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**PALYNOLOGICAL STUDY OF A HOLOCENE PEAT AND A MIOCENE  
COAL DEPOSIT FROM NW BORNEO**

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## PALYNOLOGICAL STUDY OF A HOLOCENE PEAT AND A MIOCENE COAL DEPOSIT FROM NW BORNEO

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### ABSTRACT

Anderson, J. A. R. and Muller, J., 1975. Palynological study of a Holocene peat and a Miocene coal deposit from NW Borneo. *Rev. Palaeobot. Palynol.*, 19: 291-351.

The development of a Holocene peat near Marudi (Sarawak) and a Miocene coal near Berakas (Brunei) is studied pollen-analytically and stratigraphically by comparison with present-day swamp vegetation along the NW Bornean coast. A number of 76 pollen and spore types were recognized and are briefly diagnosed.

The Marudi profile starts on mangrove sediment and shows a succession which is closely comparable to the present-day zonation of the large raised bog of which it forms part.

The Berakas profile starts on fluvial sediments and remains in the mixed swamp forest stage. This small deposit has remained close to the coast and peat growth is terminated by marine transgression.

The floristic composition of the mixed swamp forest stage in both bogs, separated in age by approximately seven million years is closely comparable. Minor differences which exist can be attributed to differences in size, ecologic conditions and accessibility from mainland reservoirs.

Only one spore type, *Stenochlaena areolaris*, has become extinct in Borneo.

### INTRODUCTION

The coastal peat swamps of Sarawak and Brunei cover more than 15,700 km<sup>2</sup> and comprise 12.5% of the land surface of this part of NW Borneo. The forests on these swamps are at present the most valuable part of the Forest Estate. The first author has been engaged on a project, included in the Forest Research Programme of the Sarawak Forest Department, to study the ecology of the peat swamps. Results were submitted as a thesis for a Ph.D. to the University of Edinburgh (Anderson, 1961a). Papers on the flora of the peat swamps of Sarawak and Brunei (Anderson, 1963), insect damage (Anderson, 1961b), climatic damage (Anderson, 1964a) and the structure and development of the peat swamps (Anderson, 1964b) have already been published. Some details of the ecology of the peat swamps are included in these papers, but the main results are now being prepared for publication. The second author became interested in the pollen content of these peat

deposits in connection with his palynological studies of Tertiary sediments of these areas. In these studies, which aimed at providing a stratigraphic zonation, it became necessary to recognize the ecological indicator value of the dispersed pollen grains. For this a knowledge of the area of production and the means of dispersal is essential. In previous studies the mangrove and montane elements have been briefly discussed already (Muller, 1964, 1965; Germeraad et al., 1968). A large proportion of the fossil types, however, soon proved to have been derived from lowland peat swamp forest and this prompted a fruitful collaboration with the Sarawak Forest Department, which could supply a complete collection of well-identified recent reference material and a vast amount of ecologic information on lowland coastal as well as on inland peat deposits. Preliminary results of the initial investigations have already been published (Muller, 1963; Brunig, 1968).

Since it proved possible to infer the ecologic succession within the peat deposits from the pollen diagrams, it was decided to extend the investigation to a Tertiary coal bed, in order to find out whether plant communities had changed since the Miocene. The two diagrams presented here, from a Holocene peat deposit near Marudi (Sarawak) and from a Miocene coal bed near Berakas (Brunei) proved to be comparable. In both, a distinct succession appeared to be present, which could be related to present-day zonation.

The Holocene peat swamps along the coast of NW Borneo are of the tropical raised-bog type, usually with a bog plain, which tends to be more extensive in more inland swamps. The peat itself is woody, acidic and markedly oligotrophic. A concentric zonation of the vegetation occurs on most swamps. The term "swamp catena" has been used to describe this zonation, and six plant communities (phasic communities) are recognized in the catena. The distribution of the phasic communities could be plotted by means of aerial photographic interpretation and checked by ground surveys. The two most advanced phasic communities in the catena occur in the centre of the most highly raised bogs which are found on the more inland peat swamps in the Baram river valley in northern Sarawak and in immediately adjacent areas in Brunei.

Previous palynological work on the peat swamps of Southeast Asia is largely confined to the pioneer studies of Polak (1933, 1949), who studied the peat swamps of southern Borneo, Sumatra and Java and established the presence of a well-preserved pollen and spore flora in tropical peats of the region.

Data on Tertiary coal of this area are even more scarce and limited to brief notes on Malayan coal (Law, 1961; Trivedi and Verma, 1969a, b).

## METHODS

### *Field technique*

Difficulties were initially experienced in obtaining core samples from the

Holocene peat bogs. "Hiller" and "Dachnowski" type borers proved a failure in the tropical woody peats, being incapable of dealing with the semi-decomposed material found at all levels in the profile. A final attempt was made in 1958 using a "Kjellerman" piston soil sampler. This heavy instrument, though cumbersome and difficult to handle in peat swamps, produced excellent results. Not infrequently, however, well-preserved undecomposed woody material prevented the sampler from being driven beyond a certain level. Further borings had then to be attempted in locations nearby. Occasionally the samples obtained contained an overabundance of semi-decomposed woody material and little pollen. The samples raised were closely inspected in order to determine the amount of contamination. In general the centre of each sample was to be considered as essentially uncontaminated.

At the Marudi location a series of 27 samples were obtained at 0.5 m intervals from the surface to a depth of 13 m. Thick samples were collected at 5, 10 and 12 m for radio-carbon dating.

The coal seam at Berakas was accessible in a shallow cut, dug for the purpose. A clean face was prepared, including a section of overlying and underlying mineral sediments, and from this a continuous series of 1 cm thick samples were collected, resulting in 100 coal and 13 mineral samples. If it is assumed that compaction of this 1 m thick coal bed has been to 1/10 of its original thickness, each cm sample would represent approximately 10 cm of peat originally and the sampling interval would then have been about 5 times more dense than in the Marudi section. The total thicknesses originally would also be comparable.

### *Laboratory technique*

The peat cores from Marudi were carefully opened in the laboratory and the undisturbed central column only was utilized for preparation. If the sample was large, a representative smaller sample was taken by random selection of a number of smaller pieces, otherwise the complete undisturbed sample was prepared. The samples were first disintegrated by boiling for a few minutes in 5% KOH. The resulting well-mixed mass was washed with water by repeated settling and decanting until the water remained fairly clear. The sample was then sieved and coarse residue retained for examination on larger plant remains. The fine residue was centrifuged and then subjected to standard acetolysis treatment. Most samples yielded a rich crop of well-preserved pollen grains and spores, but a few of the very fibrous ones had to be sieved again on a finer sieve. One sample only failed to yield sufficient pollen.

Peat stratification was studied both in the field and in the laboratory, and the results have been summarized in the columns for peat lithology and degree of humification on the pollen diagram. In the field texture, colour and macroscopically visible plant remains were recorded, in the laboratory the smaller plant remains were studied with low and high magnification

after chemical treatment of the samples. The pH and ash content were also determined. The most important recognizable peat components were remains of wood, bark, roots and rootlets, cuticles and moss leaves. Seeds were not observed. Due to lack of recent reference material, unfortunately, no opportunity existed for a thorough evaluation of the different and sometimes very typical tissue fragments which strike the eye in the microscopic preparation. The degree of humification has been estimated by a combination of observations on texture while fresh by the method of pressing a lump of peat in the hand, by the microscopical appearance of tissue fragments and by a rough colorimetric test. For the latter, striking differences in the colour of the alcohol extract of the prepared residues were utilized under the assumption that the darker the colour, the higher the degree of humification. The scale is comparable to the one originally proposed by Van Post and Granlund (cf. Faegri and Iversen, 1964).

The Miocene coal samples from Berakas could be classified in a dull, conchoidally fracturing, bituminous type or a lustrous, crumbling, lignitic type. The samples were crushed, slightly oxidized with 5% cold Schulze solution, washed with 5% KOH and acetolyzed. The mineral samples were pretreated with HF followed by bromoform separation. In general pollen and spore content was comparable to the peat samples from Marudi, although the state of preservation was less perfect. Tissue fragments were abundantly present but could not be further classified.

## POLLEN AND SPORE TYPES

### *Introductory remarks*

In the following account all pollen and spore types recognized will be briefly discussed. If not adequately described in the literature a short diagnosis will be presented and a few of the most characteristic ones will be illustrated by photomicrographs.

The affinity of the types is indicated either by direct reference to a living taxon or, if the type occurs in more than one taxon, by adding "type". The comparison was mainly limited to taxa known to occur in peat swamp forest, and in adjacent environments, e.g. mangrove and riverine vegetation. The nomenclature is based on a catalogue published in 1963 by Anderson with recent corrections based on an arboreal checklist for Sarawak (Anderson, in press).

For each genus the total number of species occurring in Sarawak, followed by the number found in the peat swamps is indicated between brackets. For arboreal genera these data are taken from the publications cited above, for the remainder they are based on comparative data available in the Kuching Herbarium.

The Miocene types have been treated in the same way as the Holocene ones, following the system outlined by Zagwijn (1960) and adopted for mangrove types by Muller (1964). Consequently no new names are proposed for new Miocene records. If not plotted on the Berakas diagram, the sample

numbers in which they were found are added.

## LYCOPODIALES

### *Lycopodium cernuum*

A trilete spore (30  $\mu\text{m}$ ) with a circular outline and a rugulate sculpture. Included by Harris (1955) in group IV together with a few species which do not occur in Borneo.

Frequent in phasic community (ph. c.) VI in the peat swamp forests, but also occurring in Kerangas vegetation.

Found only in Marudi, in low frequencies.

### *Lycopodium phlegmaria* type

A trilete spore (35  $\mu\text{m}$ ) with a rounded triangular outline and a pitted-foveolate distal sculpture (Erdtman and Sorsa, 1971). Both *L. phlegmaria* and *L. pinifolium* produce this spore type and are restricted to ph. c. VI in the peat swamp forests of the Baram swamps although occurring in the surrounding lowland forests. The type is rare in Marudi and has been found only once in Berakas (underlying mineral sediments (no. D).

## FILICALES

### *Acrostichum aureum*

A large trilete spore (75  $\mu\text{m}$ ) with, in the fossil state, a smooth exine and relatively short laesurae. Characteristic of the mangrove environment.

In Marudi restricted to the mangrove sediments underlying the peat, but in Berakas occurring in rather low frequencies throughout.

### *Asplenium* type

In this type are grouped all smooth, monolete, bean-shaped spores of approx. 60  $\mu\text{m}$  length. Most have probably originated from the genus *Asplenium*, but similar spores are produced by the genera *Crypsinus*, *Lecanopteris*, *Platyserium*, *Schizaea* and *Selliguea*. All occur in peat swamp forests, while other genera outside the swamps may also have contributed. In view of this uncertainty, without ecologic indicator value.

Dominant both in Marudi and Berakas.

### *Polypodium* type

All monolete bean-shaped spores with an areolate or verrucate sculpture and in a size range of approx. 40–60  $\mu\text{m}$  are grouped in this type. Of the ferns which have been recorded from the peat swamps, the following genera produce this spore type: *Drynaria*, *Humata*, *Nephrolepis*, *Paragramma*, *Photinopteris* and *Polypodium*. Although small differences in spore morphology exist between these genera, the dispersed spores proved to be hardly separable, without further detailed study. In consequence the type has little or no ecologic indicator value.

It is of interest, however, that the type is dominant in Berakas, but much less frequent in Marudi. Presumably supply from outside the swamps was of more significance in Berakas.

### *Stenochlaena areolaris* (Plate I, 1)

The large (80  $\mu\text{m}$ ), slender, monolete spores, apparently lacking a perispore and bearing a small number of rather large exinous spines, were first described by Holtum (1932) and are, as far as is known, unique for the species. *S. areolaris* occurs at present as

an epiphyte on *Pandanus* in the Philippines and New Guinea at an altitudinal range of 150–1200 m but has not been recorded from Borneo. The fossil record of the spores indicates that it was common in NW Borneo in the Miocene, gradually disappearing in the Pliocene.

A regular constituent of the Berakas microflora only.

### *Stenochlaena palustris*

The sparsely verrucate, monolete spores of this species have been described by Holtum (1932) and by Nayar and Devi (1964a). Although similar spores may be produced by other, unrelated genera such as *Microsorium*, these genera have not been recorded from the peat swamp vegetation. Most of the spores of this type have therefore probably originated from *S. palustris*, a characteristic climbing fern, abundant in ph. c. I, but decreasing in succeeding communities.

Dominant both in Marudi and Berakas.

### *Syngamma* type

The smooth, trilete spores of this genus have been described by Erdtman and Sorsa (1971) and those of *S. lobbiana*, the only species occurring in the peat swamp forests (ph. c. I) are characterized by a relatively small size (40  $\mu$ m), rounded outline and long laesurae. Similar spores are, however, produced by other genera, notably *Adiantum*, but the latter genus has not been recorded from the peat swamps.

Only found in low percentages in Marudi.

## CONIFERALES

### *Dacrydium* (5/1)

The bisaccate pollen grains of this type are characterized by the gradual merging of the air sacs with the body and are quite similar to the pollen grains of *D. elatum* and *D. pectinatum* (cf. Erdtman, 1957, 1965). The latter is the common species in the lowlands of NW Borneo, occurring on kerangas soils; also in one locality in the Lawas District gregariously in peat swamp forests.

The rare grains found scattered both in Berakas (no. D) and Marudi have probably originated outside the peat swamps.

### *Podocarpus* (4/0) including the new genus *Decussocarpus* (3/2)

This type is characterized by the distinctly outlined air sacs with a radial internal structure and relatively small body size. The grains are similar to those of *D. morleyi* which occurs on the coastal margins of ph. c. I.

Scattered in Marudi as well as in Berakas (nos. A, D, E, 10–12, 20, 25, 26, 30, 43, 77, 93).

## ANGIOSPERMAE

### *Dicotyledones*

#### *Alangiaceae*

### *Alangium* (6/1)

The characteristic grains of this type are closely comparable to those of *A. havilandii*, described in detail by Reitsma (1970). This is the only species of the genus recorded from the peat swamps, where it is of rare occurrence in ph. c.I.

Found scattered in low frequencies both in Marudi and Berakas (nos. 42, 47, 76, 85).

### Anacardiaceae

#### *Campnosperma* (3/2) (Plate I, 2)

The tricolporate pollen grains of this genus are characterized by their small size (24  $\mu\text{m}$ ), striate sculpture and conspicuous endoapertures. They are probably mostly derived from *C. coriacea*, which is locally abundant near the coastal margin of ph. c. I. *C. squamata*, which is much rarer, may also have contributed.

A rather frequent type both in Marudi and Berakas.

#### *Melanorrhoea* (9/3) (Plate I, 3)

This genus produces pollen grains which are 35  $\mu\text{m}$  in diameter, tricolporate with long colpi and rather small endoapertures and a very characteristic reticulate sculpture consisting of a thin, reticulate tectum, supported by rather long, decumbent verrucae. The lumina of the reticulum of the species recorded from peat swamp forests are 10  $\mu\text{m}$  in diameter and show only a faint striate alignment.

*M. beccarii* and *M. tricolor* occur in ph. c. I–IV, mainly near coastal margins.

Only found in Berakas, where it is locally frequent.

#### *Parishia* (3/2)

The indistinctly tricolporate pollen grains of this genus are mainly characterized by their spherical shape, fairly large size (45  $\mu\text{m}$ ) and coarse reticulation with high sinuose muri and distinct scattered verrucae within the lumina. Two species may have contributed, *P. maingayi* and *P. sericea*, mainly occurring in ph. c. I.

Only found in one sample in Marudi.

