadromous. The lateral veins are thin, numerous; they diverge from the midrib at a very acute angle and, curving gradually and dichotomising up to five times, reach the pinnule margin at an angle of 60-90°. There are 18-32 veins per 0.5 cm along the pinnule margin.'

In the description, Burago comments that the veins characteristically bifurcate three to four times, rarely five times. Although similar to vegetative remains of *Qasimia*, the gradually curved lateral veins and the high number of vein bifurcations set it clearly apart; in *Q. schyfsmae* the veins characteristically fork twice and rarely three times. The

Plate 16

Marattia brassii Copel

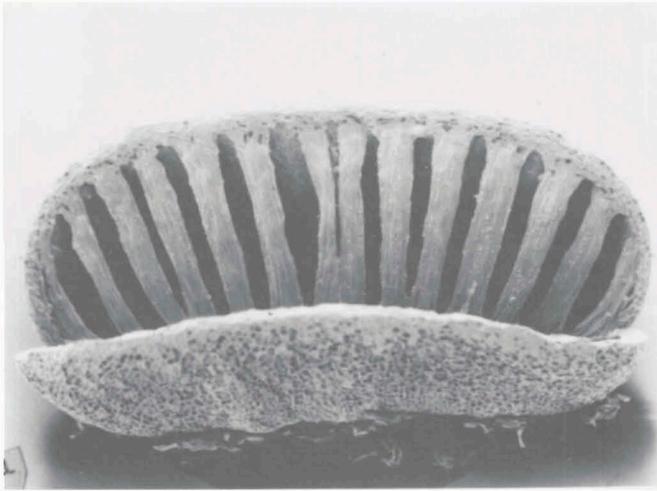
L.J. Brass, 12 117, Irian Jaya (New Guinea), (BM). Details of synangium and synangial wall, SEM.

Fig. 1. Whole synangium showing the two valves, ventral wall of one valve with gaping dehiscence slits and dorsal wall of other valve; $\times 50$.

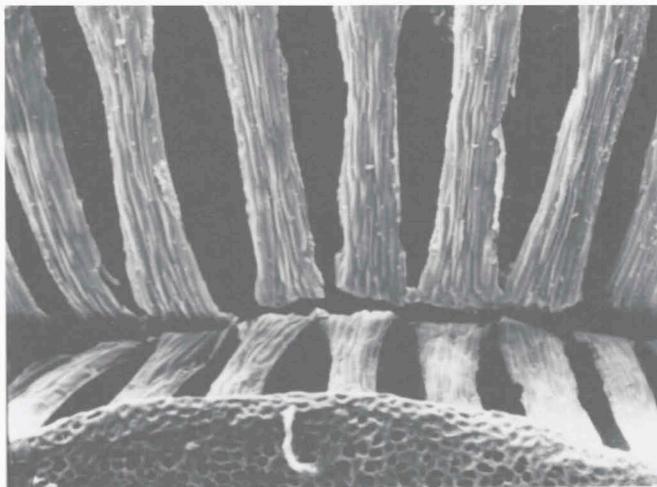
Fig. 2. Elongate cells of ventral walls of synangium; $\times 100$.

Fig. 3. Isodiametric cells of dorsal wall; $\times 100$.

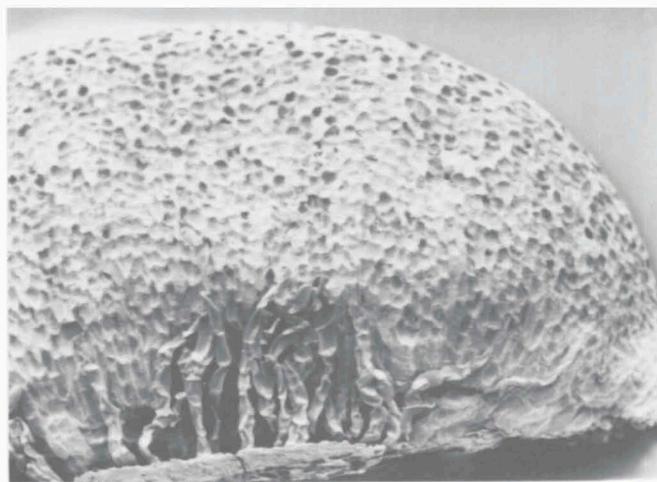
Plate 16



1



2



3

curved veins in *Marattiopsis orientalis* can be seen most clearly in Burago's pl. XXIII, fig. 2, and his pl. XXIV, fig. 4. This is very different from the taeniopteroid vein pattern of *Q. schyfsmae* in which the lateral veins in comparable pinnules run a straight course perpendicular to the pinnule margin over most of the pinnule width. Burago's material is more similar to *Neuropteridium yokoyamae* in both the number of vein bifurcations and the gradually curved course of the lateral veins.

The vein density of Burago's specimens (36-64 veins per cm at the pinnule margin) is comparable to that of both *Quasimia schyfsmae* and *Neuropteridium yokoyamae* (as figured by Kon'no and Asama, 1970), but a little higher. The description indicates that most of the specimens from South Primorye possess a vein density of 44-64 per cm, with only a few showing a lower vein density (32-40 per cm), comparable to that of *Q. schyfsmae*. Burago also mentions a few other characters unlike those found in either *Qasimia schyfsmae* or *Neuropteridium yokoyamae*, and which provide an additional hint that more than one species may be involved in his material. For instance, although the pinnule apices are characteristically rounded, as in *Qasimia schyfsmae* and in *Neuropteridium yokoyamae*, some of the pinnules described by Burago have acute apices (e.g. his pl. XXIII, fig. 2).

