# The Flora of the Peat Swamp Forests of Sarawak and Brunei, including a catalogue of all recorded species of flowering plants, ferns and fern allies

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THE COASTLINE OF SARAWAK appears to the casual observer monotonous and uninteresting. A coastal fringe of littoral forest or mangrove merges quickly into a flat plain behind which the inland mountain ranges appear in the distance. In south western Sarawak the regularity of the coastline is broken by mountains or low hills that form promontories jutting out into the sea; but from the mouth of the Batang Lupar to Kedurong Point—a distance of 200 miles—there is no high ground in the vicinity of the coast. Apart from the immediate coastal or riparian fringe, subject to regular or occasional inundation, the whole plain has been and still is largely covered in swamp forest growing on peat, recorded depths of which may exceed fifty feet. There is some evidence to show that this coastal plain has developed since the stabilisation of the sea level, about 5,500 years ago, following the last Glacial Period. Alluvium carried down by the rivers draining the interior has been deposited at the mouths of rivers or in bays along the coast and as the coastline has progressed seawards so peat has developed and accumulated under the dense forest on the plain behind. The Rejang, the largest river on the northern coast of Borneo, and to a lesser extent other rivers, has divided to form a complex deltaic system. Each island in the delta forms a distinct and self-contained swamp unit bounded by a fringe of mangrove or riparian forest.

The coastal and deltaic peat swamps cover 5,660 square miles in Sarawak and 380 square miles in Brunei, which amount to 11.9 and 12.5 per cent of the total land surfaces of the two territories respectively. Results of numerous precise level surveys prove that they are entirely of the raised bog type with a stilted water table and surface drainage. The ground water is typically tea-coloured, and the peat soils are oligotrophic and markedly acid. Similar swamps are well known elsewhere in Malaysia. Endert (5) recorded peat swamps in South Sumatra and East Borneo, and other descriptions have been made by Sewandano (11) in Central Sumatra, and by Durgnat (4) and Wyatt-Smith (16) in Malaya. Van Steenis (12-14) shows their distribution on the vegetation map of Malaysia and notes that large areas of southern New Guinea are also peat swamp. Dr. B. Polak (8) undertook fundamental research into the nature and physiognomy of peat swamps in Sumatra and East Borneo. There has been, however, no previous comprehensive study of the ecology or floristic composition of the peat swamp forests in the region.



The catalogue of the flora of the peat swamp forests includes all species of phanerograms, gymnosperms and pteridophytes collected during the course of an ecological survey of these forests. In compiling this catalogue it had been hoped initially to include records of previous collections, especially those by Beccari and by Haviland and Hose. It was found, however, that these collectors only very rarely recorded the habitat of the plant, and consequently there could be no certainty that the specimen originated in peat swamp forest; though frequently the locality of the collection indicates that this is probable. The catalogue, therefore, is confined to recent collections, largely by the author and Forest Department staff, but including a few specimens collected by Miss W. Brooke and Mr. J. Wyatt-Smith.

The species included in the catalogue are those found in the raised bog type of peat swamp forest. The marginal zones, such as the transitional zone from mangrove and near the inland perimeter of swamps, though including numerous true peat swamp species, have in addition a few species that are absent from the extensive coastal and deltaic swamps. The inland fresh-water swamp forests, which are subject to periodic inundation, and high altitude peat swamps require further investigation. These types cover a negligible area in relation to the area covered by the coastal and deltaic peat swamp forests. It is inevitable in an ecological survey of this nature that a good deal of sterile material is collected. However, during the past five years, collecting has been virtually confined to fertile material and about ninety-five per cent of the species is represented by flowering or fruiting specimens, frequently both.

One thousand seven hundred and six numbers are recorded in the catalogue. This total includes 1,528 specimens of dicotyledons, 106 monocotylons, 6 conifers and 66 pteridophytes. The complete collection is housed in separate cabinets in the herbarium of the Sarawak Forest Department at Kuching. Duplicates of early collections (1953-5) were sent to Singapore, and fertile material has in the past five years been distributed to herbaria at Kew, Leiden, Singapore and Bogor, with additional material of certain families to other herbaria. Wood specimens are available for most arboreal species.