### Apocynaceae

#### *Alstonia* (5/2)

The pollen morphology of *A. scholaris* has been described in detail by Guinet (1962). In this species grains may be tricolporate, bicolporate and occasionally syncolporate. In *A. spathulata*, which occurs in the peat swamp forests (ph. c. I, coastal margins) and in *A. pneumatophora* which is locally frequent as an enormous tree on shallow coastal peat, pollen grains are exclusively syn-dicolporate.

Rare in Marudi.

#### *Dyera* (2/1)

The relatively large (45  $\mu\text{m}$ ), suboblate grains of *D. polyphylla* are recognizable by their short ektoapertures, absence of distinct endoapertures and relatively thick exine with a very finely reticulate tectum and slightly thickened endexine in the apertural areas. The outline in polar view is rounded triangular. *D. polyphylla* is locally abundant in ph. c. I, but also occurs, less commonly, in ph. c. II–IV.

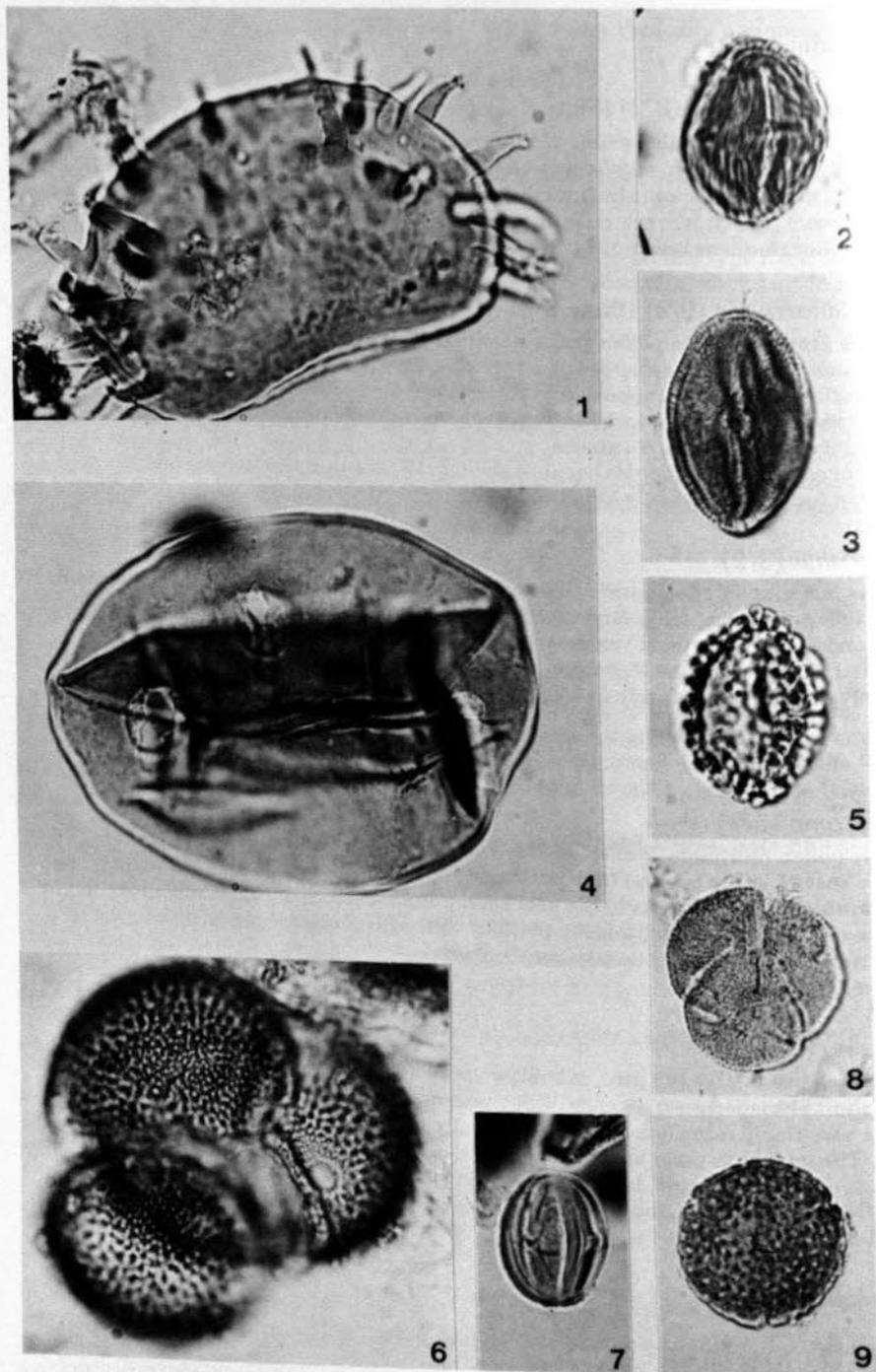
Infrequent in Marudi and found only once in Berakas, in the underlying mineral sediment (no. D).

### Aquifoliaceae

#### *Ilex* (14/3) (Plate I, 5)

For descriptions of this well-known pollen type, reference can be made to Erdtman

## PLATE I



(1952), Guinet (1962) and Huang (1972). The three species, *I. cymosa*, *I. hypoglauca* and *I. sclerophylloides* which occur in the peat swamp forests, could not be differentiated on their pollen characters. They occur in ph. c. I-V.

Frequent both in Berakas and Marudi.

## Araliaceae

### *Arthrophyllum* (4/2)

The pollen grains of *A. diversifolium*, one of the two species found in the peat swamp forests, have been briefly diagnosed by Rao and Lee (1970). They can, in addition to the characters mentioned there, be recognized by the rather thick exine and foveolate tectum. The genus is rare in ph. c. IV-V.

The pollen type occurs in low frequency in Marudi.

## Bombacaceae

### *Durio* (16/1) (Plate I, 4)

Large (80  $\mu\text{m}$ ), tricolporate, suboblate pollen grains with two ektoapertures and annular thickenings around the endoapertures are characteristic for *Durio carinatus*, which is the only species of the genus recorded from peat-swamp forests where it is found occasionally in ph. c. I. In Malaya it is locally more abundant in the same environment (Whitmore, 1972). The pollen grains of the related genus *Neesia*, of which *N. malayana* also occurs locally frequent in ph. c. I, can be differentiated on their finely reticulate sculpture (Fuchs, 1967).

A dominant type in Berakas.

## Burseraceae

### *Santiria* (12/4) and *Dacryodes* (7/2)

The pollen grains of these genera are indistinguishable. Those of the first genus have been briefly diagnosed by Erdtman (1952), of the second by Rao and Lee (1970). The pollen type can be characterized as subprolate, medium size (35  $\mu\text{m}$ ), tricolporate with long, distinctly costate colpate ektoapertures, pronounced endoapertures and a clear wall stratification. Endexine, layer of columellae and tectum are equally thick and the latter has a finely striate surface, which is only visible with 0.I.

The six species occurring in the peat swamp forests are found in ph. c. I-III.

The type has only been encountered in the clay underlying the Marudi peat.

## PLATE I (Magnification $\times 1000$ , 0.I.)

1. *Stenochlaena areolaris* (Berakas, B-83).
2. *Camposperma* (Berakas, B-27).
3. *Melanorrhoea* (Berakas, B-41).
4. *Durio* (Berakas, B-41).
5. *Ilex* (Berakas, B-83).
6. *Lophopetalum multinervium* (ph. c. I, surface).
7. *Dactylocladus* type (Berakas, B-41).
8. *Shorea albida* type (Berakas, B-83).
9. *Blumeodendron* (Berakas, B-14).

## Casuarinaceae

### *Casuarina* (3/1), including the unpublished genus *Gymnostoma*

For a detailed description of this characteristic pollen type, reference can be made to Pragłowski (1962) and Chanda (1969). Although the latter author has discovered that *Casuarina nobile* (manuscript), which occurs in Kerangas forests and in the Lawas peat swamps, has finely striate-rugulate pollen grains, while those of *Casuarina equisetifolia*, the common beach species are nearly smooth, this difference could not yet be observed in the fossil material.

The type is rare in Marudi, frequent in Berakas.

## Celastraceae

### *Lophopetalum multinervium* (8/2) (Plate I, 6)

The pollen of this genus has been described in detail by Hou (1969). Of the two species of *Lophopetalum* occurring in the peat swamps, *L. multinervium* has a distinctly coarser reticulate sculpture with fairly large columellae and a thicker wall than *L. rigidum*. The former species occurs locally on the coastal perimeter of ph. c. I.

The pollen type has been found regularly in Marudi.

## Crypteroniaceae

### *Dactylocladus* type (1/1) (Plate I, 7)

The pollen of this monospecific genus has been described by Muller (1975). It can be confused with pollen of *Axinandra* (Crypteroniaceae) and of Melastomataceae (*Medinilla*, *Marumia* and *Pogonantha*) which latter genera occur also in the peat swamps, albeit in small numbers. Outside the peat swamps, several other Melastomataceae and Combretaceae (*Terminalia*!) produce the same pollen type. Although the local abundance of *Dactylocladus* in the peat swamp forests makes it highly probable that the majority of the dispersed grains do in fact originate from this genus, some uncertainty remains. Reference is therefore made to the *Dactylocladus* type. *D. stenostachys* is abundant in all phasic communities.

The pollen type is frequent both in Marudi and Berakas.

## Dilleniaceae

### *Dillenia* (9/1)

The tricolpate, oblate, finely reticulate pollen grains of *Dillenia pulchella*, the only species of the genus which occurs in the peat swamps, in ph. c. I-II, conform to the general pattern of the genus as described by Erdtman (1952) and Dickison (1967).

The type is rare both in Marudi and Berakas.

## Dipterocarpaceae

Pollenmorphological information on this important family, which dominates a large part of the Bornean lowland forests, including the peat swamps, is very scarce. Only Erdtman and Rao and Lee (1970) present brief notes on three genera. For this reason the second author has, in collaboration with G. Maury (Paris) and B. Lugardon (Toulouse) embarked on a project to study in detail the pollen morphology of the family, especially with regard to the possibilities of identification of fossil dispersed grains. Although those studies are far from completed, it is already clear that at the level of the

light microscope, the family is pollen-morphologically rather uniform. Of the seven genera occurring in the peat swamp forests, only *Dipterocarpus* (32/1), *Dryobalanops* (6/1) and *Vatica* (28/1) have distinctive enough pollen to permit recognition. Of these, only *Dryobalanops* has been found. The pollen of *Shorea albida*, the main dominant in ph. c. II-IV, unfortunately could not be differentiated from that of other *Shorea* (120/9) species and is grouped under *Shorea albida* type (Plate I, 8). Dipterocarpaceous grains which could not be classified under these two types have been grouped as *Dipterocarpaceae varia* (Maury et al., 1975).

In general the pollen grains of the family are tricolpate with an intricate reticulate-rugulate wall structure. The pollen of the genus *Dipterocarpus* is the largest, that of *Dryobalanops* intermediate in size (50  $\mu\text{m}$ ) and suboblate obovate in shape, while *Shorea albida* pollen is almost spherical (25  $\mu\text{m}$ ), thin-walled with a very fine wall structure, appearing granular-perforate under the light microscope, but at higher magnification of the same basic type as the larger grains.

*Dryobalanops rappa* is the only species of the genus occurring in the peat swamps, locally frequent in ph. c. I-II. The species which may have been confused with the *Shorea albida* type (*Cotylelobium*, *Hopea* and *Shorea*) are widespread in ph. c. III-IV, with *Shorea albida* itself as the main dominant in ph. c. III-IV.

The *Dryobalanops* type has been recorded from the peat swamps of the *Shorea albida* type from both Marudi and Berakas.

### *Elaeocarpaceae*

#### *Elaeocarpus* (27/4)

The small, spherical, smooth, tricolporate pollen grains of this genus have been described by Erdtman (1952), Straka and Simon (1967) and Huang (1972). The four species occurring in the peat swamp forests cannot be differentiated on pollen characters and their distribution ranges from ph. c. I to IV.

Rather frequent in Marudi, but rare in Berakas (nos. C, 1, 16, 17, 19, 41).

### *Euphorbiaceae*

#### *Austrobuxus nitidus* (1/1)

The echinate, stephanoporate pollen grains of this type have been described by Punt (1962) under his *Aristogeitonia* subtype. They are characteristic for the Malesian species of *Austrobuxus* (= *Longetia*) and it should be noted that both Erdtman (1952) and Köhler (1965) only describe the aberrant pollen of the New Caledonian *A. buxoides*. *A. nitidus* occurs in the peat swamps in ph. c. I and IV.

Encountered in low frequencies in Marudi, but is absent from Berakas.

#### *Baccaurea* (28/2)

The pollen of this genus has been described by Punt (1962) under his *Baccaurea* subtype and by Köhler (1965) under his *Maesobotrya* type. *B. bracteata* and *B. javanica* cannot be differentiated on their pollen characters and are restricted to ph. c. I-III.

Rare in Marudi.

#### *Blumeodendron* (5/2) (Plate I, 9)

Punt (1962) has described the pollen of this genus under the *Blumeodendron* type. It is characterized by broad muri, supported by double rows of columellae and by small lumina. The two species occurring in the peat swamps are frequent in ph. c. I.

The type is very common in Berakas, less abundant in Marudi.

*Cephalomappa* (4/2) (Plate II, 1)

The pollen grains of this genus have been described by Punt (1962) under the *Cephalomappa* type. The two species occurring in the peat swamps (ph. c. II-III) are characterized by minute echinae positioned on top of the relatively broad muri, while the apertures are almost porate. The coarseness of the reticulum is rather variable.

Dominant in Berakas.

*Neoscortechinia* (3/2)

This pollen type is easily recognized by its finely echinate sculpture. It is assigned by Punt (1962) to the *Cheilosa* type. There are two species in the peat swamps: *N. kili* is a characteristic species of ph. c. I, and the few grains found are likely to have originated from this species.

The pollen type is very rare, both in Marudi and Berakas (no. 31).

## Fagaceae

*Lithocarpus* (46/4) and *Castanopsis* (14/1)

As has been pointed out by Soepadmo (1968), the pollen of these two genera is of the same type and characterized by prolate shape, small size (20  $\mu\text{m}$ ) and mostly smooth exine. In some species a minute perforation can be observed on the poles. The peat swamp species cannot be differentiated on their pollen. They occur in ph. c. I-IV, but species outside the peat swamps may also have contributed.

The type occurs regularly both in Marudi and Berakas.

## Guttiferae

*Calophyllum* (34/8) (Plate II, 2)

The pollen of the species occurring in the peat swamps could not be differentiated. In general, it is characterized by spherical shape, medium size (30-40  $\mu\text{m}$ ), long ektoapertures, with or without costae, equatorially elongated endoapertures and a rather uniform, finely reticulate, perforate or reticulate sculpture. The species present in the peat swamps are found in ph. c. I-IV.

Rare in Marudi but frequent in Berakas.

*Garcinia cuspidata* type (49/8) (Plate II, 3, 4)

This 4-5-porate pollen type, which had already been found by Polak (1933, plate III, fig. 99-102) has proved hard to identify. It is characterized by oblate shape, medium size (30  $\mu\text{m}$ ), an angular outline with concave sides; protruding vestibulate porate apertures, closed by a finely scabrate-echinate membrane, a distinct endexine, dense columellae and a finely scabrate tectum. In an earlier paper (Muller, 1963), it was erroneously referred to as "Symplocos" pollen. Mr. J. P. van Niel subsequently discovered that it was identical with the pollen grains of a *Garcinia* sp., which had been collected under no. S-12097 and provisionally identified as *G. cf. eugeniifolia*. They were, however, not identical with the pollen of *G. eugeniifolia* from material preserved in the Rijksherbarium (Leiden) and it later appeared that the specimen represents *Garcinia cuspidata*, described already by King in 1890 from the Malay Peninsula. Similar grains are also produced by the Formosan species *G. linii* (cf. Huang, 1972). *G. cuneifolia*, which occurs in the peat swamp vegetation has triporate grains which otherwise are rather similar. Other species of *Garcinia* have tricolporate pollen with verrucate or echinate sculpture and it appears that the genus, which is in need of taxonomic revision, produces at least two strikingly different pollen types.

