XI. SOLOMON ISLANDS BOTANY

A discussion of the Results of the Royal Society Expedition to the British Solomon Islands Protectorate, 1965. Organized by E.J.H. Corner. Phil. Trans. R. Soc. B 255 (1969) 185-631, 196 fig. University Printing House, Shaftesbury Road, Cambridge. Obtainable through booksellers or direct to the Royal Society, 6 Carlton House Terrace, London S.W.1. Price £ 14.- or $ 36.40 post free to any part of the world.

This grand, magnificently edited, and profusely illustrated book contains a wealth of information contributed by many authors. Only botany will be discussed here in more detail.

The first section (pp. 187-270) deals with the geology, climate, soils, vegetation, geomorphology, and evolution of the Solomons. The first known emergence of any of the present land area c. 40.000 sq.km (as compared to New Guinea with 895.000 sq.km) appears to have occurred at late Oligocene, the lowest unit being basalt or basaltic andesite. Lower Miocene with profuse calcareous deposition. Present form dates from Pliocene at the latest. Land surfaces are all young, only Guadalcanal and Bougainville have extensive coastal plains. Elsewhere mountains rise directly from the sea and rivers run swift and cold. Interior of all islands is a jumble of steep, unstable ridges and peaks; landslips are common. Highest elevations are in Bougainville (Emperor Range, 2835 m) and Guadalcanal (Popomanaseu plateau, 2670 m). Earthquakes are frequent. Rainfall is everywhere heavy and frequent (3120-6250 mm, in rain-shadow areas 1250-3120 mm), a tropical oceanic climate. Very occasionally cyclones may cause huge damage.

The Solomon Archipelago is part of the great Melanesian foreland from Bougainville to San Cristobal, where Malesia and Australia abut on the Pacific Ocean. It ranges as a double festoon of islands about 2500 km north-east of Australia, 1120 km long from NW to SE, separated by 176 km of open sea from New Ireland in the Bismarcks to the NW and by 352 km of open sea from the Santa Cruz Is. which are geographically a part of the New Hebrides. Within the Solomons inter-island distances are only 16 to 64 km. Lowering of the sealevel by say 60 m would provide land links between Bougainville, Choiseul, Santa Isabel, the Shortlands Group and possibly Florida and Guadalcanal.

Dr. Whitmore (pp. 259-270) sketched the vegetation: islands are entirely clothed with tropical rainforest except for small anthropogenous grass- and heathland areas in parts subject to a seasonal climate by the rain-shadow. These do not carry particular drought indicators, similar to those in

N. Australia, the Lesser Sunda Is. or S. New Guinea, testimony of their recent origin by man. Extensive areas carrying thickets of small trees and climber tangles instead of high forest are thought due to the combined influence of man, earthquake, landslip, and cyclone. Many of these species are shown to have wide ecological amplitudes.

The flora of the Solomons is in main a poor, attenuated relation of the Malesian, notably New Guinea. The diminution in flora is more strongly marked in montane than lowland groups. Absence of Fagaceae (Nothofagus, Castanopsis), Engelhardia, and the conifer genera Araucaria and Libocedrus (which are in both New Caledonia and New Guinea), and poverty in Ericaceae (only 1 Vaccinium, 1 Agapetes, and 4 Rhododendrons) is marked; Myrtaceae are common replacers (Eugenia, Mearnsia, Metrosideros, Rhodamnia). Upper montane forest is very mossy and a thick layer of peat lies over a shallow mineral soil. The two highest ranges, the Emperor Range on Bougainville and Kavo Range on Guadalcanal are forested to the summit except on the bare volcanic ash slopes around the crater of Mt Balbi (2835 m), the highest mountain in the group and patches of Sphagnum bog on the summit plateau of Mt Popomanaseu (2670 m) on the Kavo Range. Balbi, Popomanaseu, and Kolombangara all have zones with abundant scrambling bamboo (Nastus productus). Flora of Popomanaseu above 1300 m was found to be much the same as on smaller mountains half its height. Whitmore concludes that the overall poor flora of the archipelago is a result of regional geological history.

The second section of the work (pp. 271-354) deals with the land fauna (Lee concludes that probably all earthworms, 15 spp., are introduced by man!), including insects, molluscs, Collembola; "some of the curious distributions do not necessarily reflect places to which Collembola have drifted but perhaps only those to which Collembologists have been driven". A special faunal sketch is given of Rennell and Bellona islands.