The catalogue of phanerograms is arranged by families in accordance with the Bentham and Hooker system of classification with certain generally accepted exceptions. In those families revised for *Flora Malesiana* the nomenclature of the revision has been followed. For the classification of pteridophytes the system adopted by Holttum (6 and 7) has been used. Specimens of each species are recorded by administrative divisions and localities, and notes on the habit, frequence, distribution and occurrence in forest types are included. Furthermore, where species have been matched by the

author in the herbarium at Kew, the number of the matching specimen is noted with an indication by the symbols A, B, or C of the degree of reliability of the determination. All recorded vernacular names have not been included as frequently they are very unreliable. The vernacular names shown have been checked and found to have fairly consistent usage.

The completeness of the catalogue varies with the locality and the type of plant. More ecological work has been undertaken in the Rejang Delta than elsewhere and consequently the flora is better known. It also is incidentally the richest. Furthermore, collecting was originally concentrated on the tree flora, though during the past five years collections have been made of herbs, lianes, parasites, epiphytes and ferns. It is considered that for tree and shrub species the catalogue is virtually complete. Visits to peat swamps in the past twelve months have failed to yield any important unrecorded species. It has been found also that the herbaceous and climbing elements of the flora are remarkably uniform. Though the list is not as complete as that for the tree flora the same species tend to be found time and again. Even the epiphytic flora, which might have been expected to be the most variable, appears fairly constant in its distribution in peat swamps and in its occurrence in the forest types. Undoubtedly there are many species yet to be recorded in peat swamps but the most characteristic and abundant species have now been collected.

The names of some species included in the catalogue must be treated with a good deal of caution. The taxonomy of genera such as Eugenia, Garcinia and Lithocarpus is in a somewhat chaotic state and accurate specific identifications for many species will not be obtainable until the families are revised. Where matching material has not been found the species is designated by the generic name followed by the number in brackets of what is considered to be the most representative specimen.

It is impossible at this stage to say how many species new to science have been collected. This can only be ascertained with certainty when the families are revised for Flora Malesiana. In those families that have been revised or are at present in the process of revision the most important discovery has been a new species of Litsea (L. palustris Kostermans). This tree species is extremely abundant in the central areas of many swamps throughout Sarawak and Brunei; in the Rejang Delta it forms pure stands over many square miles with as many as 120 trees per acre. It is odd that it has never been collected previously. Presumably early collectors did not penetrate into the centres of the swamps. Other new species include Cephalomappa paludicola Airy-Shaw, Pandanus andersonii H. St. John and Knema uliginosa Sinclair, a small tree with a localised distribution in the Loba Kabang Protected

Forest. Mr. J. Sinclair has recently described a new species of Goniothalamus. He also considers that Polyalthia (9059) is undescribed. It is known from only one other previous collection, p.b. 3919 by Beccari. Mr. E. J. H. Corner has examined all the collections of Ficus, and has described three new species: F. callicarpides is a small root climber abundant on the buttresses of Shorea albida; F. spathulifolia and F. supperforata are stranglers or ground rooting epiphytes. In families that have not yet been revised there are a few distinctive species which are unmatched in herbaria at Kew, Leiden, Singapore and Bogor and are therefore probably new to science. These include a Parishea\* (2697), a Xanthophyllum (2614), a Piper (9234) and a Cinnamomum (4751). Finally a single collection of a small tree from the Lundu swamps has proved to belong to a new genus (Jarandersonia) in the Tiliaceae which has been described by Dr. A. J. G. H. Kostermans.

Two hundred and forty-two tree species have been recorded, including 38 small trees of the understorey which rarely or never exceed twelve inches girth. Some of the latter might be considered as shrubs, but this term has been purposely avoided as few species have a fastigiate form (except in the stunted forest in the centre of certain swamps in the Baram). The arboreal flora is somewhat greater than originally expected. Sewandano (11) estimated that the arboreal flora of the swamps of East Sumatra to be less than a hundred species. In one forest type alone in the peat swamps of Sarawak and Brunei as many as seventy-five species are found to an acre.