*G. cuspidata* is of occasional occurrence in ph. c. I-II in western and central Sarawak

and is also known from Kerangas forest throughout Sarawak.

The pollen type is frequent both in Marudi and Berakas.

### *Hypericaceae*

#### *Cratoxylum* (6/2)

The pollen of this genus has been briefly described by Erdemir (1952) and Khan (1970) and is characterized by subprolate shape, long, equatorial bridged ektoapertures and a perforate to reticulate tectum, supported by distinct reticulations which are longest on the poles, and a rather thick endexine. The two species of this genus occurring in the peat swamps are found in ph. c. I and IV.

The pollen type is infrequent in Marudi.

### *Icacinaceae*

#### *Stemonurus* (6/2) (Plate II, 6)

The small, triporate pollen grains of this genus have been described by Lobreau (1969, 1972). The two species occurring in the peat swamps, *S. scorpioides* and *S. secundiflorus* cannot be differentiated on their pollen grains. They are found in ph. c. I-II.

Frequent in Marudi as well as in Berakas.

### *Lecythidaceae*

#### *Barringtonia racemosa* type (16/1)

This pollen type has been diagnosed in Payens (1967). It is different from the pollen of *B. reticulata* which is the only species of the genus recorded from the peat swamps and the two grains found in Berakas (nos. 21, 55) have therefore probably been derived from outside the swamp.

### *Leguminosae*

#### *Crudia* type (6/0) (Plate II, 5)

The pollen of this type has been discussed by Fasbender (1959) and by Germeraad et al. (1968). It is identical with the fossil species *Striatricolpites catatumbus*. Although similar grains occur in a number of other genera of the subfamily Caesalpinioideae, the derivation from the genus *Crudia* is rather probable. According to Whitmore (1972), *Crudia* trees are rare, although *C. wrayi* is locally common on river banks and swampy places, but they do not occur in peat swamps. It could very well be this, or a related species which has produced the abundant pollen grains found in the fluvial clay underlying the Berakas coal.

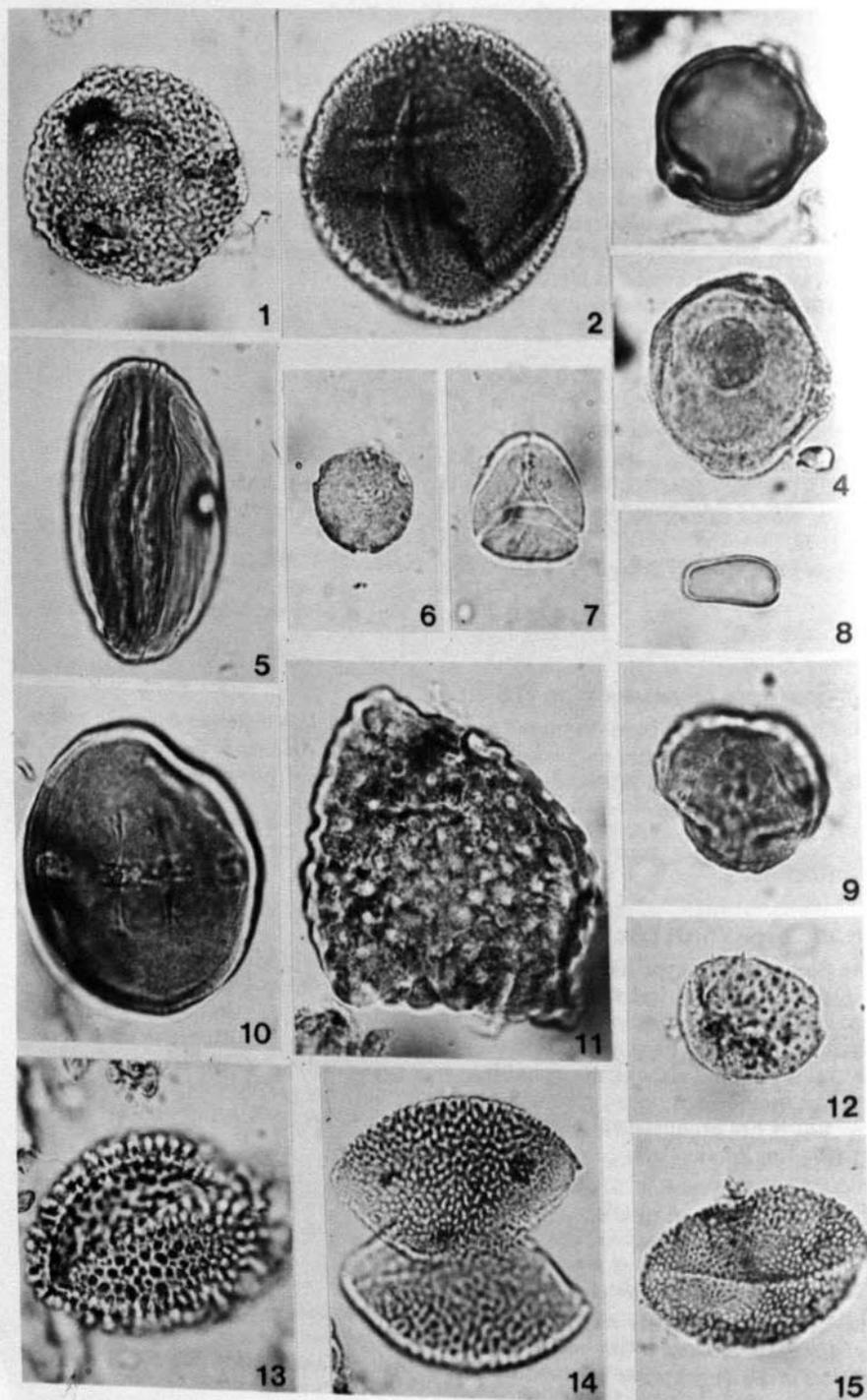
### *Linaceae*

#### *Ctenolophon parvifolius* (1/1)

This pollen type is easily recognized by its size, stephanocolpate apertures and finely reticulate tectum. It has been described by Germeraad et al. (1968). *C. parvifolius* is the only species of the genus occurring in Malesia and is found mainly in ph. c. I.

Rare both in Marudi and Berakas (nos. 39, 61, 65, 66, 68, 97).

## PLATE II



## Loranthaceae

### *Amylotheca* type

This pollen type is also found in *Lepidaria* and *Macrosolen*. The pollen of *Amylotheca* and the latter genus has been described and illustrated by Eganman (1952). *Lepidaria* and *Macrosolen* occur as crown parasites in ph. c. I.

A single specimen has been encountered in the Berakas coal (no. 26).

### *Elytranthe* type

The pollen grains of this type are slightly smaller than those of the preceding one, lobate in equatorial outline and synapophyses with a wavy surface sculpture. It may comprise more genera, which, however, are not known to occur in the peat swamp forests at present.

Rather frequent in Berakas.

## Malvaceae

### *Hibiscus* type (1/0)

The characteristic large, periporate, echinate grains of the *Hibiscus* type are included in the fossil form species *Echiperiporites estelae*, described by Germeraad et al. (1968). They may have been derived from *Hibiscus tiliaceus* or from *Thespesia populnea*, which are locally frequent in the littoral fringe and along tidal creeks.

A single grain was found in Berakas (no. 39).

## Meliaceae

### *Amoora* (3/1)

A small (25  $\mu$ m), subprolate grain with short ektoapertures, equatorially elongated ellipsoidal endoapertures and a smooth exine which is slightly thickened over a broad equatorial belt. Only one species, *A. rubiginosa* occurs in ph. c. I-II. The pollen grains of the closely related, much larger genus *Aglaiia* (43/0) are similar (Pennington and Styles, 1975). The pollen grains of *Sandoricum* are larger and possess a more equal exine thickness.

Found in Marudi in small numbers.

## PLATE II (Magnification $\times$ 1000, O.I.)

1. *Cephalomappa* (Berakas, B-41).
2. *Calophyllum* (Berakas, B-1).
3. *Garcinia cuspidata* type (ph. c. I, surface).
4. *Garcinia cuspidata* type (Berakas, B-66).
5. *Crudia* type (Berakas, D).
6. *Stemonurus* (Berakas, B-41).
7. *Eugenia* or *Tristania* (Berakas, B-41).
8. *Ficus* (ph. c. I, surface).
9. *Parastemon* (Berakas, B 31/32).
10. *Palaquium* type (Berakas, B-41).
11. *Gonystylus* (Berakas, B-30).
12. *Pandanus* (Berakas, B-41).
13. *Oncosperma* (ph. c. I, surface).
14. *Calamus* type (Berakas, B-41).
15. *Cyrtostachys* (Berakas, B-41).

*Chisocheton* (9/1)

Rao and Lee (1970) have described the pollen of *C. divergens* as triporate, while Pennington and Styles (1975) state that the genus has 3–5 colpi-porate pollen grains. *C. brachyanthus*, which is the only species of the genus occurring in peat swamp forests, has 4–5 stephanocolpate apertures with very short but distinct slit-like ektoapertures and aspidate endoapertures. It is further characterized by its large size (60  $\mu\text{m}$ ), spherical-suboblate shape and smooth exine. *C. brachyanthus* is rare in ph. c. I.

The pollen type has been encountered in small numbers in Marudi.

## Moraceae

*Ficus* (67/20) (Plate II, 8)

The small, thin-walled, smooth diporate pollen grains of this genus are very characteristic. The 15 *Ficus* species occurring in the peat swamp forests cannot be distinguished on pollen characters. They are widely distributed in ph. c. I–IV.

Rather frequent in Marudi, rare in Berakas (nos. 3, 4, 6, 14, 71, 92).

## Myrtaceae

*Eugenia* (87/13) and *Tristania* (11/3) (Plate II, 7)

The many species of these genera occurring in the peat swamp forests are hardly distinguishable on their pollen characters. The grains are generally small, tricolporate, syn- or parasyncolpate with a triangular outline and a smooth, thin exine (cf. Pike, 1956). The species of both genera occur in ph. c. I–V, but *Tristania* is much more common in ph. c. IV–V.

A common pollen type, both in Marudi and Berakas.

## Nepenthaceae

*Nepenthes*

The pollen morphology of the 5 species of this genus occurring in the peat swamp forests is quite uniform. Good descriptions of *Nepenthes* pollen are presented by Basak and Subramanayam (1966). The species range over ph. c. I–VI, but are much more abundant in ph. c. III–VI.

The pollen type is rare in Marudi and has only been found once in Berakas (no. 80).

## Olacaceae

*Anacolosia* (1/1)

The pollen grains of this genus are similar to the fossil type *Anacolosidites* cf. *luteoides*, described by Germeraad et al. (1968). *A. frutescens* is the only species recorded locally from peat swamp forest (ph. c. I).

Regularly present in low percentages in Berakas (nos. D, 2, 5, 10, 11, 15, 30, 36, 48, 51–53, 61–63, 67, 69, 80, 88, 90).

## Polygalaceae

*Xanthophyllum* (28/3)

This pollen type is characterized by 10–20 stephano- or colpi-porate apertures. The endoapertures have completely fused to form an equatorial belt of thinned endexine.

The shape is spherical-subprolate, 35  $\mu\text{m}$  in size, tricolporate with long, equatorially bridged, ektoapertures and a fairly thick tectate exine, covered with a characteristic irregularly rugulate sculpture and with a dense layer of minute columellae. The shape is similar to that of the pollen grains of the species of *Utricularia* (Thanikaimoni, 1966; Huynh, 1970) but differs in the shape of aperture development. The latter genus is common in the peat swamps. Two species of *Xanthophyllum* are also present in the peat swamps. *Xanthophyllum* *spicatum* is locally frequent in ph. c. IV.

The pollen type is rather rare in Marudi and Berakas peat, but only one grain has been found in Berakas (no. 16A).

## Rhizophoraceae

### *Combretocarpus rotundifolius*

This pollen type differs from that of *Combretocarpus* *sp.* and is easily recognized by its prolate shape, medium size, 35  $\mu\text{m}$  in size, with indistinct, polarly elongated endoapertures and a tectum which is finely subdivided into a thin endexine, a layer of very small, irregularly shaped, finely reticulate tectum (lumina  $< 0.5 \mu\text{m}$  in diameter), and a thin, finely reticulate tectum. Occurring infrequently in ph. c. II–V, but dominant in ph. c. VI.

This type is frequent in the upper part of the Marudi peat, but only one grain has been found in Berakas (no. 16A).

### *Rhizophora* type (2/0)

Described by Germeraad et al. (1968) under the name *Zonocostites ramonae*. It may include *Bruguiera* (4/0) grains (cf. Matter, 1964; Biasco and Duriani, 1973) and can only have been derived from mangrove forest.

Occurring in Marudi only in the mangrove sediments underlying the peat, but a common constituent in Berakas.

## Rosaceae

### *Parastemon* (2/2) (Plate II, 9)

The pollen grains of this genus are spherical-suboblate, 35  $\mu\text{m}$  in size, tricolporate with long, equatorially bridged, ektoapertures and a fairly thick tectate exine, covered with a characteristic irregularly rugulate sculpture and with a dense layer of minute columellae. Of the two species present in the peat swamp forests, *P. urophyllum* occurs occasionally in ph. c. I, while *P. spicatum* is abundant in ph. c. IV–VI.

The pollen type is rather frequent in Marudi as well as in Berakas.

## Rubiaceae

### *Canthium* (4/2)

For a description of the pollen of this genus reference can be made to Bronckers (1967). The two species found in the peat swamp forests have a similar pollen morphology, although the ektoapertures are even more reduced, giving the grains a triporate appearance. The tectum is finely, evenly reticulate. Occurring infrequently in ph. c. I–II.

The type is rare in Marudi.

### *Gardenia pterocalyx* type (4/1)

The large tetrads (66  $\mu\text{m}$ ) of this type are characterized by distinctly annulate pores, arranged according to Fischer's law and a relatively thin, smooth to slightly verrucate wall. *G. pterocalyx* occurs in ph. c. I–II. However, since this pollen type has only been

encountered in the mineral sediments underlying the Berakas coal (nos. D, E), but its origin is not quite certain and it may in fact have been derived from another species.

### *Jackia* (1/1)

The pollen grains of *J. ornata* have been briefly diagnosed by Mitra (1969) and are characterized by a spherical-suboblate shape, medium long colpate ektoapertures, small but distinct, circular, costate endoapertures, a thick wall consisting of distinct exine, conspicuous, fairly long columellae arranged in a reticulate pattern and supporting muri which enclose lumina of approx.  $1\ \mu\text{m}$  in diameter. The species is found occasionally in ph. c. I, mainly on shallow coastal peat.

The pollen type is rare in Marudi.

### *Timonius* (9/2)

This pollen type is characterized by three indistinct porate apertures, spherical shape, medium size ( $30\ \mu\text{m}$ ) and a very coarse reticulate sculpture, the muri being supported by few, but distinct columellae in single rows. *T. peduncularis* is the only species occurring in the peat swamps, where it is found occasionally in ph. c. I but is abundant in ph. c. IV.

Rare in Marudi.

## Sapindaceae

### *Pometia* (2/2)

The tricolporate pollen of this genus can be recognized by its suboblate shape, triangular outline in polar view with slightly protruding apertures, medium size ( $33\ \mu\text{m}$ ), very short and inconspicuous ektoapertures, circular aspidate endoapertures (cf. Erdtman, 1969: plate 37, fig. 3; and Huang, 1972: plate 139, figs. 23–30) and reticulate tectum, supported by small, but distinct columellae. The lumina are approx.  $1\ \mu\text{m}$  in diameter and rather irregularly ellipsoidal in outline. *P. pinnata* is the only species of the genus recorded from peat swamp forests and is found in ph. c. I near the inland margins.

