STUDIES IN PHYLOGENY.

II.

On the Phylogeny of the Malaysian Burseraceae-Canarieae in general and of Haplolobus in particular

by

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> "One should not make the mistake of drawing final conclusions on the basis of the "present-day distribution of anyone group "of organisms... and much less on any "single family or genus...". (MERRILL, Gardens' Bull., Straits Settlem. IX, 1935, p. 51).

Summary.

The Burseraceae comprise 3 tribes which show an increasing differentiation from West to East and have, accordingly, their points of gravity in America (*Protieae*), Africa (*Bursereae*) and Asia to Australia-Polynesia (*Canarieae*) respectively. An eastward migration of the order is probable. The easternmost tribe comprises 5 genera, viz. *Scutinanthe, Canarium, Santiria, Dacryodes* and *Haplolobus.* These are tested regarding their fundamental characters, in order to calculate their "phase indices". In these calculations 1 (of the series 1, 1½, 2, 2½, 3) means the most primitive, 3 the most advanced condition of a feature. From the figures thus obtained and from geographical data, it is concluded that *Haplolobus* (area: Borneo to New Guinea inclusive; *map 1*) is the youngest genus of the five, whilst the four others must have originated in East Asia more or less simultaneously from the "Procanarieae" which where at that time still closely related to the ancestors of *Garuga* (*Protieae*). It is further evidenced both by the characters and by area disjunction that *Haplolobus* must have originated bi- or polytopically from *Santiria* in Eastern Malaysia. *Santiria* shows a recent species explosion in the Sunda Land, *Haplolobus* in New Guinea (*map 2*). In "Wallacea" the last-named genera are apparently either in regression (*Santiria*) or scantily developing (*Haplolobus*).

The paper proceeds with considerations on migration tracks in Malaysia and adjacent regions (*map 3*), checked by a short survey of the geological history since the early Tertiary. From the last-named survey it is concluded that three different areas are in the way of genorheithra, migrating either eastward or westward in Malaysia, viz. 1. the old and large continental Sunda Land which enabled rapid migrations and large "species explosions"; 2. "Wallacea" which with its continuous insular character has always been a serious impediment to migrations and which consequently is to be considered as a sieve for potentialities; and 3. the Sahul Land which is also continental, but younger and smaller than the Sunda Land. These conditions (among others) are responsible for the fact that so much more Asiatic types have reached Australia and Polynesia than Australian types reached Asia. The paper closes with a tentative reconstruction of the tertiary and quaternary phylogeny of the Canarieae in the region under discussion (*fig. 1*).

Contents

1. INTRODUCTION.

If, in spite of Merrill's admonition, quoted as a motto at the heading of this paper, I venture to make a tentative phylogenetical reconstruction of a part of a natural order, which is more or less familiar to me, it is because I hope to add a humble stone to that splendid and solid foundation of Malaysian Phytogeography, of which Merrill is one of the most prominent constructors and one of the most competent and zealous promotors. For I think that a small number of well-checked and well-interpreted data from a thoroughly known group are at least as valuable towards historical biogeography as a great number of facts on a less trustworthy basis.

If we desire to obtain an idea on the phylogeny of a given group, we have to investigate, as far as possible, something like the following points:

1. Systematic position of the group as a whole towards related groups;
2. Systematic position of the components of the group mutually (sharing and participation of characters) and eventually in relation to other groups;
3. Specific density of genera (or generic density of families) in various parts of the area now occupied;
4. Geographic distribution of the group and of related groups;
5. Geographic distribution of components of the group;
6. Geographic distribution of some important characters;
7. Geographic distribution of subsequent phases of characters;

8. Means of dispersal;
9. Eventual fossils;
   and some still more uncertain data such as palaeo-ecology, evolutionary rate, contingencies, etc.;

and, on the basis of the foregoing points:

10. Relative age of the groups in the region;
11. Relative age of the components of the group;
12. Supposed migration of ancestors, in accordance with geologic history, etc.

These points will be dealt with underneath as far as data are adequate and investigable. As a matter of course, phylogenetic reconstructions can only be fertile if they are based on a sound and thorough taxonomic and geographic knowledge of a natural group and if they are not in contradiction with geological results; they may be of some value only when they yield any results of wider scope or demonstrate methods of wider applicability.