## Representation of families

The representation, by genera and species, of the families of phanerograms is shown in Table 1. If the arboreal species alone are considered, it will be seen that most of the principal arboreal families that occur in lowland dipterocarp forest are to be found in peat swamp forest. Of the families that have not been recorded mention may be made of the Combretaceae, Lythraceae, Styracaceae, and Proteaceae. A comparison of the arboreal flora in peat swamp forest with that recorded by Wyatt-Smith (15) in two fiveacre plots in Malaya shows an obvious similarity in the relative numbers of genera and species recorded. It should be remembered, however, that the comparison is between the total arboreal flora in peat swamp forest and species exceeding twelve inches girth in two small plots. Nevertheless most of those families, i.e. Dipterocarpaceae, Anacardiaceae, Annonaceae, Euphorbiaceae, Guttiferae, Lauraceae, Leguminosae, Myrtaceae, Rubiaceae and Sapotaceae, that predominate in lowland dipterocarp forest also provide

<sup>\*</sup> As result of a recent (1962) collection (S. 15951) this specimen has been identified as *Quassia borneensis* Nooteboom (msc.), the first representative of the Afro-American genus to be found in Asia. A previous collection (San. 20499) was made in Borneo.

most species that occur in peat swamp forest. It would appear, therefore, that specialized adaptations, such as pneumatophores, kneed roots and, perhaps, stilt roots, for growing in peat swamps do not tend to be exclusive to or predominate in certain botanical families.

In the herbaceous vegetation there is an absence of the predominantly aquatic families and genera of dicotyledons, e.g. Nymphaceae, Limnanthemum, Jussiaea, and Ludwigia. A possible cause may be the extremely acidic and anaerobic conditions of peat swamp soils. It is hardly surprising to find an almost complete absence of the calciphylous families such as Balsaminaceae (Impatiens), Acanthaceae, Scrophulariaceae, Begoniaceae, and Gesneriaceae. Aeschynanthus luans, of the last mentioned family, is the only record. Monocotyledons, and in particular the Araceae and Cyperaceae, preponderate in the herbaceous flora.

The climbing flora is drawn from many families, of which particular mention may be made of the Annonaceae, Rubiaceae and Moraceae. Species of Capparidaceae, Malpighiaceae, Solanaceae and Acanthaceae have not been recorded, and the Convulvulaceae is only represented by two species, neither of which is common.

## Floristic composition

Lists of the more important and characteristic peat swamp species are shown in Table 2. These include the more widely distributed and common species. For rarer and localised species reference should be made to the catalogue.

The arboreal flora has been subdivided into four canopy classes based on the average maximum girth attained by a species. This subdivision is somewhat arbitrary and does not presuppose that distinct canopy layers can be recognised or even exist. No consideration is taken here of the ecology of the species or their occurrence in the forest types. This will be briefly discussed later. Furthermore it should be remembered that the average maximum size class of a species varies very considerably in different forest types. For instance Dactylocladus stenostachys—the only tree species to occur in all forest types—is a massive dominant, with girths occasionally exceeding twelve feet, on the perimeter of the swamps, whereas in the stunted forest in the centre of certain swamps in the Fourth Division it occurs abundantly as a small tree rarely exceeding twelve inches girth and frequently little more than a shrub.

In the upper storey species of Dipterocarpaceae predominate. Of the six species of Shorea commonly found in peat swamps Shorea albida forms remarkable pure stands (in the upper canopy) with 40 to 160 trees per acre and covering very extensive areas in the central zones of many swamps from the Sadong river in southern Sarawak to Badas in Brunei. Other important dominants are

the timber producing species Gonystylus bancanus, Dactylocladus stenostachys, and Copaifera palustris. These three species with the Shoreas (S. platycarpa, S. rugosa var. uliginosa, S. scabrida, and S. teysmanniana) comprise on the average about 80 per cent of the upper storey (trees with girths exceeding 60 inches) in mixed swamp forest in the peripheral zone of swamps and near the coast. Litsea palustris, an associate of Shorea albida, occurs in almost pure forests in the centre of some of the larger swamps in the Rejang Delta. In Lawas District in north Sarawak, and in adjacent areas in North Borneo, Shorea albida is absent and is replaced by a unique forest dominated by the conifer Dacrydium beccarii var. subelatum and an undescribed species of Casuarina, formerly confused with C. sumatrana. Little now remains of this forest after forty years of heavy exploitation.

The middle and lower storeys include many species of the Lauraceae, Euphorbiaceae, Guttiferae, Burseraceae, Ebenaceae, Fagaceae, and Annonaceae. Some of the more abundant species in the middle storey are Alangium havilandii, Blumeodendron tokbrai, Ctenolophon parvifolius, Diospyros evena, Diospyros pseudomalabarica, Kokoona ovato-lanceolata, Palaquium cochleariifolium, Parastemon spicatum and Xylopia coriifolia. In the lower storey the most widely distributed species in mixed swamp forest are Neoscortechinia kingii, Cyathocalyx biovulatus, and Stemonurus umbellatus. Tetractomia holttumii and Cephalomappa paludicola are abundant in the lower storey of pure Shorea albida forest.