Encountered in Berakas in low frequencies (nos. 10, 15, 41, 72, 80, 85, 93).

## Sapotaceae

### *Palaquium* type (28/6) (Plate II, 10)

Fairly large ( $35\text{--}50\ \mu\text{m}$ ) tetra- or pentacolporate, subprolate pollen grains with a thick, smooth wall, medium long, slit-like ektoapertures and ellipsoidal endoapertures. The outline in equatorial view is often characteristic because of the straight sides and rounded poles. This pollen type may have been produced by the genera *Ganua* (13/4), *Palaquium*, *Payena* (7/0) and *Planchonella* (4/0). Further detailed pollen-morphological studies may make it possible to come to a further differentiation. This group of genera, totalling 10 peat swamp species is common in all phasic communities from 1 to V.

Fairly frequent in Marudi, and one of the dominant pollen types in Berakas.

## Sonneratiaceae

### *Sonneratia caseolaris* (3/0)

The pollen of this species has been described by Muller (1969) and, as a fossil form species under the name *Florschuetzia levipoli* by Germeraad et al. (1968). It is no doubt extraneous to the peat swamps and originates from mangrove.

Found in Marudi only in the mangrove sediments underlying the peat, rather frequent in Berakas.

*Florschuetzia trilobata*

This form species has been described by Erdtman (1952) and is becoming extinct in the course of the Miocene. It is now represented by species of the genus *Sonneratia*.

Found only once in Berakas (nos. 105, 106).

*Theaceae**Ternstroemia* (11/2)

The pollen grains of the species *Ternstroemia* which occur in the peat swamp forests in ph. c. I-V are well represented by small size (25  $\mu$ m), subprolate shape, tricolporate apertures with fusate long, narrow apertures, rather large ellipsoidal endoapertures and a reticulate-aperturate surface with spines, contrasting with a smooth-walled equatorial belt.

The type occurs rarely in Marudi.

*Thymelaeaceae**Gonystylus* (4/3) (Plate II, 11)

The pollen of this genus has been described by Erdtman (1952), Rao and Lee (1970) and, in detail, by Archangelsky (1971). It can easily be recognized by its indistinct periporate apertures, intricate wall structure and small, supratectate spinules. The three species occurring in the peat swamps cannot be distinguished on their pollen grains and range from ph. c. I to IV, *G. bancanus* being a dominant tree in ph. c. I.

The pollen type is locally frequent in Marudi as well as in Berakas.

*Tiliaceae**Brownlowia* type

This pollen type has been described by Muller (1964, 1968, *Discoidites borneensis*) and includes the pollen of *Pentace* and the new genus *Jarandersonia*. The latter genus is known with one species, to occur locally in ph. c. I, the former genera are found outside the peat swamp forests. *Brownlowia argentata* occurs in mangrove forests.

Frequent in Berakas, but with low percentages.

*Verbenaceae**Avicennia* type (3/0)

This pollen type has been described by Muller (1964), Assemien (1966) and Blasco and Caratini (1973). Several other Verbenaceae genera are included and of these only *Vitex* occurs very rarely in ph. c. I in the peat swamp forests. It is likely that most grains of this type have been derived from the mangrove genus *Avicennia*.

Rare both in Marudi and Berakas (nos. 61, 98, 105) and mainly restricted to mangrove sediments.

*Monocotyledones**Cyperaceae**Thoracostachyum*

The pollen grains of this genus are subspherical, rather small (25  $\mu\text{m}$ ), with a single, indistinctly outlined porate aperture which is covered by a thin, granulate membrane. The wall is composed of a thin endexine, a thin layer of scattered minute columellae and a very thin tectum with a finely scabrate surface. Total wall thickness does not exceed 1  $\mu\text{m}$ . The only species of this genus occurring in the peat swamps range over ph. c. I-VI, but is abundant only in ph. c. I and VI.

This delicate pollen type has only been found in Marudi.

*Flagellariaceae**Flagellaria*

The pollen of this genus has been described by Chanda (1965). *F. indica* occurs in the peat swamp forests, rarely in ph. c. I-III, occasionally in ph. c. IV-V and frequently only in ph. c. VI.

The pollen type is infrequent in Marudi and Berakas (nos. 23, 24, 36, 66, 88, 89).

*Gramineae*

Since this family has not been recorded from the peat swamp forests, no attempt has been made to identify the occasional grass pollen grains encountered infrequently in Marudi and Berakas (nos. C, 3, 13, 24, 40, 94, 95, 99, 108).

*Palmae**Calamus* type (Plate II, 14)

This pollen type is characterized by dicolpate apertures, a trapezoid outline and a finely reticulate wall structure. It may include pollen of the genus *Plectocomiopsis* (cf. Thanikaimoni, 1970). An unidentified *Calamus* sp. and *Plectocomiopsis wrayi* may occur in ph. c. I, but are not known from the more advanced communities. *Calamus*, however, is often abundant on the riparian margins of peat swamps beyond saline influence.

The *Calamus* type has been included in the arboreal pollen sum but, since it has been produced by a climbing rotan palm it might also have been considered as a non-arboreal pollen.

Locally rather frequent in Berakas.

*Cyrtostachys* (Plate II, 15)

The finely reticulate, colpate pollen of *C. lacca*, the only species of the genus recorded from the peat swamp forests has been described by Thanikaimoni (1970). *C. lacca* is found in ph. c. I-III, but is most common in the transition zone between mangrove and peat.

The pollen type is locally frequent in Berakas as well as in Marudi.

*Eugeissona minor*

The pollen of this species has been described by Thanikaimoni (1970) and is characterized

by its large size (70  $\mu\text{m}$ ), long colpi and finely reticulate sculpture. The pollen wall is thin, coarse, evenly distributed reticulate sculpture. The colpi are regularly shaped lumina, 1–2  $\mu\text{m}$  in diameter and the colpi are not branched. It has been recorded from lowland peat swamp forest in Marudi and Berakas.

The pollen type has been found in the peat swamp forest (ph. c. I–43, 108).

### *Nypa fruticans*

This pollen type has been described by Erdtman (1952) and Thanikaimoni (1970). The equivalent form species is *Spiniferites nypoides* (Erdtman) Thanikaimoni et al., 1968). This palm species does not occur in the peat swamp forest. The regular presence in Berakas and local occurrence in Marudi peat swamp forest. It is the regular pollen type in the peat swamp forest underlying the mangrove vegetation.

### *Oncosperma* (Plate II, 13)

The characteristic clavate pollen grains have been described by Thanikaimoni (1970). *Oncosperma* is common in the peat swamp forest of the mangrove belt.

The pollen type is in Marudi peat swamp forest. It is the mangrove pollen type underlying the peat, while it is frequent throughout the Berakas.

### *Zalacca conferta*

The pollen of this species differs from the other species of the genus, described by Thanikaimoni (1970) in its finely reticulate sculpture. It is dicolpate, with short colpi and of relatively small size (27  $\mu\text{m}$ ). *Z. conferta* is locally abundant on shallow peat near the coast (ph. c. I).

Only found in low frequencies in Marudi.

## Pandanaceae

### *Pandanus* (Plate II, 12)

The pollen of this genus has been described by Erdtman (1952) and is easily recognizable by its small size, single aperture and finely echinate sculpture, except for a few species which possess smooth pollen which cannot be separated from the related genus *Freycinetia*. It is, unfortunately, not possible to separate the species occurring in the peat swamp forests, ranging from ph. c. I to VI, on their pollen characters.

The type is a dominant constituent both in Marudi and Berakas.

## MARUDI DIAGRAM (HOLOCENE)

### Geological setting

The raised bog in which the profile has been taken forms part of an extensive area of peat swamp covering the Baram alluvial plain. On the accompanying map (Fig.1) the extent of the peat growth, the location of the boring and the main geological features of the older terrain surrounding the alluvial plain deposits, are indicated. The Baram plain can be subdivided into an upper and a lower part, because of a constriction near Marudi. SW of Marudi the plain marks a structural depression in the subsurface, N of Marudi it is underlain by the wide, undisturbed Badas syncline. As a whole the valley coincides with an area of post-Tertiary downwarp. Subsidence

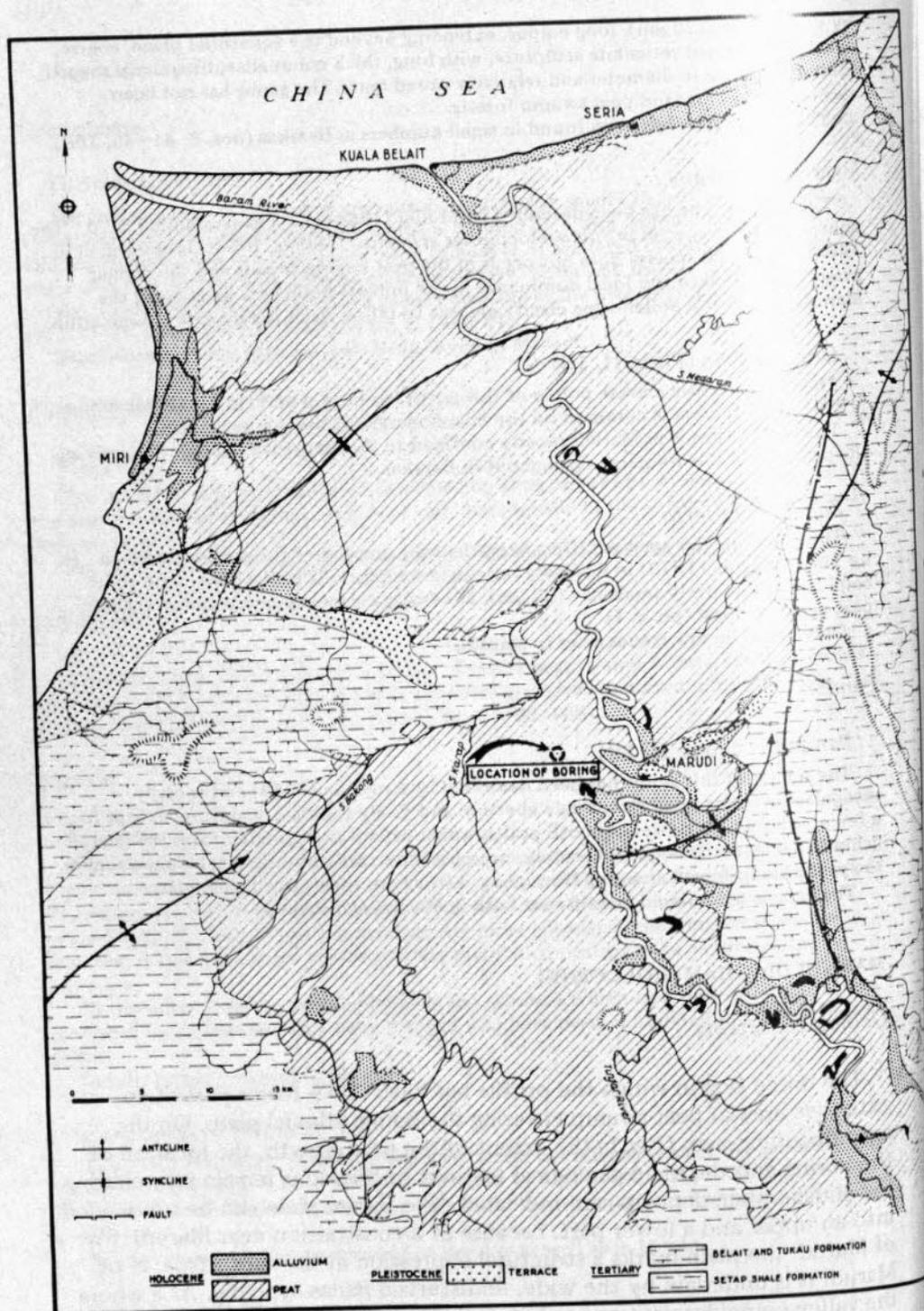


Fig. 1. Geological sketch map of the Baram alluvial plain.

is continuing into Recent times as indicated by warped Pleistocene terraces. The peat is surrounded by outcropping Tertiary and Pleistocene sediments. To the W mainly clays and shales of the Miocene Setap Formation are found. To the E and along the eastern side the more sandy Tukai and Belait formations of Mio-Pliocene age mark the border. Pleistocene terraces occur locally. No detailed information on the Quaternary sediments underlying the peat is available. It is known, however, that between Miri and Seria a thin succession of silty clays of varying thickness is underlying the recent beach and river sands. At the Baram mouth the thickness of the Holocene is estimated at 68.5 m.

During the last glacial period the valley presumably formed an area of erosion. During the postglacial a gradual process of accumulation of sediment must have started, continuing today. It is most probable that the infilling of the eroded valley by the Baram river started at the southern end and that gradually the marine influence of the rapid postglacial transgression was pushed back to its present position. The alluvial deposits which caused this infilling of the valley were probably initially colonized by mangrove, which was succeeded by peat, as the inland limits became decreasingly subjected to saline influence. The initial cause of peat development on mangrove clay is little understood but it is probably related to impeded drainage in the top layers of the clays. This impeded drainage may have been further aggravated when sea level reached its maximum height in the middle of the Holocene period. The dating of  $4270 \pm 70$  B.P. for the lowest peat in the boring studied, which will be shown to rest on mangrove clay, is in fair agreement with this, because it is generally assumed that the postglacial eustatic rise of sea level reached its maximum at approx. 5000 years ago (Jelgersma, 1961). Also in Holland, in a comparable situation, extensive peat growth on postglacial lagoonal sediments was found to start between 4800 and 4400 years B.P. (Riezebos and Du Saar, 1969). It is, nevertheless, probable that further south peat growth started earlier and to the north later, than in the central profile studied.

At present the peat is separated from the Baram river by a narrow belt of levees. In the Marudi profile, which is quite close to the river, no trace of its deposits is found, however. This suggests that during the time of peat growth the river has not shifted its course much and has stayed within a meander belt of not more than three miles width. The markedly raised surface of the bogs themselves, which prevents extensive flooding, may have been a contributing factor to this fixed course. Seawards the peat is protected by a narrow strip of beach sand deposits, built up to approx. high tide level. It is thus clear that the undisturbed development of the Baram valley peat bogs is due to an unusual combination of several favorable geological and physiological factors.

### *Ecology*

The vegetation of the peat swamps is entirely tropical rain forest which

has, until recently, been little disturbed. Each raised bog forms a unit in the ecosystem and the catenary sequence of phasic communities occurs from the perimeter to the centre of a bog. On relatively undeveloped bogs with a shallow lens-like surface structure, only the initial phasic communities occur, whereas on highly developed bogs the initial communities may be absent. The complete sequence of phasic communities occurs only in the Baram river valley. There is a tendency per unit area in the catena for the numbers of tree species to decline and the numbers of individuals to increase towards the final stage, which is correlated with a decrease in the average girth of a species. Between the first and last phasic communities there is an almost complete floristic change: *Dactylocladus stenostachys* among the trees and *Thoracostachyum bancanum* in the herbaceous layer, are the only species that occur in all communities.

Brief descriptions follow of the phasic communities. Although all the communities were not found on the Marudi bog, some details are important for the interpretation of the results of both the Marudi peat and the Berakas coal pollen diagrams.