As mentioned on p. ..., the fertile specimens of *Marattiopsis orientalis* Burago do show a marked resemblance to *Qasimia schyfsmae*. If one tries to fit any of the vegetative remains associated with the fertile pinnules of *M. orientalis* within the range of variation known for vegetative pinnules of *Q. schyfsmae*, it may be that some of the pinnules with rounded apices and a relatively lower vein density belong to the same plant. It certainly appears that Burago's material represents a heterogeneous assemblage. It also comes from a number of different localities.

The taeniopteroid aspect of the larger, more elongate pinnules of *Qasimia schyfsmae* invites comparison with certain species of the East Asian *Cathaysia* flora which have been assigned, perhaps wrongly, to *Taeniopteris* Brongniart. Most similar in this respect is *Taeniopteris tobaensis* Li, Yao & Deng (1982, pl. V, fig. 3b; pl. XI, figs. 1-4b). This species has been described as follows (translation by Dr Zhou Zhiyi):

'Frond at least once pinnate; rachis 4-5 mm broad, ornamented with longitudinal wrinkles. Pinnules 10 cm long, 2 cm broad, margin entire, base cordate, apex acutely rounded. Midrib prominent, about 1 mm wide. Lateral veins of pinnule issuing from midrib at an acute angle, then immediately bifurcating, curving towards the margin, and bifurcating once more at a point about one quarter of its length from the midrib, then running parallel towards the margin. Twenty-eight veins per cm at the margin. Vegetative pinnules similar to fertile in shape and size but with fewer veins in the latter. Sporangia arranged in rows, parallel on both sides of lateral veins on the abaxial surface of the lamina; each row the same length as that of the vein, and composed of 35-38 sporangia. Sporangia possibly elliptical in form, touching each other tightly, with their long axis perpendicular to the vein (details unknown).'

Plate 17

Qasimia schyfsmae (Lemoigne) gen. et comb. nov.

Epidermis of abaxial surface of pinnule showing more or less cyclocytic stomata; RGM 382 442. Direct views of uncoated specimen, SEM using environmental chamber.

Fig. 1. Region over vein at right lacking stomata and with rectangular epidermal cells, at left, in interveinal region, ordinary epidermal cells irregularly polygonal with numerous apparently cyclocytic stomata; $\times 500$.

Fig. 2. As for fig. 1, showing details of stomata; $\times 750$.

Fig. 3. Stomata from different region of pinnule, evidently not cyclocytic; $\times 500$.

Plate 17



1



2



3

Li, Yao and Deng also note: 'The reproductive pinnules show that the genus *Taeniopteris* may probably belong to the order Marattiales of the true ferns; but because the details of the sori are unknown the taxonomic position cannot yet be confirmed.'

Both the illustrations and the description suggest a species of *Qasimia*. In fact, the fertile pinnules (Li, Yao & Deng, 1982, pl. XI, fig. 4a) closely resemble *Qasimia schyfsmae*, particularly our Pl. 1, fig. 1 and Pl. 5. The vegetative material is also very similar, both in shape and dimensions of the pinnules and in the venation pattern. Li, Yao and Deng's species shows twice bifurcate lateral veins which follow a similar course to that of the lateral veins in *Qasimia schyfsmae*. However, the vein concentration at the pinnule margin is only 28 per cm, as opposed to 40-50 per cm in the Arabian species. We therefore retain *tobaensis* as a separate species, whilst transferring it to the genus *Qasimia*. The original attribution to *Taeniopteris* is inappropriate for a number of reasons. On a purely morphological basis *Taeniopteris* should be restricted to petiolate leaves, with a prominent midrib which extends into the normally rather acute apex. The lateral veins of *Taeniopteris* are characteristically perpendicular or nearly perpendicular to the leaf margin, and are often hardly if at all curved at the midrib. *Taeniopteris* is also known to have been the foliage of seed-bearing plants, apparently related to the Cycadopsida (Mamay, 1976). The Chinese plant is here named *Qasimia tobaensis* (Li, Yao & Deng) comb. nov.

A number of Permian plants from China have been incorrectly referred to *Taeniopteris*, e.g. *Taeniopteris crassinervis* Mo (see p. ..). Furthermore, Shimakura (1940, pl. VI, figs. 6-7) has illustrated a *Taeniopteris* sp. aff. *T. hallei* Kawasaki, which appears quite similar to the pinnules of intermediate size of *Qasimia schyfsmae*. It is even more similar to *Neuropteridium yokoyamae* Kon'no & Asama.

The Southeast and East Asian genus *Macralethopteris* Jongmans & Gothan (1935, pp. 130-132), known from vegetative remains only, shows large, elongate pinnules with similar but not identical venation to that of *Qasimia schyfsmae*. However, the attachment of the pinnules varies from a constricted base to a narrowly confluent one. In *Qasimia schyfsmae*, narrowly confluent bases only occur in the apical parts of pinnae with small, relatively short pinnules. The elongate pinnules invariably show cordate bases. The venation of the vegetative pinnules is also quite different since the lateral veins of the type species, *Macralethopteris hallei* Jongmans & Gothan, are described as being only once bifurcate near the midvein, whereas *Q. schyfsmae* has at least twice bifurcate veinlets.