In the understorey there are few species that rarely or never attain twelve inches girth, and most of these are rather rare or localised. Mention however may be made of Ixora pyrantha which is abundant in Shorea albida forest, and Tarenna fragrans in mixed swamp forest. Shrubby dicotyledons are rare. Those that do occur are largely confined to the more open forest in the centre of some swamps. Here may be found Ficus deltoidea var. motleyana, Euthemis obtusifolius, Labisia punctata f. punctata and Medinilla hasseltii. Some species, such as the Nepenthes, may have a scandent or climbing habit, but they are more commonly found on or near to the swamp surface, and may be more correctly considered as shrubs. It would appear that most of the Nepenthes in swamp forest only adopt a climbing habit when the canopy is opened. The stemless spiny palm Zalacca conferta and the large stemless pandan Pandanus andersonii frequently form dense thickets; the former in mixed swamp forest, especially on shallow peat, and the latter in association with Shorea albida. Two other pandans are common: Pandanus brevifolius in mixed swamp forest, and Pandanus ridleyi in stunted forest in the centre of some swamps in the Baram.

Herbaceous dicotyledons are practically absent. Argostemma psychotrioides is frequent in mixed swamp forest and the interesting small myrmecophyte Clerodendron fistulosum has a wide

distribution though is never common. Aroids and sedges predominate, of which the most abundant and widespread species is Thorachostachyum bancanum. Many aroids occur in damper localities where the water table is exposed or permanently near the surface. Here may be found Aglaonema pictum, Homalomena rostrata, Alocasia longiloba and Alocasia beccarii. Near streams or in particularly damp spots in the swamps where the water table is permanently exposed, the aquatic aroid Cryptocoryne pallidinervia abounds. Aroids are however almost entirely absent from the drier central areas of swamps. The large herb, Hanguana S malayana, also favours the damper localities and is frequently found in places where a hole has been torn in the swamp surface by a tree uprooted by wind. A smaller form of this species tends to occur in slightly drier habitats. The two small terrestrial orchids, Zeuxine violascens and Cystorchis variegata, with attractive variegated foliage, occur on leaf litter in mixed swamp forest.

A simple classification, such as is attempted here, for herbs, epiphytes and climbers may lead to complications. Some species, such as Ficus spp., Pycnarrhena borneensis, and Poikilospermum spp., start life as epiphytes and later, after their roots have reached the swamp surface, develop a climbing habit; whereas others, e.g. Randia sp. (7904) and Fagraea litoralis, are initially epiphytes and later become independent shrubs or small trees. Bulbophyllum beccarii, a conspicuous epiphyte on Shorea albida, is stated by Beccari(1) to start as a climber from the ground surface, but early stages in its development have not been seen by the author. The species has always been found as an epiphytic climber spiralling round the upper boles of trees. Another complication is that some crown epiphytes, e.g. Ficus deltoidea var. borneensis and Dischidia nummularia may be terrestrial in the more open forest in the centre of some swamps, where presumably the ecological conditions are not dissimilar to those found in the crowns of the upper canopy in dense forest.

Many of the commonest crown epiphytes are confined to mixed swamp forest. They are particularly abundant in the crowns of Gonystylus bancanus and Dactylocladus stenostachys, both of which have a soft fibrous bark. No attempt, however, has been made to determine host specialisation. The best represented group is the orchids, of which Bulbophyllum vaginatum, Dendrobium merrillii, Eria pannea and Eria aff. pulchella are particularly abundant. Crown epiphytes on Shorea albida are scarce. Dischidia spp., Hydnophytum formicarum and Myrmecodia tuberosa are largely confined to stunted forest where conditions are similar to open heath forest in which these species also occur. The two most widely distributed and abundant shade epiphytes are Medinilla laxiflora and the orchid Liparis lacerata. Both tend to occur as epiphytes on small trees in dense forest at heights of from two to ten feet from the ground.

The liane and climber flora is not so conspicuous as that found in lowland dryland forest. The species are relatively few and do not appear to reach as large a size. In Shorea albida forest lianes are rare, and they are almost absent in the central forest types. Rattan palms, though not rare, are small in size and commercially of no value. Of the three species recorded two, Plectocomiopsis wrayi and Korthalsia rigida, are abundant; the latter frequently in association with Shorea albida. The commonest of the larger lianes is Uncaria ovalifolia, the sap of which is drunk by the natives to quench their thirst in the forest. This species also tends to form thickets in young secondary forest following exploitation. Other common lianes are Willughbeia glaucina, Fibraurea chloroleuca, and Mitrella dielsii.