The third section (pp. 355-548) deals with marine biology including geomorphology, polychaete ecology, zoning patterns, interstitial transects, especially of opisthobranch molluscs. Dr. Womersley wrote on Algae (220 spp. of Chlorophyta and Rhodophyta are credited to the islands); in general all are common, widely distributed species. He refers to a remarkable phenomenon in the Solomons, viz. the dead coral reefs and Lithophyllum on the reef surfaces, specially those exposed to slight moderate surf, situated at 12-15 cm above to just below low tide. Both appear to have quite recently been killed. This is usually ascribed to storm deluges and heavy rainfall through excess of freshwater. It might also be ascribed to very recent tectonic upheaval.

The fourth section (pp. 549-608) deals with the flora, viz. geography by Whitmore, Ficus, Jaagi I. (S. Isabel), mountain-flora of Popomanaseu, and larger Fungi by Corner, Orchids by Hunt, Palms by Moore, and two contributions on floristic relationships by Thorne and Good respectively. This is followed by a discussion largely of botanical comments: Ashton on forest density, Burtt on Gesneriaceae, Jeffrey, Seychelles compared, Green, New Caledonia compared, Jarrett, pteridophytes, Melville, continental drift, with a summary by Corner.

Whitmore stressed the attenuate nature of the Solomon Is. flora as compared with Malesia, especially New Guinea. It is not a recent immigrant flora, and has not arrived by long-distance dispersal. The latter statement is adhered by all botanists present (Thorne excepted) and this, in passing, gave me great satisfaction. There have been stronger land connections within the Solomons and with Malesia in the past. The result is incomplete immigration from Malesia. It is a land-bridge, with proportionally few local endemics (genera: Allowoodsonia, Apoc., Kajewskiella, Rub., Homalocladium, Polygon.). I may add there may be some others e.g. in the Astronia-complex, and the newly described Icacinacea Whitmorea Sleumer. Homalocladium occurs also in Papua, and we regard this as a Muehlenbeckia.

There is a small but distinctive group of non-Malesian genera; some are Pacific wides, others are local-endemic, some of which having signs of great antiquity. There is no predominance in the flora of Melanesia of any one dispersal mechanism, apart from the mainly sea-dispersed Indo-Pacific strand flora. 35% of the genera are worldwide, 28% palaeotropical, 28% Malesian, and 2% Pacific. Allowoodsonia, allied to neotropical Malouetia, shares with Heliconia and some others a tropical trans-Pacific affinity; a list of these is given.

There is hardly any sign of the peculiar New Caledonian flora in the Solomons. Whitmore believes that the Solomon Is. landmass has foundered; they were very early cut off from invasion from the south; the "Antarctic finger pointing north from New Zealand to the New Guinea mountains skirts west of the Coral Sea". Absence of some genera is difficult to explain e.g. of Agathis, which occurs all round the Solomons (New Caledonia, Santa Cruz Is., New Britain, New Guinea); in app. B a list is given of 87 genera found in Fiji and/or New Hebrides and in New Guinea but fail to occur in the Solomons. Absence of a good mountain flora is explained e.g. on the Kavo Range because the mountain is too young (Pliocene) and that obviously the Solomons had before a period in which there were no high mountains perpetuating an

earlier mountain flora. Whitmore concludes that the Solomons act as an efficient land-bridge. Furthermore, that speciation in plants and evolution rate is slow, as the Solomons have been a scene of steadily changing environmental conditions due to geological changes in the Tertiary, and have been subjected to a whole gamut of geological vissicitudes, but show poor endemic development.

Ficus, Corner told, holds a central position in the Solomons, with radiating affinities. There is no evidence of random effect in dispersal in the distribution of Ficus, which section by section maps out migration routes and static fronts of phytogeography. There is plenty of evidence that oceans are effective barriers; Ficus is not distributable except over land or through archipelagoes. The weak part of fig-distribution seems to be in the very short life of the fig-insect; recent observations indicate that this is only 24-48 hours in the flying stage.

Corner's short note on Jaagi islet, 2 miles off Santa Isabel, is an example of the colonisation and succession in a young, very low islet.