2. THE BURSERACEAE AS A NATURAL ORDER.

The natural order of the Burseraceae may be subdivided into three tribes, which show an increasing differentiation from West to East and which have, accordingly, their points of gravity in Tropical America, Tropical Africa and Western Asia, and East-Asia to Polynesia respectively:

TABLE I (cf. lit. 12, p. 301).

Regions / Tribes	Trop. Amer.	Trop.Afr. & West-Asia	East-Asia & Polynesia	Total
Canarieae	2	38	148	188
Bursereae	± 100	163	1	± 264
Protieae	92	4	8	104
Total. . . .	± 194	205	157	± 556

These conditions strongly suggest that the Burseraceae originated in Tropical America and, in general, migrated eastward, a suggestion which has been discussed more in detail in a previous paper (lit. 12, pp. 298—306). The above table therefore corresponds, in general, to the fundamental typological phylogenetic scheme in connection with migration (cf. lit. 16, p. 179 ss. and 15, p. 111).

Having started probably some time in the Cretaceous, this migration must have been rather rapid, as the only fossils attributed to this family (and to the tribe of the Bursereae) are of Miocene age (Germany) and *Canarium* cannot have reached the North-Eastern boundary of the "Melanesian continent" much later than some time during the same period (cf. § 6 Geological evidence). Not only migration, however, but also evolution must therefore have proceeded with considerable speed, as *Canarium* shows, of all genera, the largest number of advanced character phases.

3. THE TRIBE OF THE CANARIEAE.

I will restrict myself in the present paper to the tribe of the *Canarieae* and more particularly to that part of it which is found in Eastern Asia, Malaysia and Polynesia. The central problem will be to give a tentative reconstruction of the phylogeny of the genus *Haplolobus*. This problem, however, will find its frame in a similar reconstruction of the very natural group of the Malaysian and Polynesian Canarieae.

As has been shown above, the Canarieae actually have their centre of gravity in Eastern Asia and Polynesia. The following table shows some more details concerning the distribution of their diversity:

TABLE II.

Regions / Genera	Trop. America	Trop. Afr.	Mad. & Masc	Trop. Asia, Austr. & Polynesia	Total
Haplolobus	—	—	—	13	13
Scutinanthe	—	—	—	1	1
Canarium . . . . . . (incl. Canariellum)	—	8	5	102	115
Santiria	—	6[1])	—	18[2])	24
Dacryodes	2[3])	19[4])	—	14[5])	35
Total . . .	2	38		148	188

[1]) Sect. Santiriopsis — [2]) Sections Eusantiria and Trigonochlamys — [3]) Sect. Archidacryodes — [4]) Sect. Pachylobus — [5]) Sect. Curtisina.

It appears from this table that the tribe comprises in Tropical America only 1, in Africa etc. 3 and in Asia, Australia and Polynesia 5 genera. The monotypic genus *Canariellum* from New Caledonia has been included in *Canarium*, as it is insufficiently known and as its distinguishing characters (unifoliolate leaves, two-celled fruits) are not uncommon in some representatives of *Canarium* (cf. lit. 17). In the tribe the last-named genus is distinguished by a bony axial intrusion between the bony pyrenes, which are connate with that intrusion, so that a usually hard and solid putamen is formed. On account of this important feature — which finds its counterpart among the Bursereae — I created the subtribe of the *Eucanariinae*. The four other genera, which lack such an axial intrusion are then forming the subtribe of the *Dacryodiinae*. Of these, *Scutinanthe* is rather divergent both by its features (5-merous flowers with receptacle, pyrenes bony and connate with a bony mesocarpium) and by its distribution (Ceylon, Malaya, S.E. Sumatra, Borneo). The three other genera, *Dacryodes*, *Santiria* and *Haplolobus* are closely related, particularly the two last-named ones, as *Dacryodes* is more tending towards *Canarium* in various features. In general, the taxonomic relations of the genera may appear from table III (p. 131).