Jongmans and Gothan incorporated a number of very different taxa in their genus, and it is clear that only the type species can be accepted as really belonging to *Macralethopteris*. Stockmans and Mathieu (1939, pl. X, figs. 1, 1a) illustrated a specimen of *Macralethopteris hallei* showing a narrow strip of lamina joining adjacent pinnules. They referred it to *Alethopteris*. A similar species is *Alethopteris gothani* Stockmans & Mathieu, an East Asian element which has also been recorded from Central Asia (Sixel & Savitskaya, in Sixel et al., 1975).

Plate 18

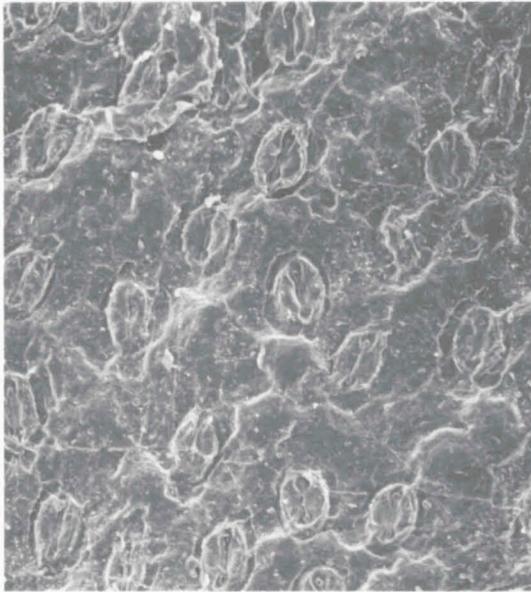
Figs. 1, 2. *Marattia wernerii* Ros.

T.G. Walker, T.8482 (sheet 2 of 2), New Guinea (BM), epidermis of abaxial surface of pinnule showing cyclocytic stomata comparable with those of *Qasimia*; SEM; 1: general view, $\times 200$; 2: detail of one stomatal apparatus; $\times 800$.

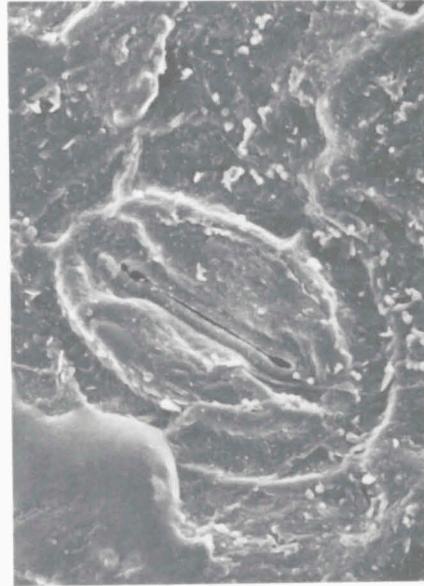
Figs. 3, 4. *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov.

Presumed hypodermis from abaxial surface of a fertile pinnule, SEM, $\times 250$; RGM 382 434.

Plate 18



1



2



3



4

An even more remote comparison involves the genus *Compsopteris*, described by Zalesky (1934, p. 263) for Permian plants from the Pechora Basin in the northern Urals. This is regarded as equivalent to *Protoblechnum* sensu Halle (non Lesquereux). Quite apart from the fact that the specimens described under these names are probably pteridosperms (in view of the lack of sporangia in the numerous remains recorded in the literature), their oblique veining and variable pinnule attachment (including markedly decurrent forms) provide clear differences from *Qasimia*.

Phylogeny

The great antiquity of *Marattia* as we know it today is attested to by the Carboniferous fern described as *Radstockia kidstonii* by Taylor (1967), which represents the earliest sphenopteroid form. The Permian remains here described as *Qasimia* underscore this antiquity and represent the earliest recorded taeniopteroid form. Notably, *Qasimia* is so similar to the taeniopteroid forms of taeniopteroid species of *Marattia* that its generic identity rests largely on the rounded pinnule apices (as against the pointed ones of *Marattia*) and on such quantitative characteristics as the length of sporangial loculi in the synangium (and of the cells of their dorsal wall), as well as the relative length of the entire synangium, which typically covers the entire half-width of the fertile pinnule. This means that most of the essential characteristics of *Marattia* were already established in Permian *Qasimia* and that only relatively minor evolutionary changes occurred in the Mesozoic, resulting in *Marattia*. Intermediate forms, particularly with regard to the length of synangia, do occur in the Mesozoic, and these are already sufficiently similar to *Marattia* to reject the use of the fossil genus *Marattipsis* for them. *Qasimia* may therefore be regarded as the direct ancestor of taeniopteroid forms of *Marattia*.