*Phasic community I (Gonystylus—Dactylocladus—Neoscortechinia association)*. Occurs on the perimeter of the peat swamps and covers very extensive areas of relatively undeveloped coastal and deltaic bogs. Canopy is uneven, dominants attaining 40–45 m in height and the floristic composition of all storeys very mixed. Average number of tree species (30 cm girth and over) per 2000 m<sup>2</sup> ranges between 35 and 55. Principal dominants include *Gonystylus bancanus*, *Dactylocladus stenostachys* (rather rare in some localities), *Copaifera palustris* and four species of *Shorea* (not *Shorea albida*). The botanical composition of the middle and lower storeys has affinities to that in Mixed Dipterocarp Forest: Myrtaceae (*Eugenia*), Sapotaceae (*Palaquium*, *Ganua*), Guttiferae (*Calophyllum*, *Garcinia*), Myristicaceae (*Horsfieldia*, *Gymnacranthera*, *Knema*, *Myristica*) are frequently represented. *Neoscortechinia kingii* and *Alangium havilandii* are the two most widely distributed species in the lower storey. The water table is partially exposed, especially during the wet season and aroids are common in the herbaceous layer. The sedge *Thoracostachyum bancanum* is usually abundant. Terrestrial ferns (*Schizoloma*, *Asplenium*, *Vittaria*, *Syngamma*) and epiphytic ferns (*Asplenium*, *Drynaria*, *Humata*, *Selliguea*, *Pyrrhosia*) are widely distributed and frequent.

On shallow peat near the coast, immediately inland from the mangrove or the littoral fringe, a subcommunity, the *Camposperma—Cyrstostachys—Zalacca* subassociation, is recognized. The principal dominant, *Camposperma coriacea*, occasionally forms almost pure stands. The spiny palm *Zalacca conferta* is often found in dense thickets. The forest tends to be more open than in phasic community I, and the number of species per unit area fewer. The climbing fern *Stenochlaena palustris* is very abundant. *Lophopetalum multinervium* and *Parishia sericea* are two species that reach their greatest abundance in this subassociation.

*Phasic community II (Shorea albida—Gonystylus—Stemonurus association).* This community occurs as a transitional zone, often of considerable extent, between phasic communities I and III. It covers extensive areas in the Rejang delta, but the zone it occupies in the Baram swamps is usually rather narrow. The structure of the forest and the floristic composition resemble those in phasic community I, with the exception that large *Shorea albida* trees, frequently exceeding 3 m girth, dominate the forest. *Stemonurus secundiflorus* var. *lanceolatus* is a characteristic species of the lower storey. Aroids, other herbs and terrestrial ferns are less common than in the preceding community.

*Phasic community III (Shorea albida consociation).* This community covers extensive areas in the Baram swamps, but is largely absent from the Rejang delta. The upper storey is composed of a pure, even canopy, ranging in height between 48 and 58 m, of *Shorea albida*, which averages between 35 and 40 stems per 4000 m<sup>2</sup>. The middle storey is somewhat sparse: *Gonystylus bancanus*, *Combretocarpus rotundatus* and *Dyera lowii* are the principal species. The understorey is frequently composed very largely of one species: *Tetractomia parviflora* (in the Baram valley), *Cephalomappa paludicola* (in the Rejang delta) and *Ganua curtisii* (Badas swamps of Brunei). *Pandanus andersonii*, a large stemless pandan, often forms dense thickets in the shrub layer, where *Nepenthes bicalcarata* is a characteristic species. Herbaceous vegetation and terrestrial ferns are largely absent, and lianes and climbers infrequent.

*Phasic community IV (Shorea albida—Litsea—Parastemon association).* Occurs in the centre, on the bog plain, of numerous swamps in all localities, especially in the Rejang delta. On the more inland Baram swamps it is found as a broad zone between phasic community III and V. The characteristic feature of this community is the relatively large number of small-sized trees per unit area: few trees exceed 1.8 m girth and the number of individuals per 4000 m<sup>2</sup> ranges between 270 and 370. The canopy tends to be even at about 30–36 m. Tree species per 2000 m<sup>2</sup> ranges between 19 and 26. The principal dominants are *Shorea albida*, which frequently exceeds 100 stems per 4000 m<sup>2</sup>, *Litsea crassifolia*, *Combretocarpus rotundatus* and *Calophyllum obliquinervum*. *Parastemon spicatum* and, to a lesser extent, *Tristania obovata* are abundant in the lower storey. Herbaceous vegetation is sparse, but small scramblers and shrubs, such as *Ficus deltoidea* var. *motleyana*, *Euthemis minor* and *Nepenthes* spp. are abundant.

*Phasic community V (Tristania—Parastemon—Palaquium association).* This community occurs as a narrow transitional zone between phasic communities IV and VI and may be considered as an extension of the preceding community. All the trees are small, few exceed 1.2 m girth and the number of stems per 4000 m<sup>2</sup> usually exceeds 450. The canopy height does not exceed 21 m, except for the occasional dominant. The principal species

include *Tristania obovata* (and *Tristania beccarii* locally), *Parastemon spicatum*, *Palaquium cochleariifolium*, *Combretocarpus rotundatus* and *Dactylocladus stenostachys*. *Pandanus sigmoideus* is the most conspicuous shrub and *Thoracostachyum bancanum* is the only common herb.

*Phasic community VI (Combretocarpus-Dactylocladus association).* This and the preceding community are only found in the centre of the more inland Baram swamps. The forest is open and all trees and shrubs have a markedly stunted appearance. *Combretocarpus rotundatus* is the principal dominant, but even this species rarely exceeds 0.9 m girth and 12 m in height. *Dactylocladus stenostachys* is abundant as a stunted small tree. *Litsea crassifolia*, *Ilex cymosa* and *Garcinia cuneifolia* occur as shrubs. Myrmecophytes, including *Myrmecodia tuberosa*, *Hoya* spp., *Dischidia* spp. and *Hydnophytum formicarum* and *Nepenthes* spp. are abundant. *Thoracostachyum bancanum* and stunted *Pandanus sigmoideus* are widely distributed and abundant. A characteristic feature of the community is the occurrence of *Sphagnum junghuhnianum*. This is the only habitat at low altitude in Sarawak where *Sphagnum* moss is found.

This brief outline of the characteristic features of the swamp vegetation is supplemented by a diagram (Fig.2) in which the distribution over the catena of those trees and shrubs which can be palynologically identified are plotted. This table will form the base for interpretation of the pollen diagrams. Further details are to be found in Anderson (1961a, 1963). A more detailed description of the Baram peat swamps will follow. These swamps cover approx. 2200 km<sup>2</sup> and extend for a distance of 116 km upstream from the mouth of the Baram river. In the lower reaches of the Baram, the swamps are contiguous with those in the Belait river in the State of Brunei. The total swamp area is subdivided by tributaries of the Baram river into numerous individual raised bogs, the largest of which covers approx. 520 km<sup>2</sup>. Level surveys undertaken by Anderson (1964b) and by the Sarawak Shell Petroleum Company prove that these swamps are all of the raised-bog type; the domed structure of the more upriver bogs has been found to be very pronounced.

The Marudi bog lies on the true left banks of the Baram and Tinjar rivers and extends for a distance of 45 km upstream in a direct line from the confluence of the Baram and Bakong rivers. On the western side the long narrow bog is bounded by the Bakong river and its tributary the Karap. The whole bog extends over an area of about 420 km<sup>2</sup>.

The location of the Marudi boring (Fig.1) was situated towards the centre of the most northerly part of the bog, 1.6 km from the Baram river. A level survey was made along a trace cut through the forest from the banks of the Baram at the first bend in the river downstream from Marudi. The gradient of the peat surface is steep on the margin of the bog: heights above the datum (approximate high water mark of the river) of 4.13 m, 4.88 m and 6.75 m were recorded in the first 103 m and 603 m respectively. Beyond this towards the centre of the bog the surface levels off to an almost flat bog plain: 2610 m from the river bank, the height above the datum was



7.8 m. The maximum depth of peat recorded was 11.7 m at the location of the boring. The subsoil below the peat was found to be below the datum, a feature that is characteristic of most of the bogs surveyed in Sarawak and Brunei. In the Marudi bog, phasic community VI entirely covers the bog plain and the other communities are constricted in narrow zones between the bog plain and the rivers. Phasic community I is absent. The distribution of the vegetation communities over the Marudi bog and surrounding swamps, as interpreted from aerial photographs is shown on Fig. 3.

A transect was cut from the first bend in the Baram river downstream from Marudi and 2000 m<sup>2</sup> plots were enumerated at 402 m, 804 m and 1608 m along the transect. The forest on the perimeter of the bog, within the first 300 m, is composed of phasic community II. No sampling was undertaken here, however, as the vegetation had been disturbed by the felling and extraction of some *Shorea albida* trees.

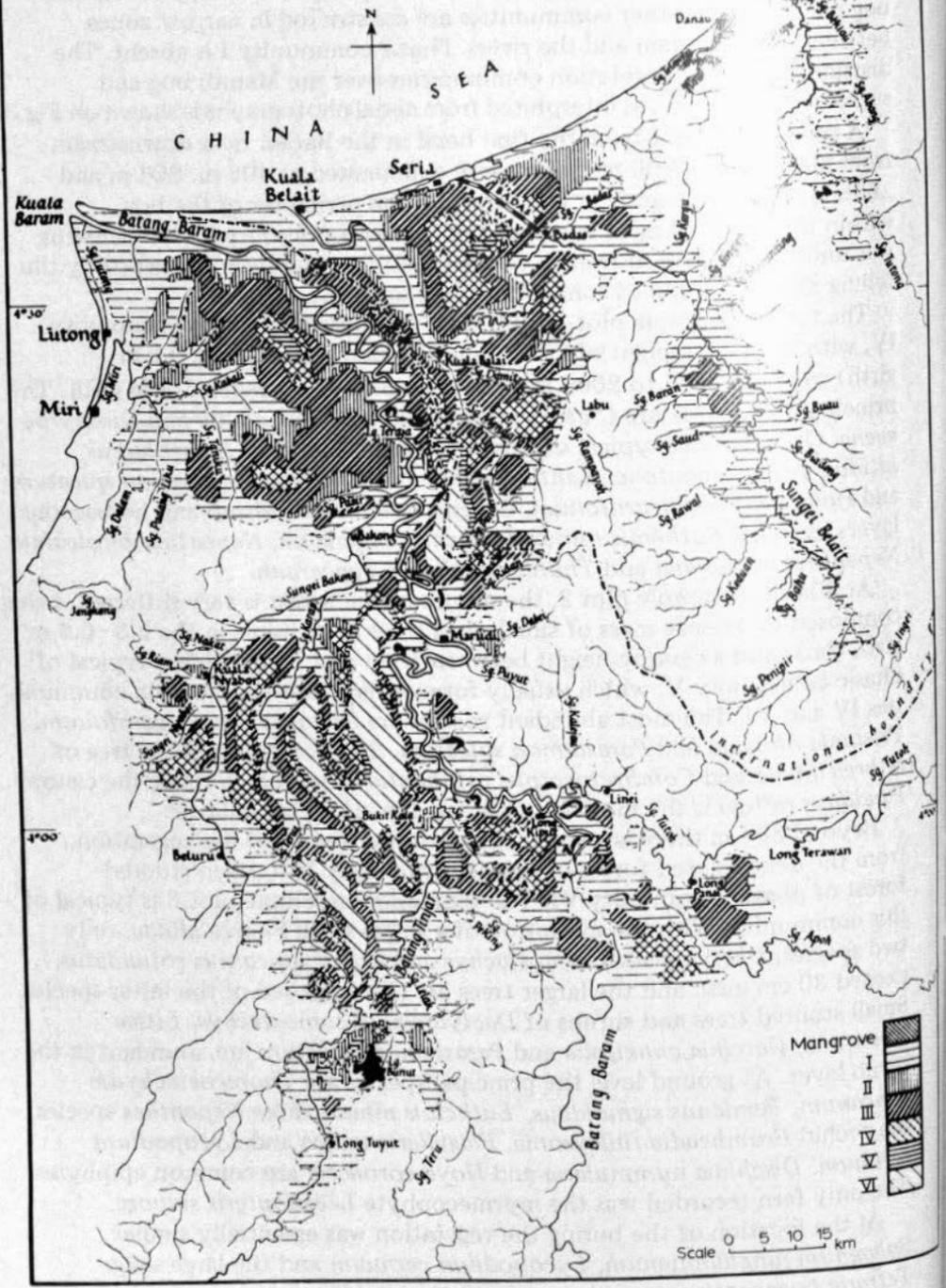
The forest in sample plot 1 (400 m) is composed of phasic community IV, with a canopy height of 27–30 m. 150 stems (exceeding 0.3 m girth) were recorded to 2000 m<sup>2</sup> and only 3 trees exceeded 1.8 m girth. The principal dominants are *Cratogeomys glaucum*, *Shorea albida* and *Diospyros eben*. Other species typical of this community included *Austrobuxus nitidus*, *Litsea crassifolia*, *Xanthophyllum ramiflorum*, *Parastemon spicatum* and *Palaquium cochleariifolium*. Species noted in the shrub and herbaceous layers included *Euphorbia minor*, *Pandanus andersonii*, *Nepenthes bicalcarata*, *Nepenthes rafflesiana* and *Thoracostachyum bancanum*.

At 804 m, in sample plot 2, the nature of the forest is very different, being composed of a dense mass of small-sized trees (176 stems in the 0.3–0.6 m girth class) and a canopy height between 18 m and 21 m. This is typical of phasic community V, which usually forms a narrow zone between communities IV and VI. The most abundant species are *Palaquium cochleariifolium*, *Tristania obovata* and *Parastemon spicatum*. The occasional larger tree of *Shorea albida* and *Combretocarpus rotundatus* is emergent above the canopy. *Pandanus ridleyi* is the most frequent species in the shrub layer.

Beyond 804 m there is a sharp change in the aspect of the vegetation, from the dense closed forest of phasic community V to open stunted forest of phasic community VI. The vegetation in sample plot 3 is typical of this community. With the exception of a single small *Shorea albida*, only two species, *Dactylocladus stenostachys* and *Combretocarpus rotundatus*, exceed 30 cm girth and the larger trees are all composed of the latter species. Small stunted trees and shrubs of *Dactylocladus stenostachys*, *Litsea crassifolia*, *Garcinia cuneifolia* and *Parastemon spicatum* are abundant in the shrub layer. At ground level the principal species are *Thoracostachyum bancanum*, *Pandanus sigmoideus*, *Euphorbia minor*, three *Nepenthes* species, the orchid *Bromheadia finlaysonia*, *Flagellaria indica* and *Lycopodium cernuum*. *Dischidia nummularia* and *Hoya coronaria* are common epiphytes. The only fern recorded was the myrmecophyte *Lecanopteris sinuosa*.

At the location of the boring the vegetation was essentially similar. *Sphagnum junghuhnianum*, *Lycopodium cernuum* and the large sedge *Tetraria borneensis* were common in the ground layer.

# PEAT SWAMP FORESTS OF THE BARAM, SARAWAK AND THE BELAIT, BRUNEI



Mangrove

I	[Horizontal hatching]
II	[Vertical hatching]
III	[Diagonal hatching /]
IV	[Diagonal hatching \]
V	[Cross-hatching]
VI	[Dotted pattern]

Scale 0 5 10 15 km

## Pollen analysis

The aim of the palynological investigation was to provide factual evidence of the vegetational succession from the basal clay to the present-day forest. This aim can only be realized if the pollen and spore flora preserved in the peat represents the contemporaneous swamp flora to a sufficient large degree. This proved to be largely the case as only a small amount of extraneous pollen was found. The large size of the peat swamp investigation and its dense forest cover, causing over-representation of the local vegetation were probably largely responsible for this. The closeness of the bog to the location to the river bank had no discernible influence. It should be stressed here that, since the aim of the present study was concerned with the development of the swamp itself and not with changes in vegetation outside the swamp area, this lack of outside influence was a great advantage. However, in planning the present study and in evaluating the results a number of handicaps and sources of error remain and these will be now briefly reviewed.