As may appear from this table, the sharing of the fundamental characters is rather irregular. This and the fact that some of the fundamental (nrs. 2, 4, 7 and 9) and many of the less important characters not mentioned here show transitions from one genus to one or more others, shows that the evolution of the group is probably in full swing and its present configuration of probably recent date. This is probably especially true for the genera *Dacryodes, Santiria, Haplolobus* and *Canarium*; *Scutinanthe* shows a singular mixture of primitive and advanced character phases and its average phase index is therefore little significant. I consider its classification with the Canarieae as a rather artificial one. Its flower strongly recalls that of *Garuga* (Protieae) and its fruit may have been subject to a development parallel to that of the Canarieae. It might be considered as a sort of tentative canarioid fruit, in the way the *Pteridospermae* showed a tentative gymnospermy. Detailed evidence concerning these tendencies may be found in lit. 14 (regarding character 5: pp. 155—158, cf. also SINIA; char. 11: pp. 159 ss.; and char. 12: pp. 171 ss. and 184) and in lit. 17 (regarding character 9).

In the paper already mentioned (lit. 14) I have placed the Malaysian genera of the Burseraceae in regard to a still greater number of tendencies, viz. 23. The phase of each genus in a certain tendency was

TABLE III.

Genera / Characters	Dacryodes	Santiria	Canarium	Scutinanthe	Haplopus
1. Axial intrusion extant or not in fruit	none	none	**extant**[1]	none	none
2. Pyrenes ± free or connate	± free	± free	**connate with axial intrusion**	**connate with bony mesocarp**	**connate**
3. Pyrenes: constitution	± cartilaginous	bony	bony	bony	**papyraceous**
4. Stigma on fruit	± apical or nearly so	**excentric**	apical	apical	apical or nearly so
5. Cotyledons: shape	compound or lobed	lobed	compound or lobed	**entire**	**entire**
6 Cotyledons: folded or flat	folded	folded	folded	folded	**flat**
7. Receptacle in the flower	slightly developed (esp. ♀ fl)	slightly developed (esp. ♀ fl.)	slightly developed (♀ flowers)	**extant**	none
8. Number of flower parts	**3**	**3**	**3**	5 (carpels 3)	**3**
9. Number of steeds in the fruit	**1** (rarely 2)	**1** (rarely 2 or 3)	3—1	**1** (rarely 2)	**1** (always)
10 Stipular organs	none	none	usually **extant**	none	none
11. Resiniferous vasc. strands in the medulla of the branchlets	extant in 7 (out of 14) species	extant in 3 (out of 18) species	**extant** in almost **all species**	none	extant in only 1 species (out of 13)
12. Ditto in the petioles	reduced in 6 species	reduced in 8 species	**numerous** in almost all species	none	reduced in 6 species

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[1]) Heavy type indicate advanced phases.

indicated by one of the numbers 1, 1½, 2, 2½ and 3, of which 1 represented the most primitive and 3 the most advanced condition (l.c., table on p. 186). From these calculations the following figures may be derived, representing the average phase indices for the 5 genera under discussion concerning all the 23 tendencies:

1. Canarium: 1.93
2—3. Santiria and Dacryodes: 1.69
4. Haplolobus: 1.65
5. Scutinanthe: 1.63

As a matter of course, these figures have only a relative significance; and as differentiation is, in general, a function of time, they may tell

TABLE IV.

Characters \ Genera	Dacryodes	Santiria	Canarium	Scutinanthe	Haplolobus
nr. 1 (Table III) .	1	1	3	1	1
„ 2 „ „ .	2	2	3	3	3
„ 3 „ „ .	1½	1	1	1	2
„ 4 „ „ .	1½	2	1	1	1½
„ 5 „ „ .	1½	2	1½	3	3
„ 6 „ „ .	1	1	1	1	2
„ 7 „ „ .	1½	1½	1½	3	1
„ 8 „ „ .	3	3	3	1½	3
„ 9 „ „ .	2½	2	1½	2½	3
„ 10 „ „ .	1	1	2½	1	1
„ 11 „ „ .	2	1½	3	1	1
„ 12 „ „ .	2	2	3	1	1½
13. various differentiations in the flower (androeceum, disk, etc.)	1	1½	2½	1½	1
Total . . .	21½	21½	27½	21½	24
Average . . . . . (first case)	1.65 (1.69)	1.65 (1.69)	2.12 (1.93)	1.65 (1.63)	1.85 (1.65)

us something about the relative age of the genera. It would then appear that *Canarium* as a phylogenetic discontinuity (a genorheithrum) is older than the four other genera, whose age is not very much divergent.