Figs are particularly abundant in peat swamp forest; twenty-four species have been recorded. True strangling figs, that after killing the host develop a trunk of their own, are relatively rare. Ficus crassiramea is the most conspicuous example. This species is confined, however, to shallow peat near the coast. Many of the figs start as epiphytes but though adopting a strangling habit rarely, if ever, kill the host tree. They might be considered as partial stranglers, or, as is preferred, ground rooting epiphytes. These are especially abundant in mixed swamp forest on Gonystylus bancanus and Dactylocladus stenostachys. The most common species are Ficus acamptophylla, Ficus consociata, Ficus spathulifolia, Ficus xylophylla and Ficus sundiaca. Some tend to be rather localised: Ficus xylophylla, for instance, is very abundant on Pulau Bruit in the Rejang Delta but rather rare elsewhere in swamps. Of the small root climbing figs Ficus callicarpides is abundant on buttresses of Shorea albida.

Of the small climbers, generally confined to the lower storey, though some may reach the crowns of middle storey trees, the most numerous are Lecananthus erubescens, Lucinaea morinda, Medinilla scandens, Aeschynanthus hians, and the climbing aroid Rhaphidophora lobbii. Nepenthes ampullaria almost invariably has a climbing habit in peat swamps, though in heath forest the whorls of pitchers are not infrequently found embedded in the litter layer. Gnetum neglectum, a small twining climber which rarely attains a height of more than fifteen feet has been found throughout the Rejang Delta and Maludam Peninsula but is never common.

The myrmecophytes form an interesting group. They include two trees, Macaranga caladifolia and Macaranga puncticulata. The former is a primary forest species, whereas the latter has been only rarely recorded in primary forest, though it frequently forms almost pure dense stands in secondary swamp forest, especially along rail lines and on shallow peat cleared for cultivation. Of the other myrmecophytes only the herb Clerodendron fistulosum occurs in

dense forest, the remainder, which includes the epiphytic climbers. Dischidia nummularia and Dischidia rafflesiana and the two conspicuous epiphytes Myrmecodia tuberosa and Hydnophytum formicarum, occurs in open stunted forest.

Parasites are not common in peat swamps. Lepidaria oviceps, a very conspicuous species, is found as a crown parasite of upper storey trees, whereas Macrosolen beccarii occurs as a parasite of lower or middle storey trees in the shade. It can be quite abundant locally. The parasitic shrub Henslowia varians is found in open stunted forest.

A list of the common ferns of peat swamp forests is included in Table 3. Terrestrial ferns are limited in number. The most typical species are Vittaria elongata, Schizoloma coriaceum, and Syngramma lobbiana, all of which occur in mixed swamp forest on roots and pneumatophores above the water table. The stemless tree fern Cyathea glabra is locally abundant in Shorea albida forest. Schizaea malaccana, more usually a montane species, occurs in stunted forest often in association with Lycopodium cernuum, which is so common on degraded soils. The interesting and rare Ophioglossum intermedium has only been recorded from one locality in the Rejang Delta. Nephrolepis biserrata is rare in primary forest but forms dense thickets in completely open secondary forest, especially where the slash has been burnt.

The epiphytic ferns are more difficult to classify into crown and shade epiphytes as they appear to be more tolerant than flowering plants of light and humidity conditions. Many of the common epiphytic ferns of gardens, rubber plantations, etc., such as Asplenium nidus, Asplenium phyllitidis, Pyrrosia longifolia and Paragramma longifolia are to be frequently found in peat swamp forest. Humata angustata and Humata parvula may be found as either crown or shade epiphytes and are occasionally even terrestrial in the central forest types. The most consistent shade epiphyte is Lycopodium phlegmaria var. divaricatum which occupies a similar habitat to Medinilla laxiflora and Liparis lacerata. Only two climbing ferns have been recorded: Stenochlaena palustris which clothes the lower stems of many trees on shallow peat near the coast, but becomes progressively rarer further inland; and Teratophyllum ludens which is confined to dense or moderately dense shade in the understorey.