First of all, very little is known of the floral biology of most trees from the peat swamp forest. It is generally stated that in the tropical rain forest, flowers are insect-pollinated, but it is not known how far this condition restricts the dissemination of pollen after opening of the anthers. The unexpected occurrence of fairly large quantities of *Ficus* type pollen in the peat forms a case in point, because *Ficus* fertilization procedures hardly give opportunity at all for airborne dispersal. Here, as well as in other cases, it seems most likely that the flower or inflorescence as a whole dropped and disintegrated on the soil. This phenomenon is of common occurrence in the tropical rain forest and has been observed for instance in *Dactylocladus* (inflorescence) and *Palaquium* and Dipterocarpaceae (flowers). It results in a very localized pollen accumulation, without much vertical transport.

Whatever the means by which it was achieved, the result has been that a major part of the trees, shrubs and herbs growing in the peat swamps have produced considerable quantities of pollen and spores which were embedded and perfectly preserved in the peat soil underneath. Pollen production is, however, markedly different between various species. At one end of the scale are found *Dactylocladus*, *Camptosperma* and *Rhizophora*, which produce large quantities of pollen, at the other end trees like *Alangium*, *Canthium* and *Neoscortechinia*, which, although by no means being less abundant, produce far less pollen. A more serious disadvantage is that of other groups, like for instance Myristicaceae and Lauraceae, which occur abundantly in the vegetation and are ecologically significant, no pollen at all is preserved. The pollen production of these trees appears to be low, as is

Fig. 3. Vegetational zonation of the Baram peat swamps. I: *Gonystylus*—*Dactylocladus*—*Neoscortechinia* association. II: *Shorea albida*—*Gonystylus*—*Stemonurus* association. III: *Shorea albida* consociation. IV: *Shorea albida*—*Litsea*—*Parastemon* association. V: *Tristania*—*Parastemon*—*Palaquium* association. VI: *Combretoarpus*—*Dactylocladus* association. Dominance of species in IV: *Shorea albida* (A); mixture (Mx).

shown by the very small quantities which are recovered from acetolysed flower material. In addition, the delicate pollen especially of these two families is probably easily destroyed during fossilization.

Another phenomenon which may have left its mark in the data is the periodic flowering of certain trees, notably the Dipterocarpaceae. This is one of the reasons which has led to the sampling procedure adopted for the cores.

From the systematic description of the pollen and spore types it has already become clear that in certain cases a type may represent a whole genus of which the species differ markedly in their ecological preference. This is for instance the case with *Palaquium* and Myrtaceae. If it were possible to split these pollen types in future investigations, much more detailed ecologic information would result.

Pollen dispersal above peat bogs is mainly dependent on wind and in this respect the situation in a tropical rain forest, such as covers the Bornean peat swamps, is not favorable. Only in the relatively open vegetation of phasic community VI a certain amount of atmospheric mixing and long distance transport could be expected. Winds in a humid equatorial climate are characteristically weak. The occasional strong wind is usually associated with squalls and accompanied by heavy rainfall. The latter circumstance effectively limits, through washout, atmospheric pollen dispersal as has been recently verified by McDonald (1962).

Even in Europe, where strong, persistent unidirectional winds in early spring are frequent, pollen dispersal within the closed forest is extremely limited. Studies by Jonassen (1950) and Tauber (1965) in Danish forests have shown conclusively that the spectra here are strongly locally marked and generally reflect only the very nearest growth, i.e. the forest in a circuit of a few hundred metres only. Long distance transport therefore appears to be without significance within the forest.

Provided the dispersal is not too limited, this facilitates the investigation of the local succession.

The pollen content of surface samples, which can be directly related to the contemporaneous vegetation on the sampling spot provides a quantitative estimate of the errors involved, but for the present study it was not possible to do more than a very restricted preliminary survey.

In the lower part of the Marudi pollen diagram (Fig.4), the spectra of nine surface samples are shown, but only the numbers A—C are from the Marudi area itself. The samples 1—6 originate from other areas and they show general agreement with what is known of the floristic composition at present. One pronounced difference is their extreme richness compared to equivalent strata in the boring. As this richness is mainly related to the rate of peat accumulation, it suggests a certain difference in ecologic conditions, which, however, cannot be further evaluated without additional study.

The samples 1—3 were taken in the general area of the bore hole location within phasic community VI at three spots by random collection of five

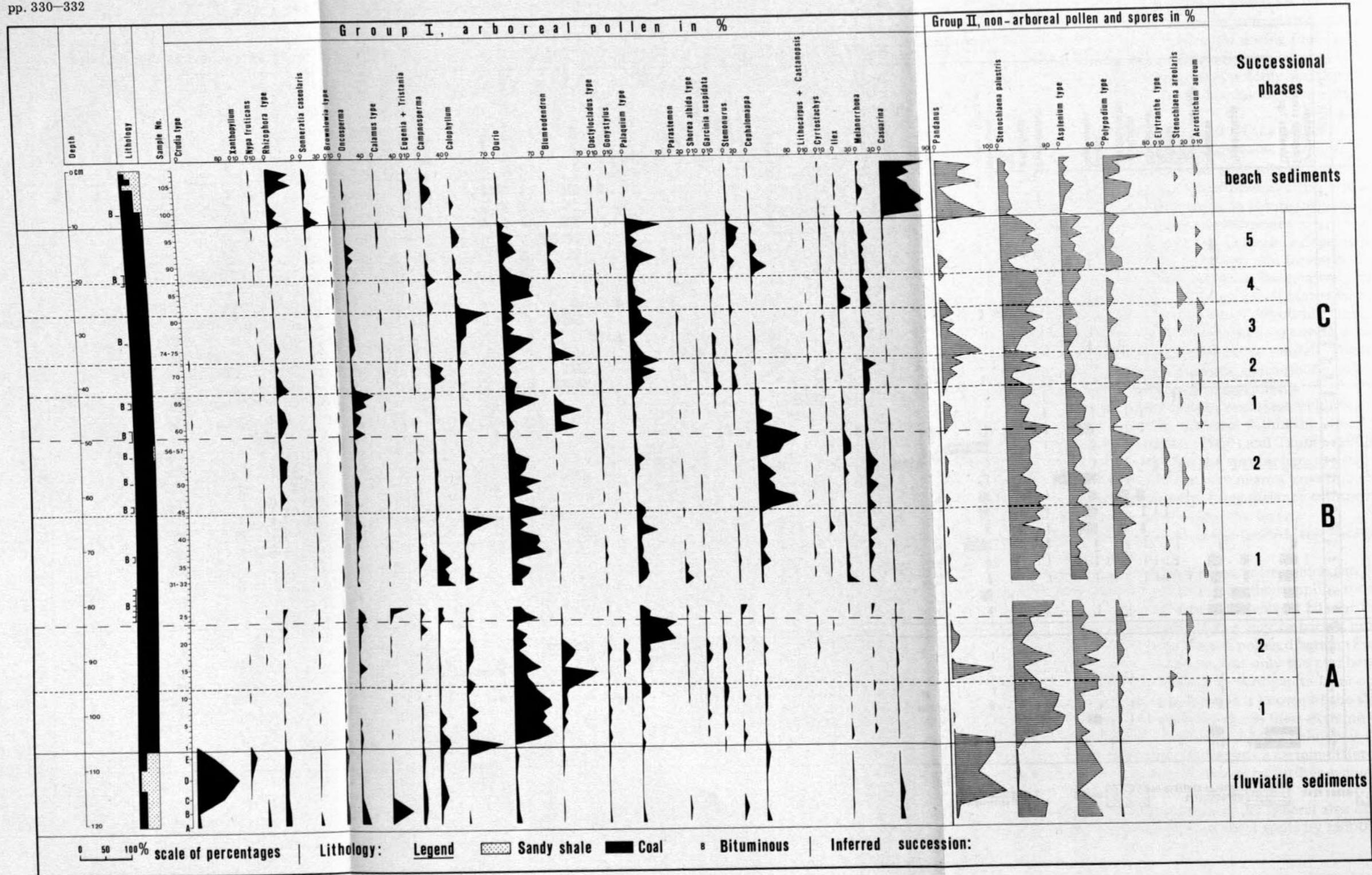


Fig. 5. Berakas diagram (Miocene).



growing magnam polsters over an area of approx. 100 m<sup>2</sup>. The samples of each spot were then carefully mixed before preparation, eliminating as far as possible random errors. The spectra indicate that even within the relatively open vegetation of phasic community VI they reflect mainly local dominants of respectively *Dactylocladus* (1), *Palaquium*, *Ilex* and *Combretocarpus* (2) and *Parastemon* (3). The *Casuarina* grains could have originated from Keruas vegetation near Marudi, a distance of approx. 10 km. The genus may also occur in the Baram swamps, since it has been recorded elsewhere in peat swamp forest.

The need for caution in the interpretation of a single profile is thus amply demonstrated. As mentioned already, it was attempted to minimize the sources of error caused by local over-representation as much as possible by taking a well-mixed, representative sample of each separate core. Based on the growth rate of the peat as indicated by <sup>14</sup>C dating, it may be estimated that one core sample is representative of maximally 50 years of peat growth. This is probably less than one tree generation. In evaluating the final diagram, the rule can be followed that any percentage maximum, if confined to one sample only, is likely to be caused by local over-representation. If a maximum is spread out over two or more consecutive samples, the chances are of course better that this represents more than local dominance of the tree involved. For future work it is strongly recommended to base an investigation such as attempted here on at least two borings and a suitable number of carefully selected surface samples.

A last important point to consider is the choice between one or more pollen sums and the subsequent design of the pollen diagram. It is evidently undesirable to include all pollen and spore types distinguished in one sum for percentage calculations, as some shrubs and epiphytes like *Pandanus* and *Stenochlaena* would then, by their excessive pollen production effectively swamp the trends in the curves of the rarer tree pollen types. Also there is at the present stage of investigation not much point in including in the sum unidentified pollen types, or those that could not be identified with any degree of certainty.

It was therefore decided to restrict this study to the positively identified pollen and spore types only. These were split into two groups and the percentages were calculated separately for each group. Group I contains all tree species, larger shrubs, palms and rotans and Group II all smaller shrubs, herbs, epiphytes and climbers. These two groups can be compared to the Arboreal Pollen and the Non-Arboreal Pollen groups, respectively, as generally distinguished in pollen-analytical studies in Quaternary sediments in temperate climates. Both groups include large pollen producers as well as small ones, but nevertheless it was found that the resulting diagram shows little obvious over-representation. It is also possible in this way to compare the floral changes within group I with the independently calculated ones in group II. In future studies a more strongly differentiated grouping of types may be advisable, however. A curve showing the relation between group I and group II has not been presented but can easily be constructed from the

pollen sums given on the diagram.

On the Marudi diagram (Fig.4) the following data are presented from left to right.

- (1)  $^{14}\text{C}$  determinations. Age has been given in years before present, corrected for a Suess-effect of 230 years.
- (2) Peat lithology in a simplified way, giving rough quantitative relations between amounts of clay, wood peat, fibrous peat (cuticles and rootlets) and remains of leaf mosses (sphagnum leaf fragments were not observed).
- (3) Degree of humification on conventional scale.
- (4) Depth in metres below the peat surface.
- (5) Percentages for all types included in group I and in group II. One sample only proved too poor to permit a percentage calculation. In some other cases the number of grains belonging to group II was too low. In such cases the actual number of grains found is stated. The pollen and spores of all types have, within each group, been arranged in stratigraphic order as they occurred in the boring.
- (6) The inferred succession which will be discussed in greater detail below.
- (7) The results of the surface peat samples were calculated in the same way but plotted separately on the bottom part of the diagram.

### *Peat stratigraphy*

By combination of the data obtained by the various methods discussed previously, the sedimentary column could be roughly subdivided into four stratigraphic units:

(A) The basal clay and transition to peat from 13 to 11.5 m. The clay is very humic at the bottom and semi-decayed plant fragments, possibly derived from *Nyssa* are frequent. Microscopically the large amount of iron sulphide, visible as small, black, angular or spherical concentrations inside the plant tissue fragments, is conspicuous, suggesting brackish influence in the depositional environment. The assumption that this clay represents a mangrove sediment is supported by its pollen content, as will be shown below.

(B) From 11.5 to 5.5 m a rather compact, strongly humified wood peat of a typical crumbling granular texture occurs. Minor variations between the amount of wood and bark remains, cuticles and rootlets are present and are indicated as far as possible in the column for peat lithology. The sample at 9.5 m consisted almost entirely of wood, but this may have been accidental since remains of very large logs are found scattered throughout the profile.

(C) At 5 m the character of the peat changes markedly. From 2 to 5 m few wood remains are found, the peat has a very high water content, is sloppy and less humified and, because of this, very difficult to sample. Root fragments of a monocotyledonous type, both large and very small, are a conspicuous constituent. It is possible that *Pandanus* roots occur since its pollen is well represented within this interval. Also other, peculiar tissue

fragments are found, which do not occur either below or above this interval. At 4 m and from 3 to 2 m leaf moss remains are conspicuous under the microscope. They occur in a perfect state of preservation and complete cathegonia even are found regularly.

(D) From 2 to 0 m the peat is heavily compacted, fibrous and highly humified. Small pieces of wood occur, but roots, rootlets and cuticles are the main constituents.

#### *Description of the diagram*

From 12 to 11.5 m, *Rhizophora* type, *Nypa* and *Oncosperma* pollen is dominant in the arboreal pollen sum (AP). In the non-arboreal pollen sum (NAP), *Arctostichum* spores characterize this interval, while spores of *Stenochlaena palustris* and *Asplenium* type are dominant. It will be evident, that the transition between clay and peat, which starts at 12 m is only expressed in the increase from 0% to very low percentages of *Amoora*, *Arthropodium* and *Cyrtostachys*.

The sample at 11 m shows a decrease in the mangrove elements and *Oncosperma* as well as a marked increase in Myrtaceae and *Ficus* pollen. This is also the first sample in which no mineral matter is present.

Between 11 and 10.5 m a major change in the curves is present. Mangrove elements and *Oncosperma* virtually disappear while *Cyrtostachys*, *Camposperma*, *Palaquium* type and *Dactylocladus* show a marked increase. In the NAP, in contrast, no such marked change is apparent.

From 10.5 to 9 m a rather uniform microflora is present, characterized by the dominance of *Cyrtostachys*, *Lophopetalum*, *Camposperma* and *Stenochlaena palustris*.

The interval between 8.5 and 6.5 m shows a rather sharp alternation in dominance of various pollen types. At 8.5 m, *Gonystylus* and *Stenochlaena palustris* are dominant, to be followed in the next sample by Myrtaceae. At 7.5 m, *Camposperma*, *Elaeocarpus* and *Ficus* pollen is abundant, while the samples at 7 and 6.5 m are characterized by dominance of *Garcinia cuspidata* type and *Pandanus*.

Between 6.5 and 6 m another major floral change is indicated more or less coinciding with a change in the degree of humification of the peat. *Cyrtostachys* and *Garcinia cuspidata* type decrease, while *Castanopsis* type and *Dactylocladus* increase.

Between 5 and 4 m, in addition, *Canthium*, *Shorea* cf. *albida* type, *Ilex*, *Combretocarpus*, *Parastemon*, *Nepenthes* and *Lycopodium cernuum* start increasing.

Between 4 m and the surface only minor changes are apparent. *Castanopsis* type decreases, *Dactylocladus* shows strong fluctuations, *Combretocarpus*, *Parastemon* and *Thoracostachyum* increase, while *Pandanus* decreases. The slight increase in *Oncosperma* and *Casuarina* pollen is most likely due to long-distance dispersal.