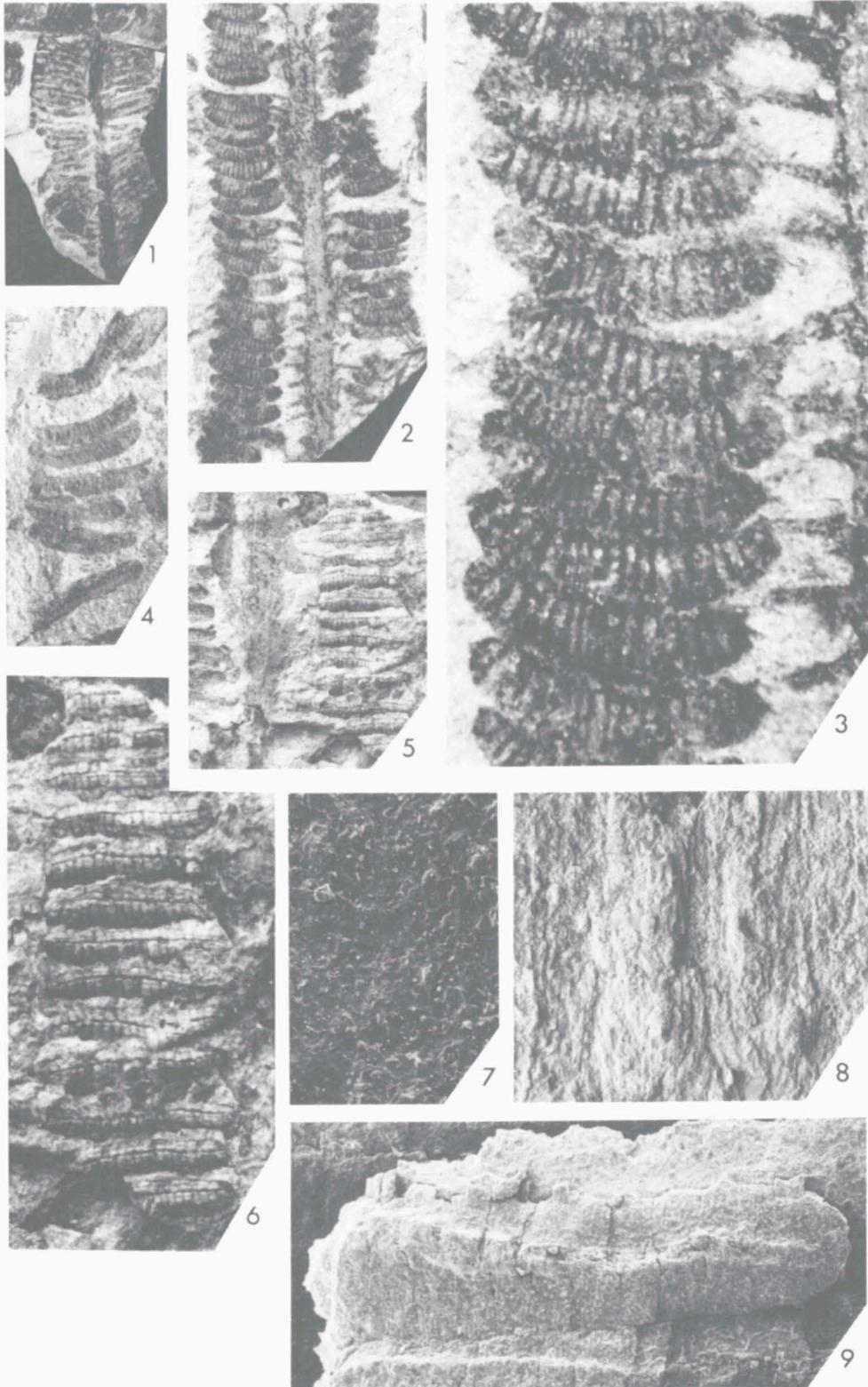
Plate 19

Marattia anglica (Thomas) Harris

Middle Jurassic (Saltwick Formation) of North Yorkshire, U.K.

- Fig. 1. Pinnule in which synangia extend across the full half-width from midrib to margin of the lamina. Hasty Bank main plant bed, coll. J.D. Lovis, 1975, $\times 1$; V. 58 557W (B.M.(N.H.)).
- Figs. 2, 3. Synangia tilted sideways and lamina of pinnule not preserved, thus appearing like *Lophotheca* Zhao. Roseberry Topping plant bed, coll. J.D. Lovis, 1979; V.62 045 (B.M.(N.H.)); 2: $\times 3$; 3: $\times 12$.
- Fig. 4. Specimen like that in figs. 2, 3, but in which the synangia are somewhat displaced from their original position on the lamina. Roseberry Topping plant bed, 580-600 cm beneath the sandstone capping, coll. C.R. Hill, 1977; $\times 3$; V.62 046 (B.M.(N.H.)).
- Figs. 5, 6. Showing bivalved organisation of the synangium as in extant species. Roseberry Topping plant bed, 20-40 cm beneath the sandstone capping, coll. C.R. Hill, 1976; V.62 047 (B.M.(N.H.)); 5: $\times 3$; 6: $\times 5$.
- Fig. 7. Dorsal wall of tilted synangium, showing more or less square or rounded isodiametric cell outlines. Hasty Bank main plant bed, coll. J.D. Lovis, 1975, silstone matrix; SEM, $\times 100$; V.60 675, (B.M.(N.H.)).
- Fig. 8. Ventral wall of synangium, showing elongate cell outlines. Roseberry Topping plant bed, 760-780 cm beneath sandstone capping, coll. C.R. Hill, 1978; SEM, $\times 100$; V.62 050, (B.M.(N.H.)).
- Fig. 9. Showing bivalved organisation of the synangium. Roseberry Topping plant bed, 760-780 cm beneath the sandstone capping, coll. C.R. Hill, 1978; SEM, $\times 30$; V.62 048, (B.M.(N.H.)).