## Peat swamp endemics

A far greater knowledge of the flora of Borneo and of the ecology of the species is required before it can be stated with any authority which species are confined to peat swamp forest. There are probably very few. That there are similarities in the floras of heath and peat swamp forest is well known, and has been mentioned by Richards (9 & 10) and Browne (2 & 3). The author has recorded

ninety-eight species which occur in both vegetation types and Dr. P. S. Ashton has recently added to the list. A note is included in the catalogue under each species where its occurrence in heath forest has been recorded. Dr. E. F. W. O. Brunig is at present engaged on an ecological study of heath forests and when this is in a more advanced state a comparison of the two floras will be possible. Some typical peat swamp species are also to be found in lowland dipterocarp forest. A recent enumeration of a thirty acre block on a largely clay ridge in the Semengoh Forest Reserve near Kuching showed the presence of Neoscortechinia kingii, Shorea scabrida, Swintonia glauca, Mangifera havilandii, Koompassia malaccensis, Santiria tomentosa, Bhesa paniculata, Endospermum malaccense, Cratoxylon arborescens, Litsea grandis, Dialium laurinum, Sindora leiocarpa, Carallia brachiata, Mussaendopsis beccariana and Pometia pinnata f. acuminata. All these occur in peat swamp forest and there are probably others in this area which have not yet been definitely identified. It is significant that all these species, without exception, occur and are largely confined to the peripheral zone of mixed swamp forest, where the drainage is better and the peat soil probably more fertile. The species that occur in the forest types in the centre of the swamps are largely those that are also found on poor, frequently podzolic, soils found in heath forest.

# Distribution of peat swamp species

The peat swamps form an almost continuous strip along the coast of Sarawak and Brunei from south western Sarawak to the Tutong river in Brunei. The only major breaks in their distribution occur between Bintulu and the Nyalau river, a distance of forty-five miles, and eight miles which separate the swamps in the Sibuti river from those in the Baram river. Conditions of development of peat swamps and the nature of the peat soils themselves are similar over the whole area. It can be expected, therefore, that the flora is relatively uniform. In comparison with the flora of other soil types, where marked discontinuities occur, this is generally so. Nevertheless it has been found that the flora of the Rejang Delta is richer than that of swamps elsewhere in Sarawak or Brunei. Further collecting in less frequented areas will no doubt reveal a more widespread distribution of some species that are at present recorded from only the Rejang Delta. But there are in the Rejang Delta species such as Lophopetalum rigidum, Blumeodendron subrotundifolium, and Stemonurus scorpioides which occur so frequently that if present elsewhere it is unlikely that they would have been overlooked. Moreover, in ecological sample plots, recording all trees exceeding twelve inches girth, it has been found that the species per acre tend to be consistently more numerous in the

Rejang Delta than elsewhere. The following tree species are known in peat swamp forest only from the Rejang Delta: Anacalosa frutescens, Blumeodendron subrotundifolium, Ellipanthus tomentosus spp. tomentosus, Parishea sp. (2697), Swintonia glauca, Lophopetalum rigidum, Castanopsis foxworthyi, Cephalomappa beccariana, Mangifera havilandii, Campnosperma montana, Linociera sp. (9042), Stemonurus scorpioides, Kibatalia sp. (9300), and Kibessia coriacea. In contrast there are few species apparently absent from the Rejang Delta yet recorded in other swamps. Neesia malayana has a localised distribution in Lawas swamps and has also been recorded from the Setapok Forest Reserve near Kuching. Tristania maingayi is abundant in the central forest types in the Baram and in the Maludam Peninsula, but has not been recorded in similar forest in the Rejang Delta. Ganua curtisii is known in swamp forest only in the Badas forests of Brunei, where it occurs abundantly in association with Shorea albida.

In general it has been found that upper storey species tend to have a more widespread distribution than smaller tree species of the lower storey, and understorey trees are frequently very localised. Typical examples of the latter are Knema uliginosa in the Loba Kabang Protected Forest, and Kibatalia sp. (9300) and Lophopetalum rigidum which are confined to the apex of the Rejang Delta. An interesting exception to this generalisation is the distribution of the Dipterocarpaceae which is shown diagramatically in Table 4. Six species occur in peat swamp forest throughout the two territories. Cotylelobium flavum has a widespread distribution in heath forests but in peat swamps it has only been recorded from the Rejang Delta and Brunei. Shorea macrantha and Shorea pachyphylla are also more frequently found in heath forest but both have a limited and localised distribution in neath and peat swamp forests. In peat swamps they are only found near the inland margins of the swamps. Dipterocarpus coriaceus, which is only known from localised areas in the Second Division and in the Sekai Forest Reserve in the Mukah river, is confined to peat swamps. It has not definitely been recorded from the Rejang Delta, but seedlings, probably of this species, have been found in the Naman Forest Reserve at the apex of the delta. The distribution of the gregarious species, Shorea albida, extends in peat swamps from the Sadong river to the Badas swamps of Brunei. It has also been recorded in heath forest near Lundu. Shorea inaequilateralis has a similar, though somewhat narrower, distribution.