In the list of the mountain-flora of Popomanaseu, Guadalcanal, Corner found very few true subalpines, the conifers being Dacrydium and Podocarpus. The occurrence of Acianthus, Orch., Carex cf. dietrichiae, Cyp., Ascarina, Chlor., and Belliolum, Wint. are interesting; otherwise there is nothing thrilling in the way of mountain plants.

Hunt's report on orchids is general in nature; c. 350 collections were made; c. 230 spp. are known to occur in the Solomons of which 90 endemic (70 undescribed); a new genus record is Galeola, hitherto known from the Mascarenes as far as Australia and New Guinea. The composition of the orchid flora is similar to that in New Guinea; very few appear to terminate their eastern extension in the Solomons except those which occur only in New Guinea as well. Wide-reaching genera, e.g. from the Himalayas to the Solomons generally reach Fiji and Samoa as well, exceptions being Paphiopedilum and Thrixspermum. One species is found of the Australasian-New Caledonian genus Acianthus. About 80 spp. are found in New Guinea and the Solomons only, and 10 others in New Guinea sens. lat. and the Solomons.

Mr. Hunt extended his general views with some wider considerations, for example tentatively concluding from Orchid ranges – despite certain zoological evidence to the contrary – towards an ancient Lemurian land-bridge ('dispersal route' probably insular), as the route via NE. Africa and Arabia seems less likely in view of geological and palaeoclimatical evidence. Eulophidium pulchrum and Liparis caespitosa reach from Africa over this range to the Solomons, and Fiji. He

remarked on the numerous synonyms in tropical orchids and lack of correlation in species concepts and description; see elsewhere in this number some quotations. Hunt made also some remarks on the importance of pollinators, saying amongst others that the Papuan-New Britain Dendrobium lawesii is pollinated by a red-breasted honey-eater. He remarked also on the dispersal of seed very worth reading. Within the islands orchids are - as far as habitats are available - rather uniformly distributed. The Solomons are still far from being saturated with orchids.

Collecting and cultivation of orchids is also carried out by the Islanders and Hunt was told that some coastal species of Kolombangara had been brought from New Georgia and Gizo by native Melanesians and Gilbertese.

Dr. H.E. Moore surveyed the Solomon Is. palms, giving a preliminary list. Here also shows an attenuated Papuan flora. There is an enigmatic palm found, viz. Pelagodoxa henryana Becc. native of the Marquesas in San Cristobal but Mr. Dennis suggested that the grove at Makiri Harbour is probably derived from introduction through the nearby Catholic Mission from the Marquesas. However, it is established and Corner stresses that also in the way of palms, the vegetation of the Solomons is far from being saturated, a suggestion also mentioned by Whitmore for trees and Hunt for orchids.

Thorne, in comparing the Solomons and New Caledonia, put two questions: (i) Why is New Caledonia so much richer than the Solomons, despite covering only 6400 sq.miles against the Solomons 15.000 sq.miles? (ii) Why do these islands separated only by 700 miles (over 1100 km) and more or less linked by the New Hebrides and Santa Cruz chain have such relatively distinct floras?

To the first question he serves that New Caledonia has greater variability in climate and distinctive substrates, and its flora has a greater age and suffered a greater isolation. He states bluntly that the lack of certain indigenous groups "rules out land connection with any continental mass". A remarkable statement for a botanist who admits that 15 genera are confined to Australia and New Caledonia and who says that the more recent, particularly herbaceous Angiosperms consist of waifs that have reached the island over wide sea gaps.

His answer to the second question is not quite clear; he stresses that 3 genera are restricted to New Zealand and New Caledonia (out of 118 shared) and none to New Caledonia and the Solomons, but 15 are restricted to Melanesia. He speaks about continuous isolation and ancientness of New Caledonia. A further remarkable statement is that "If a relict flora

comparable to that on New Caledonia ever existed in the Solomons, it has largely been crowded out by the highly adapted Papuan lowland tropical rain-forest flora". He forgets then suddenly climate, soil, ancientness, etc. in this wild guess, without any scientific argument behind it. He summarizes then, saying: "that the floristic relationships between the Solomon Islands and New Caledonia are what one might expect considering the relative proximity of the two island groups to the same Papuan Region source areas and to the intermediate Santa Cruz and New Hebrides islands, the 700 miles of ocean between the Solomons and New Caledonia, and the climatic, elevational, geological, and consequent vegetational differences between the two island groups".