However, the figures mentioned are also based upon tendencies which may be of importance concerning the Burseraceae as a whole, but which are of smaller significance for the Canarieae of East Asia and Polynesia only. If we therefore apply the same method to Table III and add a few tendencies that may better be estimated by a number than described, table IV results (p. 132).

This table shows therefore the following arrangement:

1. Canarium: 2.12 (formerly: 1.93)
2. Haplolobus: 1.85 („ : 1.65)
3. Santiria: 1.65 („ : 1.69)
4. Scutinanthe: 1.65 („ : 1.63)
5. Dacryodes: 1.65 („ : 1.69)

The most striking feature of this arrangement is the position of *Haplolobus*, the young differentiations of which are more exactly appreciated.

As taxonomical data apparently cannot bring us nearer to the solution of phylogenetical questions, geographical evidence has to be introduced. And even then a number of uncontrollable points lead us to scepticism, e.g. the individual rate of evolution that may be widely different in related genorheithra, the influence of contingencies (Palmgren, lit. 23), the possible explosive outburst of new species in a newly gained part of the area, etc. In regard to the last-named point, it may be recalled that Merrill (lit. 20, p. 146; lit. 21) has shown on various occasions that at least two big centres of dispersal are to be traced in Malaysia, viz. one in the Sunda Land and one in the Sahul Land (New Guinea and North Australia; Merrill calls this Papualand, but as the names Sunda and Sahul are traditional counterparts, I prefer to maintain them). I may add (cf. *map 3*) that the Philippines may form a third centre (cf. Dickerson, fig. 10), or in general, that any region of a certain extent and of sufficient ecological isolation may form such a centre, whose importance towards this point is, according to Palmgren (lit. 22, pp. 28, 76, 104, 120—125), more or less proportional to the size of the region (i.e. island).

Table V (p. 134) gives the diversity of the five genera in East Asia—Polynesia:

TABLE V.

Numbers of species; endemics between brackets.

Regions / Genera	Total in Far East	Asia Cont. & Ceylon	West Malaysia			Centr. Mal.		East Mal.		Austr. & Polyn.
			Mal.	Sum.	Born.	Phil.	Cel.	Mol.	N.G.	
Haplolobus	13	—	—	—	1 (1)	—	1 (1 ?)	1 (1)	**10** (10)	
Scutinanthe	1	1[1]) (—)	1 (—)	1 (—)	1 (—)	—	—	—	—	—
Canarium (Canariellum incl.)	102	**20**[2]) (19)	12[3]) (1)	16[3]) (2)	25[3]) (9)	**19** (13)	11 (1)	**13** (2)	**18** (10)	**17** (14)
Santiria	18	—	10 (1)	10 (—)	**14** (5)	1 (—)	2 (—)	1 (—)	1 (1)	—
Dacryodes	14	1[4]) (—)	**11**[5]) (2)	8[5]) (—)	**11**[5]) (3)	4 (—)	1 (—)	—	—	—
Grand Total	148	22 (19)	34 (4)	35 (2)	52 (18)	24 (13)	25 (1+1?)	15 (2)	29 (21)	17 (14)

It may be seen that *Haplolobus* is endemic in Eastern Malaysia and Celebes, with a centre in New Guinea (cf. *maps 1* and *2*). *Santiria* and *Dacryodes* have evident centres in the Sunda Land and cross its limits only with a few species. I consider these "species explosions" as a product of the Tertiary and Pleistocene Sunda Land, when Malaya, West Borneo, East Sumatra and probably for some time also North or West Java were united.

As far as *Canarium* is concerned, this large genus, whose area reaches from West-Africa and Madagascar to Southern China, Palau, Samoa and North-Australia, seems to have found new stimuli for differentiation in almost every new area gained during its apparently rapid eastward migration (cf. lit. 17). It is not improbable that the last-named condition is due

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[1]) Ceylon, Malaya, S.E. Sumatra and Borneo (1 sterile specimen) — [2]) 1 Sunda Land species in Andamans and Bengal — [3]) 3 widely spread species also in Java, moreover in Java 1 endemic with Sumatran relation and 1 Eastern element on Bawean Isl. The other genera are not represented in the Java flora except 1 species of *Dacryodes* (in West-Java only) — [4]) also in Western Malaysia — [5]) 1 species also in West-Java.

to the fact that especially *Canarium* fruits with their fleshy though resiniferous pericarpium are not seldom dispersed by fruit eating pigeons, megapodes and cassowaries (RIDLEY, p. 501 ss.)[1]).