There are many factors involved in determining the geographical distribution of peat swamp species. Unpublished pollen evidence indicates that many of the species have been present in peat swamps in Borneo for millions of years. Recent changes in sea level during and immediately after the Glacial Period with consequent erosion and deposition along the coasts may have been an important factor.

Some species confined to peat swamps may have been eliminated from swamps in minor rivers yet retained a foothold in the Rejang river. After the stabilisation of the sea level, some 5,500 years ago, the spread of species may have been obstructed initially until the seaward development of peat swamps on alluvium had progressed sufficiently for the swamps to coalesce along the coast. There are, however, many other factors to be considered. Even if species were eliminated from coastal swamps, they would, no doubt, be preserved in heath forests and in small localised hill and montane peat swamps and thus be able to spread down again to the coast. Moreover, some of the species, such as Swintonia glauca, Stemonurus scorpioides, Mangifera havilandii and Quassia borneensis, which in peat swamp forest have only been recorded in the Rejang Delta, may be considered more accurately as constituents of dry land forest, and only in the Rejang Delta have they become adapted to growing and regenerating in peat swamps. Further understanding of the distribution of the peat swamp flora is only likely to be achieved after greater knowledge has been gained of the Bornsan flora as a whole. Later a comprehensive study of the peat swamp flora in the Malaysian region might yield some interesting and valuable information on the phytogeography of Malaysia.

## Ecology of the peats swamp forests

It is not intended to describe in any detail the ecology of the peat swamp forests in this paper. This will be discussed at greater length elsewhere. However, as some details of the occurrence of the species in recognised forest types are included in the catalogue a few remarks by way of explanation are necessary.

The coastal and deltaic peat swamps are all of the raised bog type, each swamp or bog forming a separate unit in the ecosystem. Well developed raised bogs have a structure similar to that found in temperate raised bogs. The vegetation types are found in a catenary sequence from the perimeter to the centre of a raised bog. The term "Phasic Community" has been used to designate a vegetation or forest type. This term is particularly appropriate as a recent pollen analysis indicates that the horizontal pattern of vegetation types found on the ground is also likely to be found in a vertical succession in the centre of the raised bogs. Six phasic communities have been recognised and they are differentiated on floristic composition and structure of the vegetation. Two phasic communities (Nos. 5 and 6) occur only in the most highly developed raised bogs in the Baram river. Brief descriptions of the phasic communities follow:

## Phasic Community 1

Gonystylus—Dactylocladus—Neoscortechinia association. (Mixed swamp forest). Occurs on the perimeter of swamps and covers extensive areas of relatively undeveloped coastal bogs. The canopy is uneven, with dominants attaining 130 to 150

feet in height, and the floristic composition of all storeys very mixed. Of the phasic communities it most closely resembles lowland dryland forest. Principal dominants include Gonysty-lus bancanus, Dactylocladus stenostachys and four species of Shorea (not Shorea albida). Numerous species occur in the middle and lower storeys, of which the most widely distributed and abundant are Neoscortechinia kingii and Alangium havilandii. Tree species, twelve inches girth and over, recorded in ecological plots average between sixty and seventy per acre. The water table is frequently exposed and aroids and the sedge Thorachostachyum bancanum are abundant. Zalacca conferta may form dense thickets especially on shallow peat.

## Phasic Community 2

Shorea albida—Gonystylus—Stemonurus association. (Locally known alan forest). Occurs as a transitional zone, often of considerable depth, between phasic communities 1 and 3. The canopy is uneven, and large trees, frequently exceeding twelve foot girth, of Shorea albida, dominate the forest. These are almost invariably hollow and have the appearance of being moribund with large stag-headed crowns. Mid-girth trees and regeneration of Shorea albida are almost entirely absent. The moderately dense middle and lower storeys are large composed of species of Phasic Community 1. Stemonurus umbellatus is a characteristic species of this community.