Plate 19



The ancestry of *Qasimia* itself is more speculative. Two lines of evidence may be explored. Firstly, the foliage shows considerable size variation, particularly in pinnule length, from 11 mm to 110 mm, whilst the pinnule width varies from 6 mm to 12-15 mm. This is the kind of variation that is normally associated with pinnae of the last order rather than pinnules. It is also of note that the midrib of the larger, elongate pinnules shows longitudinal striations which are more usually found in rachises. Thus it seems likely that the large pinnules of *Qasimia schyfsmae* represent totally fused, condensed pinnae of the last order, which are, in fact, still represented in *Qasimia* by the rarer form of pinna which has small, neuropteroid pinnules. Fusion of pinnules to produce an entire lamina is discussed by Asama (1960).

Stidd (1974) and others have pointed out that a pectopterid ancestor must be envisaged for present day Marattiales. Since the pinnae of the last order in Carboniferous pectopterids with marattialean characteristics show a rounded apical pinnule, it is reasonable to compare with the rounded apices of the pinnules of *Qasimia schyfsmae*, particularly the taeniopteroid ones that are supposed here to represent condensed pinnae. These rounded apices would therefore reflect the shape of the pinna apex in a supposed Carboniferous ancestor; the pointed apices of the taeniopteroid pinnules in Mesozoic and living *Marattia* would represent a later modification.

The possibility that the taeniopteroid pinnules of *Qasimia* represent condensed pinnae of the last order is also suggested by the evolutionary changes which seem to have taken place in the Mesozoic. *Qasimia* shows a much higher vein density than comparable vegetative pinnules of Mesozoic and extant *Marattia*; this reduction in the number of veins (and, perhaps more significantly, in the number of vein bifurcations) is matched in *Qasimia* itself by the fewer bifurcations and consequently lower vein density of the fertile pinnules. These show venuli recurrentes alternating with the veins.

The venuli recurrentes (fibre bundles) of Marattiales have long been regarded as a curiosity, and have given rise to a certain amount of speculation without any firm evidence as to their origin and function. In general, however, they have been considered to represent the byproduct of fusion of an originally more divided frond. For instance, Holtum (1954) regarded them as representing the fused margins of neighbouring pectopterid pinnules. *Qasimia* provides the first direct evidence that this suggestion is probably incorrect. The vegetative pinnules of *Qasimia* (which show no evidence of venuli recurrentes) indicate that fusion had occurred without their formation. We conclude that the venuli recurrentes in fertile pinnules of *Qasimia* merely represent degenerate surplus branchlets left over from vein branches in excess of those needed to service the synangia. Perhaps they served a purpose in strengthening the lamina, since the weight of the large synangia must have been considerable. Whatever the case, by Mesozoic times both the fertile and vegetative pinnules of *Marattia* uniformly had a low vein density, rather like that of fertile *Qasimia*, and showed a uniform association with venuli recurrentes. By the time the Recent species had evolved, with their generally smaller synangia, the venuli recurrentes had disappeared; leaving no trace, as it were, of their former and transitory existence.

The evolutionary history of the *Qasimia* fructification is more speculative. Its synangia consist essentially of two strips of laterally joined, elongate sporangia, which are united into a bivalved structure. The presumed orientation of the sporangial loculi in life was with their long axes perpendicular to the pinnule lamina (Fig. 5), and the whole synangial structure is aligned with a lateral vein branch. An ideal ancestral form might be considered to have possessed pendant, rather elongate sporangia occurring in single file on both sides of the mid-vein of pectopterid pinnules. However, the smaller pinnules of

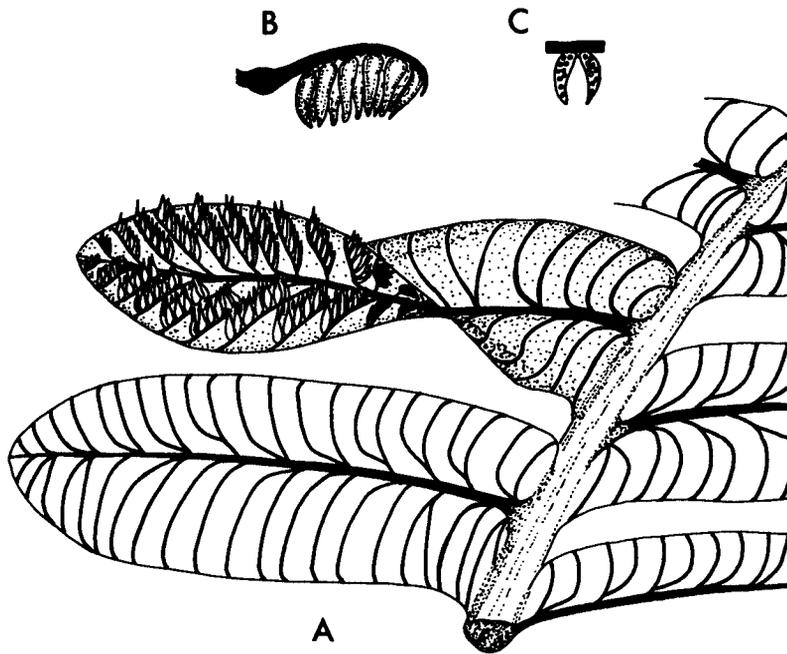


Fig. 6. *Danaeites saraepontanus* Stur. Restoration based on Corsin, 1951, and Laveine, 1969; A: a portion of a fertile pinna, with 'Moulin Rouge' display of pinnule on the left in order to illustrate the sori; each sorus consisting of two rows of separate sporangia, approx. $\times 5$; B: diagrammatic transverse section of a sorus, $\times 10$; C: transverse section of one side of a fertile pinnule, $\times 10$.