### Interpretation of the diagram

A cautious approach must be made to the ecological interpretation of the pollen diagram for reasons that have previously been outlined. Lack of precise knowledge on floral biology and pollen production, inability to differentiate pollen at the species level and absence of data on pollen dispersal are all important factors on which further research is needed. Furthermore, the results from a single core can at best give only a preliminary indication of the succession. However, despite these limitations there is clear evidence from the pollen diagram that the Marudih swamp originated over mangrove clay and that an ecological succession, bearing similarities to the catenary sequence of phasic communities, has taken place over the past 4000 years. This is best shown by comparison with Fig. 2 on which the distribution over the catena of those taxa which could be identified is plotted in the same sequence as on the pollen diagram. From this it is clear that the correlation between the two is most marked at the lower and upper limits of the peat. Certain zones are indicated on the inferred succession on the diagram but these, at this stage, must be considered as only a tentative interpretation. Further palynological investigations are required to determine the hydrosere with greater accuracy.

In the following discussion first the arboreal pollen and then the non-arboreal pollen and spore distribution will be compared.

#### Arboreal pollen

The abundance of *Rhizophora*, *Nypa* and *Oncosperma* pollen in the zone between 13 and 11 m clearly demonstrates the former presence of mangrove. *Nypa* and *Oncosperma* indicate an inland zone of mangrove vegetation, subject to periodic, non-diurnal, inundation and where saline influence is less strong. It is probable that a deeper boring might show the ecological succession in the mangrove itself. The non-mangrove pollen types, particularly Myrtaceae and *Elaeocarpus*, in this zone may be extraneous, having been carried in by tidal action. It is significant, perhaps, that *Eugenia* and to a lesser extent *Elaeocarpus*, are common constituents of riparian vegetation in Sarawak. It is suspected that the mangrove may have been bordering a former estuary of the Baram river.

The sharp floristic boundary, coinciding with the decrease in mangrove pollen, between 11 and 10 m clearly demonstrates the succession from mangrove to peat swamp. More information is required before even this boundary can be placed with certainty: the lithology indicates that it might be half a metre lower. Recent observations indicate that shallow peat forms under mangrove vegetation, but under these conditions the mangrove species are unable to regenerate and are succeeded by peat swamp species. In the zone between 10.5 and 9 m the abundance of *Camposperma* (probably *C. coriacea*) and *Cyrtostachys* (certainly *C. lacca*) pollen is clear evidence of the former presence of the *Camposperma*-*Cyrtostachys*-*Zalacca* subassociation. This is further confirmed by the occurrence of

*Lophopetalum* (probably *L. multinervium*) and *Zalacca* (probably *Z. confusa*) pollen. The distribution of both these species is at present largely confined to shallow peat.

Above 0.5 m the pollen representation is almost entirely confined to genera occurring in peat swamp forest. Some of this, of course, may have originated from species that do not, or no longer grow in the swamps, but this appears unlikely. The only probably extraneous pollen is that of the conifers (*Dacrydium* and *Podocarpus*) and the *Casuarina* pollen. *Dacrydium pectinatum* is a dominant species in peat swamp forests in the Lawas district, 100 km to the northeast, and has now also been recorded in ph. c. VI of the Marudi swamps. *Podocarpus maximus* has been recorded in peat swamp forests from a number of localities, but not in the Baram area and it is always a rare species. It therefore seems more probable that the pollen of both genera is of windborne origin outside the peat swamp, possibly from a heath forest on terrace sands in the lower Baram valley where both species are known to occur, accompanied by *Agathis*. The pollen of the latter is not found but this was certainly due to its low pollen production and lack of characteristic features which make it hard to recognize with certainty. The *Casuarina* type pollen at lower depths (13–9 m) is likely to have originated from *Casuarina equisetifolia*, which was probably present in the littoral fringe at the former mouth of the Baram river. No *Casuarina* has been recorded in peat swamp forests in the Baram valley; it is suspected, therefore, that the pollen of this type found at higher levels has the same origin as the conifer pollen; *Casuarina nobile* occurs near Marudi.

When considering the inferred succession, the representation of monospecific genera and, to a lesser extent, genera that in the Baram swamps are only represented by one species, is likely to be significant. *Dactylocladus stenostachys*, which is monospecific, is apparently a large pollen producer. Surprisingly it is absent from the zone 8.5–6.5 m, as the species at present occurs throughout the catena. It may have flowered less abundantly in this interval and it is necessary to check this absence in further cores. The distribution of *Combretocarpus* pollen is in accordance with the occurrence of *Combretocarpus rotundatus*, also monospecific, in the catena, where it is absent or rare in phasic communities I and II but becoming increasingly more abundant in the more central communities. Though the genus *Gonystylus* is represented by two species in peat swamps (a third, *Gonystylus maingayi*, is marginal), *Gonystylus forbesii* is a small or medium-sized tree that at present is rare. Most pollen, therefore, probably originated from *Gonystylus bancanus*, an important, widely distributed and abundant dominant. The regular occurrence of *Gonystylus* pollen between 9.5 and 4.5 m indicates the former presence of phasic communities I and possibly II. This is further confirmed by the presence of *Stemonurus*, *Ctenolophon*, *Blumeodendron* and *Lophopetalum* pollen. *Shorea albida* is the principal, frequently the sole dominant in phasic communities II–IV. The distribution of the pollen of this species is therefore

of great importance. It is unfortunate, however, that its pollen could not be identified with certainty and is liable to be confused with other species and even with that of other genera of Dipterocarpaceae. Nevertheless, it is perhaps significant that *Shorea albida* type pollen is well represented from 4.5 m to the surface, indicating that the species was probably an important component of the forest. Furthermore, the distribution of *Canthium*, *Longetia*, *Ilex* and *Ternstroemia*, all associates of *Shorea albida*, tends to confirm this.

There are of course certain anomalies. The occurrence of *Alchornea* and *Dillenia* pollen, though in very small quantities, is contrary to the inferred succession and the distribution of these genera in the catena. The frequent occurrence of *Oncosperma* pollen above 11 m may perhaps be attributed to wind dispersal of this palm pollen type, since no *Oncosperma* pollen is found in peat swamp forest.

The main enigma, however, is the abundant representation of *Marattia cuspidata* type pollen, especially at 7 and 6.5 m, but also at other levels as well as in the surface samples. The species is at present of rare occurrence in phasic communities I—II. Its dominance would fit in with a transition between phasic communities I and II at this level, although it seems to have been much more abundant than it is at present.

#### Non-arboreal pollen

The evidence of the non-arboreal pollen and spores, shown in group II on the pollen diagram, but omitted from Fig. 2, generally confirms the interpretation derived from the distribution of the arboreal pollen. The wind-dispersed spores of ferns and fern allies are likely to have a wider distribution than pollen and hence they are expected to be found in a wider range of strata in the profile. *Acrostichum*, which is not represented in peat swamp forest, would appear to be an exception to this generalization, as its distribution is confined to lower levels, 12.5—11.5 m. *Acrostichum aureum* is usually abundant towards the inland margins of the mangrove vegetation. The abundance of *Stenochlaena palustris* at lower levels is significant, as this climbing fern is largely confined to shallow peat (*Camptosperma*—*Cyrtostachys*—*Zalacca* subassociation) and to phasic community I. Especially the decrease between 8.5 and 6.5 m faithfully records its gradual disappearance. The low values in the upper part of the profile are, no doubt, indicative of transport from the receding coastal zone inwards. Five *Asplenium* species — three terrestrial and two epiphytes — have been recorded in peat swamps, while the epiphytic species also occur in mangrove. The abundance of spores of this type is therefore to be expected, but produces no information on ecologic succession. The distribution of the two types of *Lycopodium* spores, in contrast, is again of interest. *Lycopodium phlegmaria* is an occasional epiphyte in phasic community I, whereas *Lycopodium cernuum* is terrestrial in phasic communities IV—VI, becoming more frequent in the more advanced community. The spore representation of this genus is therefore in accordance with the inferred succession.

Other significant non-arboreal pollen types are *Zalacca*, *Nepenthes* (more frequent at higher levels) and *Thoracostachyum*. The latter genus occurs throughout the catena, though rare in phasic communities III and IV and therefore greater representation at lower levels might have been expected. Three *Pandanus* species occur in the peat swamp forest. It is unfortunate that the pollen cannot be differentiated as the species have restricted ecological distributions in the catena. The largest and most abundant species, *Pandanus andersonii*, forms thickets in phasic communities II and III and the high percentages of *Pandanus* pollen between 6.5 and 2.5 m may perhaps indicate the former presence of this species.

#### *Inferred succession*

Based on these considerations, the succession presented in the right-hand column of the diagram may be tentatively inferred.

From 11 to 10.5 m mangrove vegetation is clearly indicated.

The *Casipouita*—*Cyrtostachys*—*Zalacca* subassociation, which represents a transitional phase between mangrove and phasic community I is evident from 10.5 to 9 m.

It is normally succeeded by phasic community I which is certainly present between 8.5 and 7.5 m.

The *Garcinia cuspidata* phase between 7 and 6.5 m is certainly a conundrum. It may well represent somewhat different conditions pertaining at the time, preceding the invasion of the swamps by *Shorea albida*. This latter occurrence and the subsequent dominance of the species over vast areas is the most significant phenomenon in the catena. Further palynological research should be devoted to elucidating the problem.

Above 6.5 m interpretation of the succession is difficult; the forest may well have been dominated by *Shorea albida* and floristically the differences between phasic communities III and IV are relatively small. Phasic community V, which in the catena is little more than a narrow transitional zone between phasic communities IV and VI, is not indicated on the diagram. It would appear, however, that phasic community VI occupies at least the upper metre.

It may thus be concluded that the peat originally formed on mangrove clays, and that the succession thereafter bears resemblances to the present-day zonation.

#### BERAKAS DIAGRAM (MIOCENE)

##### *Geological setting*

The coal layer sampled at Berakas is one of several, occurring in sediments of the Belait Formation and outcropping in the Kianggeh valley near Brunei town (State of Brunei). The geology of this area has been described in detail by Wilford (1961). For a geological map of the area reference can be made to his fig. 31. The Belait Formation here consists of alternating sandstone,

sand, shale and clay with scattered coal seams not exceeding in thickness. The age of the formation is assumed to be Tertiary, possibly Lower Tertiary (Upper Miocene — lowermost Pliocene). This is based on strike correlation with the more marine time-equivalent Serianth and Miri Formations, in which a few diagnostic animal fossils are found and confirmed by the palynologic evidence. The scarcity of the diagnostic pollen type *Florschuetzia trilobata* indicates a post-Lower Miocene. The formation has been deposited in a littoral to deltaic environment, clearly comparable to the one in which the previously described Berakas valley Holocene peat and fluviatile sediments are still being deposited.

The locality of the seam which was sampled is given on Ward's detailed geological sketch map of the coal bearing strata in the Kiang valley (1961, fig.36, seam no. 67). The fixed carbon content of the coal is 70% on a dry ash-free basis, the moisture content 10–12%, and it ranks therefore as a high-grade lignite. The horizontal extent of the coal bed is not known but probably does not exceed 1 km.

#### *Pollen analysis and stratigraphy*

The aim of the investigation of this coal bed was similar to the one for the Marudi peat deposit and much of the general discussion found in pp. 325–333 applies here too. It may already be stressed in this connection, that the general similarity of the microflora found in both deposits allows such a close comparison.

The design of the pollen diagram (Fig.5, pp.330–332) was similar to that of Marudi. AP and NAP were distinguished and the types within each group were also arranged in a stratigraphical sequence. The two diagrams are thus directly comparable although the sequence of types within the groups is not the same and each diagram of course has a number of characteristic types besides the ones which are common to both.

A number of rare types were not plotted on the Berakas diagram. The sample numbers in which they occur are listed with the type descriptions.

It may be mentioned here already, that the Berakas diagram shows a more frequent occurrence of pollen types which must have originated outside the peat swamp area and this is, no doubt, a consequence of the much smaller size of the original deposit. Only the most important curves are shown on the Berakas diagram, but notes on the rarer types are to be found in the section on pollen and spore types (p. 295–311).

The coal deposit consisted mainly of lignitic coal, but the presence of bituminous layers is indicated. The under- and overlying mineral sediments consisted of sandy shale with variable amounts of organic matter.

#### *Description of diagram*

The samples from the underlying sandy shale show a fairly uniform pollen content and are characterized by dominance of the *Crudia* type and

of *Pandanus*, while *Xanthophyllum*, *Rhizophora*, *Oncosperma*, *Calamus* and *Casuarina* show minor concentrations.

The stratigraphical transition to the overlying coal bed is well reflected in the diagram by the decrease of the *Crudia* type and of *Pandanus* and by the increase of *Camptosperma*, *Calophyllum* and *Durio*.

The lowermost zone A of the coal succession is marked by high percentages of *Blumeodendron*, *Gonystylus* and *Garcinia cuspidata*. This zone can be subdivided into A1, characterized by dominance of *Durio* and *Stenochlaena palustris* and A2, characterized by a decrease of *Durio* and increase of the *Palaquium* type, while *Blumeodendron* and *Pandanus* show short-lived maxima.

The transition to the overlying zone B is marked by increase of *Oncosperma*, *Calamus*, *Camptosperma*, *Durio* and *Stenochlaena palustris*, while the *Palaquium* type and *Stenochlaena areolaris* decrease. A short barren interval follows, probably due to a high wood content of the samples, and the zone is further characterized by high values for *Cephalomappa* and *Melanorrhoea*, while *Blumeodendron* and *Pandanus* are conspicuously low. A further point of interest is the high frequency of bituminous coal, starting right at the A/B boundary. The zone can be subdivided into two subzones. B1 is characterized by high values of *Camptosperma* in the lower part, followed by *Durio* dominance and, finally a single *Calophyllum* maximum. B2 shows fairly high values for *Rhizophora* and *Melanorrhoea*, but is above all characterized by two major maxima of *Cephalomappa*, separated by minor *Durio* and *Melanorrhoea* maxima. *Ilex* is prominent in the upper part.

The transition with the uppermost zone C is marked by increases in *Oncosperma*, *Blumeodendron* and *Pandanus* and a decrease in *Cephalomappa*. Zone C shows a much greater variation in dominance of types and is thus difficult to characterize as a whole. Compared to B, *Blumeodendron*, *Garcinia cuspidata*, *Stemonurus* and *Pandanus* are more prominent, while *Cephalomappa* has decreased in importance. Five subzones can be distinguished. C1 is characterized by dominance of *Oncosperma* and *Blumeodendron*, C2 by dominance of *Camptosperma*, *Palaquium* type, *Garcinia cuspidata*, *Stemonurus* and *Melanorrhoea*, while *Pandanus* increases. C3 shows a return to dominance of *Blumeodendron*, coupled with a pronounced *Pandanus* maximum and followed by a single *Calophyllum* peak. C4 is characterized by dominance of *Durio*, *Ilex* and *Stenochlaena palustris*, with a maximum of *Stenochlaena areolaris* at its base. C5, finally, shows a return of *Cephalomappa* coupled with high values for *Palaquium* type and *Stemonurus*.

At the first influx of clastic sedimentary material a very sharp change is present, characterized by decrease of *Durio*, *Palaquium* type, *Stemonurus*, *Melanorrhoea* and *Stenochlaena palustris* and increase in *Rhizophora*, *Sonneratia*, *Casuarina* and *Pandanus*. Thus, while the lithological column shows a gradual change, from pure coal to coaly shale and sandy shale, the floristic change appears instantaneous, as it also was at the lower boundary of the coal succession.