Rather a mouthful of self-satisfaction. I estimate that, given the knowledge of the surrounding floras, but of the Solomons and New Caledonia only the physical features, nobody could ever have made a guess, even approximately, of the composition of these floras. I challenge Dr. Thorne to give the expected composition of the New Hebrides flora which is yet virtually unknown.

Dr. R. Good contributed also some phytogeographical remarks on the Solomon Is. flora based on genera of floristic lists. He points to the absence of an 'Australian element' and the little particularity of their flora, which is an attenuated Papuan flora. The rest of his argument is lost in some hazy speculation on the flora of Australia.

In the Discussion (pp. 609-623) Mr. Peake (British Museum) tried to mathematize distribution of Ficus and Cyathea showing that the larger the island the more endemics (Java excepted as an 'anomaly'). Deriving from Mayr: "this relationships probably being due to continual extinction of species on islands at a much higher rate than hitherto suggested", whatever this means. Because the same rule holds for continental areas, the number of species and the number of endemics increase proportionally to surface: this is not peculiar to islands! Ficus behaves differently as to degree of endemicity as compared with Cyathea.

Whitmore commented as follows: "Most botanists would probably not wish to deny that in certain circumstances the theory and its explanation of size-area relationships and species replacements can occur. At present, however, the evidence for it in the Solomons remains very slender. Further it is unlikely that the same theory can be applied to plants and animals without modification because of the major differences in population structure and dynamics. Many plants (and certainly woody ones) persist many years without the necessity to reproduce, so they can outride temporary unfavourable fluctuations in the environment, which may have

drastic selective effects on short-lived organisms such as insects or birds. The old plants live alongside their progeny with the possibility of crossing, so genetic stability is enhanced. Some trees live several hundred years."

"The Island Theory of Biogeography has not yet been demonstrated adequately, and the most encountered hypothesis to account for the existing conditions in Melanesian plant geography remains that there were more land connexions in the past, although how these lay is a detail undecided. There is no need for stronger wording. Concerning the graphs of flora size against island area, the islands lie from west to east. The diminishing flora eastwards into the Pacific may depend on the distance from source, and any apparent correlation with area may be fortuitous. Actually we have to explain not just the distribution patterns of a few species but of whole floras. If chance dispersal operated, species distributions would be at random and one would not find whole groups of species with identical ranges. As a striking example, 2400 of the 2600 species growing in New Caledonia are endemic; although the island lies in a cyclone belt, none of these species has been found in the nearby Solomons, New Hebrides, or Fiji archipelagos. Then, in as striking contrast by their extended range, several kinds of plant, such as Sararanga, and some birds and butterflies are distributed from the Solomons through the Bismarcks, along the north coast of New Guinea or offshore islands to the Philippines."

"One may recall that 15 years ago geophysicists refused to countenance continental drift despite strong biogeographical evidence. In the present case it is the botanists who have the evidence and need to stand firm. The distribution of flowering plants demands a historical explanation in the former existence of a greater Melanesia. Studies of regional geology are incomplete and of the sea bottom almost nonexistent, though they have been started."

Ashton remarked: "The relative floristic poverty of the Solomons forest suggests a less evolved forest ecosystem than that of Malaya. Would this not emply less stringent competition and hence the broader ecological ranges? Could the lower density of individuals in Solomons forest, compared with those in Malaya, also be explained in the same way? If the ecosystem were less evolved, many niches would remain unexploited and production per unit area, of which forest density is a manifestation, would be lower."

I believe talking about niches is talking about something very hypothetical. What means a 'niche' to any tree, liana, shrub or herb in the tropical rain-forest? They belong to strata.

Burtt made some good concise conclusions: "The frequent glib comparisons that we have heard between the Solomon Islands and New Guinea, as though they were equivalent regions, are dangerous. (Lippincott's gazetteer gives the area of New Guinea as 304200 square miles, that of the Solomon Islands as 16000.) There are greater differences between the floras of north-eastern and south-western New Guinea than are found through the Solomons. As exemplified by Gesneriaceae the Solomon Islands behave as a small land-mass with few internal barriers: Fiji behaves as an oceanic archipelago with much insular endemism: New Guinea behaves as a continental land-mass with considerable internal barriers and much internal differentiation."

Mr. Jeffrey compared the plant geography of the Solomons with that of the Seychelles, the latter having less native species, no doubt due to their smaller size. Essentially there is a great similarity.