Qasimia (Pl. 3, figs. 3, 4) show synangia along the lateral veins, an arrangement just like the larger, taeniopteroid pinnules. This indicates that developmental processes resulting in condensation, presumably involving a genetic 'switch', could in practice occur from pecopterid forms with sori arranged parallel to the lateral veins. This is also evident in extant Marattiales, for instance from *Angiopteris monstrosa* Alderwerelt Hill & Camus, 1985, fig. 23), which shows some pinnules of normal *Angiopteris* form and other, condensed ones, of normal *Macroglossum* form. The only intermediate 'pinnules' are peculiar lobes that resemble the condensed *Macroglossum* form more than the *Angiopteris* one. Thus there is in Marattiales no necessary requirement that a pecopterid ancestor had sporangia arranged parallel to the pinnule midrib. Such a requirement (see also Stidd, 1974) is an artefact of idealistic comparative morphology, and is probably of no empirical significance.

A fairly appropriate possible ancestor of *Qasimia*, therefore, is the Carboniferous pecopterid *Danaeites saraepontanus* Stur. Laveine (1969) has reinterpreted the fructification of this Westphalian D fern as composed of elongate, pointed sporangia occurring in double rows along the lateral veins of a pecopterid pinnule (Fig. 6). If these sporangia were joined laterally, they would form strips rather like the valves of the *Qasimia* synangium, and condensation of the pinnae would produce a taeniopteroid lamina (though the venation density of *D. saraepontanus* is too low for *Qasimia*). *Qasimia* is of exceptional interest in that although taeniopteroid pinnules are predominant, some remain small. However, these are neuropteroid rather than pecopteroid in their venation, representing a major difference from *D. saraepontanus*.

Conclusions

(1) *Qasimia schyfsmae* (Lemoigne) gen. et comb. nov., from the Permian of Saudi Arabia, is closely similar to taeniopteroid forms of Mesozoic and extant *Marattia*. Megascopically, it differs principally in the rounded rather than pointed apices of its pinnules, in the higher vein density of vegetative vs fertile pinnules, and in the occurrence of some pinnae which have more or less neuropteroid pinnules. The synangia characteristically extend across the full half-width of the fertile pinnules. Microscopically, these synangia have comparatively long sporangial compartments, which also possess longer cells on their dorsal walls. Details of dehiscence and of the ventral wall of the synangium are still unknown.

A number of other Permian occurrences of *Qasimia*-like ferns exist in the East Asian Cathaysia Province, and these include most notably *Qasimia tobaensis* (Li, Yao & Deng) comb. nov. Many such ferns have been wrongly determined as *Taeniopteris* or *Neuropteridium*. Some of the material figured and described from the Soviet Far East by Burago (1977) may also belong to *Qasimia*.

(2) *Qasimia schyfsmae* provides the earliest stratigraphic record of a fern closely related to the taeniopteroid species of *Marattia* (which occur from the Triassic onwards), and may be regarded as directly ancestral to them. Mesozoic species such as *Marattia anglica* (Thomas) Harris provide a link between *Qasimia* and the extant species, particularly with regard to synangial length and venuli recurrentes. One of several interesting features of *Qasimia* is its dimorphism, expressed by the difference in vein density between its vegetative and fertile pinnules. The lower vein density of the fertile pinnules is apparently associated with the occurrence of venuli recurrentes, which seem to mark the vestiges of surplus veins in the fertile pinnules relative to the vegetative ones. In Mesozoic *Marattia*, which shows lower vein densities for both the vegetative and fertile pinnules, there are venuli recurrentes in both. Extant species of taeniopteroid *Marattia* also have lower vein densities in both fertile and vegetative pinnules but have lost the venuli recurrentes entirely.

(3) Although speculative, it is assumed that the Carboniferous ancestor of *Qasimia* was a pecopterid form with elongate, pendant sporangia in double rows along the veins; lateral joining of sporangia would have produced the valves of the synangium. In *Qasimia*, some pinnules remain small, thus providing some evidence of such ancestry, but they are neuropteroid/alethopteroid rather than pecopteroid. The larger, taeniopteroid pinnules of *Qasimia* were presumably produced by the fusion of such small pinnules, that is, by developmental 'condensation' of pinnae of the last order. The ancestor may have been similar to *Danaeites saraepontanus* Stur.

References

- Andrews, H.N., 1970. Index of generic names of fossil plants, 1820-1965.— *Bull. U.S. Geol. Survey*, 1300: 1-354.