### Interpretation of the diagram

Compared to the Holocene Marudi diagram, the Tertiary Berakas diagram has one great advantage in interpretation: it is much more densely sampled. Taking a compaction ratio of approximately 10 to 1, it would appear that the original thickness of the coal seam was comparable to that of the Marudi deposit and that in consequence the Berakas sampling density was five times higher. This allows a much better judgment of the significance of short-lived maxima and one of the characteristic features of the Berakas diagram actually is that some species do show well-defined single or even paired maxima. This is most clearly visible in the *Calophyllum* curve, which shows between samples 40 and 44 a peak followed by an abrupt decrease. It is likely that this represents a single generational peak. *Cephalomappa* and the *Palaquium* type show more symmetrical maxima, while the *Blumeodendron* curve exhibits four paired maxima. If the sedimentation rate of the Marudi peat is extrapolated to the Berakas, 1 cm would be roughly equivalent to 40 years. A peak like that of *Calophyllum* covers 5–7 samples, which would yield an age of 200–300 years for a single generation. This figure appears somewhat high. It is estimated that the age of *Calophyllum* trees in present-day peat swamps is not likely to exceed 150 years and it appears unlikely that *Cephalomappa* and *Blumeodendron* could exceed a hundred years of age. In *Palaquium* the maximum life span could be more variable but is unlikely to exceed that of *Calophyllum*. Thus, a certain discrepancy appears to exist between the assumed compaction rate and the suggestion of single tree generation peaks in the diagram. This suggests that the compaction ratio was slightly less than 10 to 1, which is quite possible. As in Marudi, however, it is in such a case not possible to conclude on the basis of a single diagram to a regionally extended phase of a single dominant. Due to the limited pollen dispersal in peat swamp forest, it may have been a single tree which has produced the maximum. If this is true, the succession described previously may represent no more than a mosaic-like succession of individual trees instead of communities characterized by one or more dominants. This makes it advisable to restrict the interpretation of the diagram to the major features, as expressed by zonal and subzonal subdivisions, only.

The threefold subdivision into zones A, B and C, each covering probably more than a thousand years, is likely to reflect distinct shifts in the peat swamp vegetation. The subdivision of these zones may, of course, be already of less significance. However, if the changes between these subzones can be correlated with the differences in floristic composition known from the recent communities, these too may indicate a more general aspect of the succession.

This raises the vital question, how far it will be possible to compare two peat swamp hydroseres, which are separated by a time interval of approximately seven million years and including the upheavals of the Pleistocene. The fact that virtually all pollen and spore types found in the coal are either

comparable to recent swamp or to mangrove species in principle permits such a comparison. Only the spores of *Stenochlaena areolaris* form an element of which, in Borneo at least, no recent counterpart is known. According to Holttum (1932), the nearest present-day localities of this fern species are in the Philippines and New Guinea where it occurs epiphytic on *Pandanus* at altitudes varying from 150 m to 1200 m.

Also the degree of association between the pollen types in Berakas will have to be analyzed carefully, before the fossil communities can be compared with the recent ones.

The mangrove elements *Nypa*, *Rhizophora*, *Sonneratia* and *Acrostichum* are closely associated and form a well-defined element which is extraneous to the peat swamp vegetation. The remaining types, with the exception of *Eugenia*, *Hibiscus* and *Stenochlaena areolaris*, are known today to occur in coastal peat swamp communities. Within this latter group the following associations of types can be distinguished:

- (a) *Durio* and *Stenochlaena palustris*.
- (b) *Cephalomappa*, *Ilex* and *Melanorrhoea*.
- (c) *Camponia cuspidata* and *Stemonurus*.

The curves of the other types show more independent maxima, while the *Palaquium* type, *Blumeodendron* and *Durio* are alternating in dominance. The latter phenomenon may of course be a spurious statistical effect since these abundant types are included in one percentage sum.

Any repetition in the succession would of course also be significant in the interpretation but this is not apparent.

Proceeding next to a comparison with the recent distribution pattern in the peat swamp catena, the following types can be assigned indicator value, arranged in sequence of succession.

*Brownlowia (argentata and tersa)* and *Oncosperma (tigillarum)* are now found on the inner perimeter of mangroves, where the ground water is still saline but with an influence of fresh water.

*Camposperma (coriacea)* and *Cyrtostachys (lacca)* are abundant in the transitional mangrove peat vegetation, but the former species may also be found less frequently in the more advanced communities of the succession.

*Durio (carinatus)* is particularly indicative of phasic community I and its nearly continuous presence strongly suggests that the Berakas swamp did not progress beyond this stage of the succession.

The present-day distribution of *Blumeodendron (tokbrai and kurzii)* is confined to phasic communities I and V, but it is more abundant in the former. The curve for this genus corroborates the evidence of *Durio*. *Stemonurus* also falls more or less in the same category.

*Stenochlaena palustris* is invariably abundant on the margins of peat swamps, especially on shallow coastal peat. On smaller swamps, like Berakas must have been, where, moreover, the nearness of the coast is evident from the regular influence of mangrove pollen, the species may very well have occurred throughout.

In phasic community I, *Cephalomappa (beccariana)* and *Melanorrhoea*

(*beccarii* and *tricolor*) are more typical of well-developed swamps with deep peats. The increased abundance of those two types in the upper part of Berakas may very well be due to this, but they also occur in phasic communities II-IV.

The *Calamus* peak may be attributed to local dominance of *Calamus* palms which may occur in ph. c. I. It may also indicate riparian influence.

The low percentages of the *Shorea albida* and associated *Decaspermum* type are inadequate to indicate dominance of *Shorea albida* and *Decaspermum* *locladus stenostachys* and, hence, it seems unlikely that the vegetation progressed beyond phasic community I. This is also indicated by the absence of *Combretocarpus* pollen and of certain NAP types like *Lycopodium* *cernuum*, and *Nepenthes*.

The Berakas peat as a whole thus has evidently not progressed beyond phasic community I. However, the various boundaries recognized in the diagram indicate that certain changes took place and in the following they will be ecologically interpreted as far as is possible.

The Berakas swamp evidently originated on a fluvial deposit as indicated by the dominance of the *Crudia* type which probably originated from a river bank species and by the low values for mangrove pollen. It would appear that *Calophyllum* was dominant in the initial phase of peat formation.

The transition A1/A2 is difficult to interpret, but the boundary A/B probably signifies some disturbance in the vegetation, as indicated by the *Calamus* peak followed by a barren interval. The following increase in *Camposperma*, *Durio* and *Stenochlaena palustris* suggests a change towards more marginal conditions of the swamp.

The increase of *Cephalomappa* at the boundary B1/B2 is very noticeable and this type remains dominant in B2. This is probably due to the development of a deep peat soil and lack of marginal influence. The relatively high values for *Rhizophora* during this phase would then be due to a minor change in the physiography of the area surrounding the swamp, which caused the extraneous pollen to increase, without as yet influencing the peat development itself.

However, this physiographic change has ultimately influenced conditions inside the swamp area itself as witnessed by mineral influx at the well-marked boundary B/C. The reaction of the swamp vegetation is expressed by relatively high values of *Oncosperma* and *Rhizophora* and the further increase within C2 of *Camposperma*, all indicative of presence or nearness of the transition zone mangrove/peat.

The increase of *Garcinia cuspidata*, *Stemonurus* and *Pandanus*, which follow the *Oncosperma* and *Rhizophora* maxima in C2, appear to indicate next a receding danger of inundation and a renewed development towards a more stable situation within phasic community I.

Within the succeeding subzone C3, the high values, first for *Pandanus* and later for *Calophyllum* are indications for a continuation of this trend.

In the remaining part of the peat succession several quick changes follow each other which are difficult to evaluate ecologically. *Stenochlaena*

*areolata* shows a maximum at the base of C4. Although from the present-day ecology of this species a correlation with *Pandanus* peaks could be expected, this is evidently not the case. The most which can be said is that *S. areolata* maxima appear to follow *Pandanus* peaks.

At the top of zone C the marked increase of *Rhizophora*, *Sonneratia*, *Casuarina* and *Pandanus* leave no doubt that a marine transgression has terminated peat growth.

In conclusion it may be stated that the pollen and spore associations found in the Miocene Berakas coal are sufficiently comparable to the recent ones to permit the inference that a vegetation type closely similar to the present phasic community I, was present at that time. Furthermore, while peat growth started on fluvial deposits, it was evidently terminated by marine transgression. In the following section a detailed comparison between the data from Berakas and Marudi will be attempted.

#### COMPARISON BETWEEN THE MARUDI AND BERAKAS DIAGRAMS

In the preceding chapters the succession in the two diagrams has been independently compared with the recent vegetation, but it is also of importance to make a mutual comparison. For this purpose the pollen and spore types will be discussed grouped in several categories. The main subdivision will be between types which have in all probability originated from outside the peat swamp area and those produced by the peat swamp vegetation itself.

Mangrove pollen types belong to the first category and occur both in Marudi and Berakas. The following recent taxa can be identified: *Acrostichum*, *Avicennia*, *Nypa*, *Rhizophora* type, *Sonneratia caseolaris*, and only in Berakas, the extinct pollen type *Florschuetzia trilobata*, which is most probably derived from an ancestral *Sonneratia* species. The mineral deposits underlying the Marudi peat carry, in addition to the dominant mangrove pollen types, rare *Santiria* and *Jackia*. In Berakas the main dominant in these deposits is *Crudia*, while *Dacrydium*, *Dyera*, *Eugeissona* and *Gardenia* occur with low frequencies here and mangrove pollen is nearly absent. The organogenic deposits carry a number of other types which are probably derived from outside the peat vegetation and to this category belong Gramineae and *Podocarpus*, both found scattered in Marudi as well as Berakas, while *Eugeissona minor* and the *Hibiscus* type occur in Berakas, in low frequencies. *Casuarina* and *Dacrydium* in the Marudi peat also belong to this category, but whether the regular occurrence of *Casuarina* pollen in Berakas is derived from the peat vegetation or not, is less certain, since in the recent Lawas swamps the genus is locally frequent. However, the *Casuarina* pollen grains in the overlying mineral sediments of the Berakas profile are certainly derived from beach barrier vegetation and it could be argued that the nearness of the coast, as indicated by the regular occurrence of mangrove pollen in the coal itself, has also caused the influx of, presumably, *Casuarina equisetifolia* pollen.

The groups of types to be discussed next are assumed to have originated in the peat swamp vegetation. A first group is formed by a large number of types which have comparable frequencies in the interval inferred to represent ph. c. I-II in Marudi and which occur in Berakas throughout the coal. To this group belong the frequent *Cyrtostachys*, *Parastemonurus*, *Pandanus*, *Stenochlaena palustris*, the *Asplenium* and the rare *Alangium*, *Flagellaria*, *Ctenolophon*, *Dillenia*, *Neoscortechinia* and the *Xanthophyllum*. *Campnosperma*, *Gonystylus*, Myrtaceae and *Cuspidata* could also be assigned to this category, except that they are more abundant in Marudi than in Berakas. *Lophopetalum*, restricted to the lower part of the peat succession in Marudi (ph. c. I-II) and *Austrocladus* are absent in Berakas. In contrast, the following types are more abundant in Berakas: *Blumeodendron*, *Calophyllum*, *Ilex*, *Palaquium* type, *Nephrolepis* type. *Melanorrhoea*, although absent in the Marudi profile, does occur in the Baram swamps and should therefore be included in this category.

A very interesting group is formed by those types which are absent from the Marudi profile as well as from the recent Baram swamp vegetation, but which occur frequent to dominant in Berakas and also occur in the recent Rejang delta peat swamps: *Anacolosia*, *Cephalomappa* and *Durio*. *Durio* is the most important of this category and occurs in ph. c. I all over the Rejang delta and W Sarawak.

In the upper interval of Marudi, representing ph. c. III-VI, a number of types are frequent, which are rare in Berakas because the latter peat swamp is not likely to have transgressed much beyond ph. c. I. They are: *Canthium*, *Combretocarpus*, *Dactylocladus*, *Lithocarpus* type, *Shorea albida* type, *Nepenthes*, *Lycopodium cernuum* and *Thoracostachyum*.

A special category is formed by *Calamus* and *Stenochlaena areolaris*, both absent from Marudi and probably indicating some local disturbance in Berakas. Of less significance are a large number of rare types in Marudi, the absence of which in Berakas may be accidental: *Amoora*, *Arthrophyllum*, *Baccaurea*, *Chisocheton*, *Cratoxylon*, *Dryobalanops*, *Dyera*, *Jackia*, *Parishia*, *Ternstroemia*, and *Timonius*. *Pometia*, in contrast, is a rare type in Berakas, which is absent in Marudi. Probably under-represented in Berakas because of poor preservation are *Elaeocarpus*, *Ficus* and *Zalacca*.

Before a further evaluation is attempted, it must be stressed that this is possible only for phasic community I and that the similarities far outweigh the differences.

In all probability the climatic conditions must have been nearly identical because they permitted the development of a similar kind of peat swamp vegetation. This is also clear from the general similarities between the microflora contained in the mineral sediments of the Miocene and the Recent one.

It is, however, unlikely that ecological conditions were precisely the same and small differences in this respect may have caused the dominance of *Durio* and *Calophyllum* in Berakas. Also the fact that the Berakas peat started in a fluvial environment and the Marudi peat on mangrove must have influenced the development of the vegetation.

Although the possibility has to be taken into account of a shift in ecological requirements with time for certain species, this is only suggested for *Stenochlaena areolaris*, which has become extinct in NW Borneo in the course of the Pliocene. But even in this case, competition or climatic change may have been responsible.

Finally, the possibility that the differences are due to chance colonization of the peat swamps has to be considered. It has been pointed out earlier (Anderson 1963) that there are very few peat swamp endemics and that great similarity exists between Kerangas forests on bleached sands and peat swamp forests. Also, the peat swamp environment is, geologically speaking, ephemeral, being dependent on a rather exceptional coincidence of physiographic conditions. It must be emphasized in this connection that the present-day large extension of the NW Bornean peat swamps is due to the exceptional event of postglacial termination of the eustatic rise in sea level in a flat coastal area. Such an event is not known from the Miocene.

The colonization of the initial peat environment will be by species which happen to grow near, and this is largely determined by the presence of acidic Kerangas soils. Repeated geographic changes, such as can be expected in a deltaic area, will tend to disrupt the geographic distribution pattern, and to some extent, determine colonization and subsequent vegetational succession of a newly developed peat swamp.

#### CONCLUSIONS

In contrast to pollen-analytical studies of Quaternary peats in temperate areas, this investigation of tropical Holocene peat and Tertiary coal deposits concentrates on the local succession of peat swamp vegetation. This was possible because extraneous pollen forms a minority due to the dense forest cover and limited dispersal of the pollen released largely by insect-pollinated flowers. In fact, it appears probable that only a very local picture of the vegetational succession, not exceeding 100 m in diameter, is reflected in the diagrams.

The rich flora of the peat swamps is only partially preserved as pollen and spores, but a sufficient number of taxa are found which, alone, or in combination are indicative of the successional stages to permit an approximate reconstruction of the course of development.

The succession found in Marudi is closely comparable to the zonation present at the surface of the peat deposit, which started on mangrove clay and forms part of a very extensive raised-bog area, covering 420 km<sup>2</sup>.

In Berakas, in contrast, we deal with a very small deposit, not exceeding 1 km in width. Peat growth here has started on fluvial sediments, has not proceeded beyond the first stage, phasic community I of the present-day catenary sequence and which remained in close proximity of the coast.

The differences in floristic composition between Berakas and the comparable interval in Marudi are relatively minor and of the same order as those found today between swamps along the coast of NW Borneo.

Whether peat growth starts on mangrove clay or on fluvial deposits seems to make little difference in this respect. Studies on the zonation have also shown that beyond a certain stage of the development, the floristic composition of the vegetation shows little or no difference on fluvial clay or mangrove sediment.

In general the close correspondence in composition and ecological succession between the Holocene and the Miocene peat swamps, which are separated by approximately seven million years, testifies to little change in the peat swamp flora. This is especially remarkable in view of the fact that peat swamp environments are geologically ephemeral and have to be populated anew from mainland reservoirs each time a new peat swamp system develops. Only the fern *Stenochlaena areolaris*, even if originally a peat swamp type, has suffered local extinction.

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