"This indicates that the similarity in these floristic features of the two areas is largely a result of the fact that they are both island groups, probably with similar geological histories. The peculiarities of the Seychelles flora and its geographical affinities are consistent with the hypothesis that the Seychelles bank represents a continental area comparative to the ancient blocks of India, Africa, Madagascar and Australia, and that the floras of all had a common source, from which they have diverged subsequent to the splitting-up of the Gondwana continent. In Permian times, it is probable that the Seychelles were part of a land-locked area lying between Madagascar, Ceylon, Borneo and Eastern Antarctica. The Seychelles flora (apart from its strand-flora elements), seems to be one that has evolved in situ and is no doubt a remnant of an originally much richer vegetation which has throughout its history formed closed communities on a land-area constantly being reduced by denudation and marine erosion. The inland endemics of the islands (of which Lodoicea is the most striking) are not, and could never have been, capable of dispersal across large oceanic distances, and only the strand flora seems to have reached the islands in this way."

"The Solomons (unlike the Seychelles) have been subjected to considerable volcanic and tectonic activity, by which old land surfaces have disappeared and new ones formed. Nevertheless, new land areas have probably always been formed near enough to those already present for the Solomons to be regarded as also having had throughout their history a vegetation forming closed communities in which competition, marine erosion and tectonic subsidence have all contributed to keeping the flora numerically small. This too can be re-

garded as an ancient flora that has largely evolved in situ. Its geographical affinities are consistent with the hypothesis that in pre-Cretaceous times the proto-Solomons formed a land-area or archipelago inclusive also of the fore-runners of the present Celebes, northern New Guinea, New Britain, the New Hebrides and Fiji, which was probably situated at about where the Line Islands are now found."

Mr. Green observed that the lowland New Caledonian vegetation is an open "maquis" on soil derived from other bedrock and under less heavy rainfall conditions than the lowland rain-forest in the Solomons.

Miss Jarrett found the fern flora of the Solomons uniform, with lack of endemism, which is unexpected as New Guinea has a rich fern flora. She suggests this could be attributed to an extreme in climate, in this case wetness. I cannot share this suggestion, as New Guinea, Malaya, Borneo, etc. are all very wet.

Dr. Melville digressed on several general subjects. First, he is against random long-distance dispersal for an explanation of the greater part of these island floras, sharing this with all other botanical participants, Thorne excepted. Second, he is against the ideas expressed in my land-bridge theory as "no geophysical mechanism is known that could temporarily raise the ocean floor over such vast distances to comply with this theory. It is much more probable that the true explanation is to be found in continental drift". He then proceeds that he "was led to the conclusion, that from the Late Palaeozoic and through a large part of the Mesozoic, a continent existed in the Pacific centred over the present Mid-Ocean Rise known as the Darwin Rise". This North Pacific continent was disrupted early in the Cretaceous. "When the Pacific continent was severed the two portions of the Permo-Carboniferous Cathaysian (Gigantopteris) flora were drifted apart and are now found in China and western North America on either side of the Pacific ocean. In the South Pacific there is evidence for a smaller continent contemporaneous with the North Pacific continent. This consisted of the submerged platform on which now stands New Zealand, New Caledonia, Fiji and Samoa, united with Peru, Chile, and western Antarctica. It was probably disrupted at the end of the Cretaceous or in the Palaeocene".

"If the convection theory of continental drift is accepted, many puzzling plant and animal distributions can be accounted for. The theory requires a rising convection current along the line of the Darwin Rise. This would have raised up a mountain range through the centre of the continent to a height which has been estimated at 3-4 km. The Rise must have extended far enough to the south to bridge the strait

between the northern and southern Pacific continents in the Triassic. Early Angiosperms were then able to migrate northwards from their southern homeland".

I really cannot visualize that Dr. Melville has taken my use of the word 'land-bridge' in its strict sense. It seems that other botanists have taken this narrow view. It might have been better, for those, in order to prevent this literal reading, to have termed it "Land-Theory" instead of "Landbridge-Theory", as the essence of my theory is that 'land' is required for the dispersal, hence distribution, of the bulk of the plants growing now on islands.