- Archangelsky, S. & O.G. Arrondo, 1971. Palaeophytologia Kurtziana III. 2. Estudio sobre el género *Botrychiopsis* Kurtz (= *Gondwanidium* Gothan) del Carbónico y Pérmico gondwánico. — *Ameghiniana*, 8, 3/4: 189-227, pls I-VI.
- Archangelsky, S. & R.H. Wagner, 1983. *Glossopteris anatolica* sp. nov. from uppermost Permian strata in south-east Turkey. — *Bull. Br. Mus. nat. Hist. (Geol.)*, 37, 3: 81-91.
- Asama, K., 1959. Systematic study of so-called *Gigantopteris*. — *Sci. Rept. Tohoku Univ., Sendai, Japan*, 2 (Geol.), 31, 1: 1-72, pls I-XX.
- Asama, K., 1960. Evolution of the leaf forms through the ages explained by the successive retardation and neoteny. — *Sci. Rept. Tohoku Univ., Sendai, Japan*, 2 (Geol.), Special Vol., 4 (Hanzawa Mem. Vol.): 252-280, pls 26-29.
- Asama, K., 1976. *Gigantopteris* flora in Southeast Asia and its phytopalaeogeographic significance. — *Geol. Palaeont. SE Asia*, 17: 191-207, pls 28-30.
- Brousriche, C., 1982. Sur la synonymie de *Crossotheca boulayi* Zeiller, 1886-88 et *Crossotheca bourozii* Danzé, 1956 avec l'espèce-type du genre: *Crossotheca crepinii* Zeiller, 1883. Une nouvelle interprétation de la fructification. — *Géobios*, 15, 5: 679-703, pls 1-5.
- Brousriche, C., 1983. Les Fougères sphénoptéridiennes du Bassin Houiller Sarro-Lorrain (Système-matique-Stratigraphie). — *Soc. géol. Nord, Publ.* 10: 1-480, pls 1-100 (Thèse Univ. Sci. techn. Lille).
- Burago, V.I., 1977. Elementy mezozojskoj flory v pozdnepermskoj flore yuzhnogo Primorya. (Elements of Mesozoic floras in the Late Permian floras of South Primorye.) In: V.A. Krassilov, (ed. Paleobotanika na Dalneya Vostoka Palaeobotany in the Far East.) — Vladivostok, Akad. Nauk SSSR, Far-Eastern Sci. Centre: 45-51, pls XXIII-XXVII (in Russian, with English abstract).
- Corsin, P., 1951. Pécoptéridées. In: *Etudes des Gites Minéraux de la France. Bassin houiller de la Sarre et de la Lorraine. I. Flore fossile*, 4. — Impr. Petits-fils de L. Danel, Loos (Nord): 175-370; pls CVIII-CIC.
- Cotthem, W. van, 1970. Comparative morphological study of the stomata in the Filicopsida. — *Bull. Jardin Bot. Nat. Belgique*, 40: 81-239.
- El-Khayal, A.A., W.G. Chaloner & C.R. Hill, 1980. Palaeozoic plants from Saudi Arabia. — *Nature*, 285 (No. 5759): 33-34.
- El-Khayal, A.A. & R.H. Wagner, 1985. Upper Permian stratigraphy and megaflores of Saudi Arabia: Palaeogeographic and climatic implications. — *C.R. X Congr. Int. Strat. Géol. Carbonifère, Madrid*, 1983, 3: 17-26
- Gothan, W., 1927. Gondwanapflanzen aus der Sierra de los Llanos und benachbarten Gebieten. — *Abh. Senckenberg. Naturf. Ges.*, 31: 341-344.
- Gothan, W., 1941. Paläobotanische Mitteilungen. 5-7. — *Paläont. Zeitschr.*, 22: 421-438.
- Gu & Zhi, 1974. An Introduction to Chinese Fossils. Chinese Plant Fossils. I. Chinese Palaeozoic Plants. — *Sci. Publ. House, Peking*: 1-277, pls 1-130 (in Chinese).
- Halle, T.G., 1927. Palaeozoic Plants from Central Shansi. — *Palaeont. Sinica*, A, II, 1: 1-316, pls 1-64.
- Harris, T.M., 1931. The fossil flora of Scoresby Sound, East Greenland. 1. Cryptogams (exclusive of Lycopodiales). — *Meddel. Gronland*, 85, 2: 1-104, pls 1-18.
- Harris, T.M., 1961. The Yorkshire Jurassic Flora. I. Thallophyta-Pteridophyta. — *Br. Mus. nat. Hist., London*: 1-212.
- Hemer, D.O., 1965. Application of palynology in Saudi Arabia. — *V Arab Petroleum Congr., Cairo*, 1965: 28 pp., 14 pls.
- Hill, C.R. & J. M. Camus, 1985. Evolutionary cladistics of the marattialeans ferns. — *Bull. Br. Mus. Nat. Hist. (Botany)*, 14, 4.
- Hill, C.R. & A.A. El-Khayal, 1983. Late Permian plants including Charophytes from the Khuff Formation of Saudi Arabia. — *Bull. Br. Mus. nat. Hist. (Geol.)*, 37, 3: 105-112.
- Holtum, R.E., 1954. Flora of Malaya 2. Ferns. — *Govt. Printing Office, Singapore*: 1-653.
- Hull, D.L., 1968. The operational imperative: sense and nonsense in Operationalism. — *Systematic Zoology*, 16: 438-457.
- Jongmans, W.J. & W. Gothan, 1935. Die Paläobotanische Ergebnisse der Djambi-Expedition 1925. — *Jaarb. Mijneuzen Nederl. Oost-Indië*, 1930, Verh.: 71-201, pls 1-58.
- Kawasaki, S., 1931, 1934. The Flora of the Heian System, Pt 2. — *Bull. Geol. Survey Chosen*, VI, 2: pls 16-99; 47-311; pls 105-110.
- Kawasaki, S. & E. Konno, 1932. The Flora of the Heian System, Pt 3. — *Bull. Geol. Survey Chosen*, VI, 3: 31-44, pls 100-104.