## Phasic Community 3

Shorea albida consociation (alan bunga forest). This community covers very extensive areas in the second and fourth divisions and in the Badas swamps of Brunei, but is largely absent from the Rejang Delta. The upper storey is composed of a pure even canopy, ranging in height between 160 and 190 feet, of Shorea albida which averages between thirty-five and fifty trees per acre. The middle storey is largely absent and the moderately dense understorey is frequently dominated by a single species: Tetractomia holttumii, Cephalomappa paludicola or Ganua curtisii. Herbaceous vegetation is largely absent. Pandanus andersonii frequently forms dense thickets in the shrub layer.

# Phasic Community 4

Shorea albida—Litsea—Parastemon association (padang alan or padang medang forest). Occurs in the central area of numerous swamps in all localities, particularly in the Rejang Delta, and as a transitional zone in certain of the Baram swamps. The canopy is unbroken and even at heights ranging from 100 to 120 feet. All trees are relatively small in girth, few exceeding six feet, and the forest has a marked pole-like

and xerophytic aspect. Principal dominants are Shorea albida (padang alan), which may be represented by 180 stem per acre and Litsea palustris (padang medang). Other characteristic species are Parastemon spicatum, Combretocarpus rotundatus and Calophyllum obliquinervum.

## Phasic Community 5

Tristania—Parastemon—Palaquium association. Occurs as a narrow zone between phasic communities 4 and 6. The canopy is dense and even, with a few emergents, and an average height of between fifty and seventy feet. The forest has between 400 and 500 stems (12 inch girth and over) per acre, all of which are small; few exceeding three feet girth. The most abundant species are Tristania obovata, Tristania aff. maingayi, Parastemon spicatum, Palaquium cochleariifolium and Dactylocladus stenostachys. Herbaceous flora is largely absent.

## Phasic Community 6

Combretocarpus—Dactylocladus association (padang keruntum). The last known phase in raised bog development. It covers extensive areas of deep swamps in the middle reaches of the Baram, near and upriver from Marudi. The forest is open and markedly xerophytic. All trees and shrubs tend to have a stunted appearance. Combretocarpus rotundatus is the only species that exceeds three feet girth, and it rarely attains a height of more than forty feet. Dactylocladus stenostachys, Litsea palustris and Garcinia rostrata are abundant, but frequently little more than shrubs. Myrmecophytes and Nepenthes spp. are particularly numerous. Thorachostachyum bancanum and Pandanus ridleyi are abundant on the swamp surface, where sphagnum moss (Sphagnum junghuhnianum) also occurs.

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Herb, 9-18 ins. h., occasional in P.C. 1. Recorded only from II and III Divs.

#### Alocasia Neck.

## 1. Alocasia longiloba Miq.

birah hutan (Mil.).

II Div.: Triso 12218, Saribas F.R. 8507; III Div.: Pulau Bruit 9219, 8018; IV Div.: Sg. Dua 4195.

Distinctive herb, rare in P.C. 1, occasional and localised in P.C. 2; throughout Sarawak and Brunei.

## 2. Alocasia beccarii Engl.

II Div.: Triso 3174, Saribas F.R. 8364; III Div. Naman F.R. 9299.

Small herb, occasional in P.C.'s 1 & 2. Recorded from only II & III Divs.

## Cryptocoryne Fisch.

## 1. Cryptocoryne pallidinervia Engl.

II Div.: Triso 12212; III Div.: Pulau Bruit 8022.

Aquatic herb, occasional, locally frequent, in wetter localities of P.C. 1; throughout Sarawak and Brunei.

# Cyrtosperma Griff.

# 1. Cyrtosperma lasioides Griff.

III Div.: Pulau Bruit 9021, Lepah P.F. 8066.

Large herb, rare in P.C. 1, more frequent in areas where there has been an opening in the canopy and on shallow peat; throughout Sarawak and Brunei.

# Epipremnopsis Engl.

# 1. Epipremnopsis media Engl.

teririp (Mil.).

III Div.: Daro F.R. 9707.

Climber to height of 15-20 ft., rare in P.C. 1. Recorded in peat swamps from only the Rejang Delta and V Div.

#### Homalomena Schott.

#### 1: Homalomena rostrata Griff.

II Div.: Triso 10020; III Div.: Pulau Bruit 8012, Loba Kabang P.F. 2813.

Herb, occasional and localised in P.C. 1 in wetter localities where the water table is exposed. Occurs throughout Sarawak, but not recorded from Brunei.