Now it is extremely strange that whereas Dr. Melville agrees with the 'Land-Theory', he refutes the 'Landbridge-Theory' because of no geophysical mechanism known, but accepts at the same time a Pacific Basin almost filled with two continents, one southern and one northern, at least through a large part of the Mesozoic, separated by a strait "allowing for plant dispersal through land-connections and island hopping".

This means more land area in the Pacific than I anticipated to have ever existed!

A corollary of his view is that Angiosperms derived from this connection between the two early Pacific continents, must date from the Triassic. I doubt whether this will find approval; at least not by palynologists.

My viewpoints and those of Dr. Melville are of course not wide apart in essence: both require land in the past where none is today.

They could be reconciled in a general theory, the possibility of which I have hesitatingly mentioned in passing in my book, on the 'Expansion of the Earth' (Hilgenberg, 1933; Halm, 1934; Egued, 1955), which would pre-suppose an ancient Pangaea, not in Wegener's outline, but one which would envelop almost the entire globe. Gradual decrease of gravity in the universe (Dirac, 1938) and a slowing down of the rate of rotation of our globe (as shown by growth rings of corals; Wells, 1963) may have been connected with the process of expansion. During the process probably an enormous amount of gases contained in the mantle has gradually been freed. Among them water, partly also produced through recrystallisation of minerals. This would then mean that the amount of water contained in the oceans has been increasing to a large degree, as a distinct corollary of the expansion theory is, of course, that at the time of the crust enveloping the smaller globe, the amount of liquid water must have been substantially less than it is at present; otherwise there could have been no landsurface at all.

The expansion theory would also reconcile with the idea of continental drift, as the slowly bursting open of the crust (forming the oceans) would produce a pseudo-drift. And connected with it, one could easily derive that steady expansion could lead to mid-ocean rifts, producing an effect of pseudo-convection, and to the enormous troughs, trenches and graben, found in both the Ocean floors (notably the Pacific) and on continents (African rift valley). This would exclude the existence of a downward convection current under the continents.

As with the continental drift theory the geological dating of major events would be a critical issue, although we botanists can also not say much precise about the geological age of our plants. We know that Nothofagus dates from the Cretaceous, but what do we know about Spathiphyllum and Heliconia? 'Advanced' in morphology need not necessarily mean 'young in age', although these concepts are frequently identified and thus confused.

Anyway, with a suitably dated expansion theory plant geography would be extremely happy, and palaeontology as well, both being bound to the steady state advocated by me.

C.G.G.J. van Steenis.

VARIA

FLOWER TRANSPARENCIES OF TROPICAL PLANTS

It has been announced (in Brittonia 21, 1969, 194) that 200 items (representing 100 species belonging to 40 families) of transparencies of flowers grown in the Botanic Gardens, Bogor, Java, are made available through Mr. M.R.Straw, Department of Botany, California State College, 5151 State College Drive, Los Angeles, Cal. 90032, U.S.A. The proceeds will be added to the Bogor account to cover purchases for books and other necessary supplies. Price $ 1.25 each.

VARIA

ORCHIDOLOGISTS AT WORK

"The science of orchidology has never attracted many workers, never as many as, say, the fungi or the grasses or the ferns. The orchidologists there are and have been and probably will be are mostly involved in describing new species and relegating to synonymy those species described by their past and present colleagues!"

"During my study of the Orchids I collected I was rather disturbed by the seemingly large number of endemic species in each Pacific and Malesian island. It is only in the last 30 years or less that, in orchidology at least, have taxonomists really considered there to be sizeable number of widespread species at all. Many needless endemic species were described; in many the differences quoted were of a very minor character, decidedly not of specific status, but always they were reinforced by remarks about being distinct species as they were on different and distant islands! Much more correlation needs to be done before one has a true picture of orchid species' distributions in the area - and I daresay this applies to other plants as well." 1)

After having given some examples of the suggested Lemurian land-bridge, Hunt wrote: "The two Solomon Islands species Eulophidium pulchrum and Liparis caespitosa could have reached eastern Malesia via this postulated land connection" - their present range is from Africa, through Madagascar and the Mascarenes, through tropical Asia and Malesia to the Solomons and Fiji - "each species gathering incidentally about a dozen synonyms in the process."

(P.F. Hunt, Orchids of the Solomon Is., Phil.Trans.R.Soc. B 255, 1969, 581, 584)

1) As appears from scanning the synonymies in the Flora Malesiana and its precursors. - Ed.