- Kilpper, K., 1964. Über eine Rät/Lias-Flora aus dem nördlichen Abfall des Alburs-Gebirges in Nordiran. Teil I: Bryophyta und Pteridophyta. — *Palaeontographica*, B, 114, 1-3: 1-78, pls 1-15.
- Kon'no, E., 1968. The Upper Permian Flora from the Eastern Border of Northeast China. — *Sci. Rept. Tohoku Univ.*, Sendai, 2 (Geol.), 39, 3: 159-211, pls 11-25.
- Kon'no, E. & K. Asama, 1970. Some Permian Plants from the Jengka Pass, Pahang, West Malaysia. — *Geol. Palaeont. SE Asia*, 8: 97-132, pls 17-24.
- Kon'no, E., K. Asama & S.S. Rajah, 1970. The Late Permian Linggiu Flora from the Gunong Blumut Area, Johore, Malaysia. — *Bull. Nat. Sci. Mus.*, Tokyo, 13, 3: 491-580, pls 1-17.
- Konijnenburg-van Cittert, J.H.A. van, 1975. Some notes on *Marattia anglica* from the Jurassic of Yorkshire. — *Rev. Palaeobot. Palynol.*, 20: 205-214, pl. I.
- Laveine, J.P., 1969. Quelques Pécoptéridinées houillères à la lumière de la Palynologie. — *Pollen et Spores*, 11, 3: 619-668, pls 1-17.
- Lemoigne, Y., 1978. Sur l'individualité de la province paléofloristique gondwanienne. — *Ann. Soc. géol. Nord*, 97: 383-404.
- Lemoigne, Y., 1981a. Présence d'une flore comprenant des éléments cathaysiens, dans le centre de l'Arabie Saoudite au Permien supérieur. — *C.R. Acad. Sci. Paris*, II, 292: 1231-1233 (= III, 292: 975-977).
- Lemoigne, Y., 1981b. Flore mixte au Permien supérieur en Arabie Saoudite. — *Géobios*, 14, 5: 611-635, pls 1-6.
- Li Xingxue & Yao Zhaoqi, 1983. Fructifications of gigantopterids from South China. — *Palaeontographica*, B, 185, 1-3: 11-26, pls 1-6.
- Li Xingxue, Yao Zhaoqi & Deng Longhua, 1982. An early Late Permian flora from Toba, Qamdo District, Eastern Xizang. — *Palaeont. Xizang*, V: 17-44, pls I-XIII.
- Lorch, J., 1967. A Jurassic florule from Sinai. — *Israel J. Bot.*, 16: 29-37, pls 1-3.
- Mamay, S.H., 1976. Paleozoic origin of the Cycads. — *U.S. Geol. Survey Prof. Paper*, 934: 1-48, pls 1-5.
- Mapes, G. & J.T. Schabillion, 1979. *Millaya* gen.n., an Upper Paleozoic genus of marattialean synangia. — *Am. J. Bot.*, 66, 10: 1164-1172.
- Schimper, W.P., 1869-1874. *Traité de Paléontologie végétale, ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel.* — J.B. Baillière & Fils, Paris, Tome I: 1-738, Atlas: pls 1-LIII (1869).
- Schimper, W.P. & A. Mougeot, 1844. *Monographie des plantes fossiles du Grès bigarré de la chaîne des Vosges.* — Leipzig: 1-83, pls I-XL.
- Shimakura, M., 1940. Permian Plants from the Lungtan Coal Field, Kiangsu, China. — *Journ. Shanghai Sci. Inst.*, Section II (III): 1-21, pls I-IX.
- Sixel, T.A., L.I. Savizkaja & T.A. Iskandarkhodjayev, 1975. Rasteniya srednego karbona, verkhnego karbona i nizhnej permi Fergany. (Plants of the Middle Carboniferous, Upper Carboniferous and Lower Permian of Fergana.) In: T.A. Sixel (ed.) *Biostratigrafiya verkhnego paleozoya gornogo obramleniya yuzhnoj Fergany.* (Biostratigraphy of the Upper Paleozoic of the mountains bordering South Fergana.) — Izdat. 'Fan', Uzbek. S.S.R.: 77-143, tab. XXI-L.
- Stidd, B.M., 1974. Evolutionary trends in the Marattiales. — *Ann. Missouri Bot. Garden*, 61: 388-407.
- Stockmans, F. & F.F. Mathieu, 1939. La flore paléozoïque du Bassin houiller de Kaiping (Chine). — *Mus. Roy. Hist. nat. Belgique*: 49-164, pls I-XXXIII.
- Taylor, T.N., 1967. On the structure and phylogenetic relationships of the fern *Radstockia* Kidston. — *Palaeontology*, 10, 1: 43-46, pls 6-7.
- Wagner, R.H., 1962. On a mixed Cathaysia and Gondwana flora from SE. Anatolia (Turkey). — *C.R. IV Congr. Int. Strat. Géol. Carbonifère, Heerlen, 1958*, III: 745-752, pls 24-28.
- Zalessky, M.D., 1934. Observations sur les végétaux permien du bassin de la Petchora, I. — *Bull. Acad. Sci. U.R.S.S., Classe Math. Nat.*, 1934, 2-3: 241-289.
- Zhao Xiuhu, Mo Zhuanguan, Zhang Sanzhen & Yao Zhaoqi, 1980. Late Permian Flora in western Guizhou and eastern Yunnan. In: *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formations in Western Guizhou and Eastern Yunnan.* — *Inst. Geol. Palaeont. Acad. Sinica, Science Press, Beijing*: 70-99, pls I-XXIII (in Chinese).

Errata Scripta Geol. 79

p. 40, line 18: p. .. should read p. 31

p. 42, line 21: p. .. should read p. 26