As a matter of course, the group of plants that may be called the East-Asiatic *Procanarieae* that reached the Far East must, in view of what is left or displayed in recent forms, at least have comprised such potentialities as might allow the origin and the maintenance of those forms. As has been mentioned above it must be accepted, in accordance with the results of the Tables III and IV and with the present areas and their supposed eastward migration, that *Dacryodes*, *Santiria* and even *Canarium* are, as genera, older than *Haplolobus*. As I have discussed earlier (lit. 12, p. 304—305), I accept for *Dacryodes* a trirheithric and for *Santiria* a birheithric origin. This implies at any rate (whether polytopic or not) an origin from genorheithra having at least enough genes in common to give rise in two or more regions to such taxonomic units as may be comprised by the same taxonomic definition. It implies also migration of such genorheithra, and if we find such relatively primitive genera as *Dacryodes* and *Santiria* as disjunct as they are and suggesting by their character phases and their distribution about the same evolutionary development and therefore possibly about the same age, we may accept a relatively old polyrheithric or polytopic origin as the most probable explanation for their disjunctions.

For *Canarium* such an explanation is not necessary; its area is much less disjunct and its sections are not geographically correlated in the way they are in *Dacryodes* and *Santiria*.

Some words must be added concerning the area of *Scutinanthe*. Both its systematic isolation and its disjunct area might suggest its nature of a relatively old relic, maybe as a consequence both of palaeoclimatological influences and of a restricted genetic property. Its disjunction cannot be explained on the basis of geologic history. The suggestion of its relic nature is supported first of all by its primitive features and further by the recent detection of the species in S.E. Borneo (Tanahmerah) where it is reported to be very rare. Though there is only one single sterile specimen available, its identification is pretty certain. The species seems to be frequent only in certain parts of S.E. Sumatra (Palembang); in Malaya it is rare, in Borneo very rare, in Ceylon rare. Moreover, in Ceylon it is an inhabitant of mountainous regions between 600 and 900 m, in the Sunda Land it is a tree from the lowlands.

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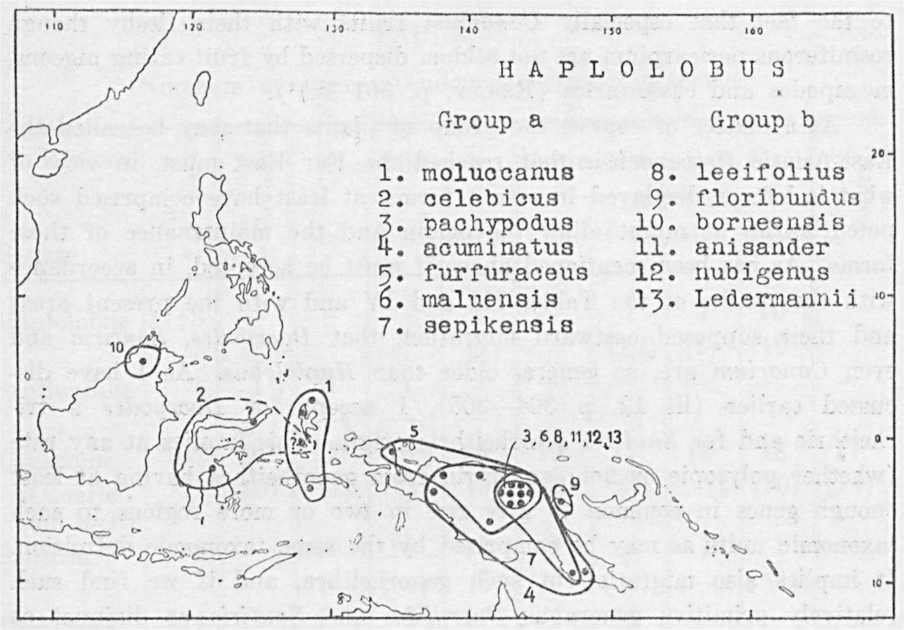
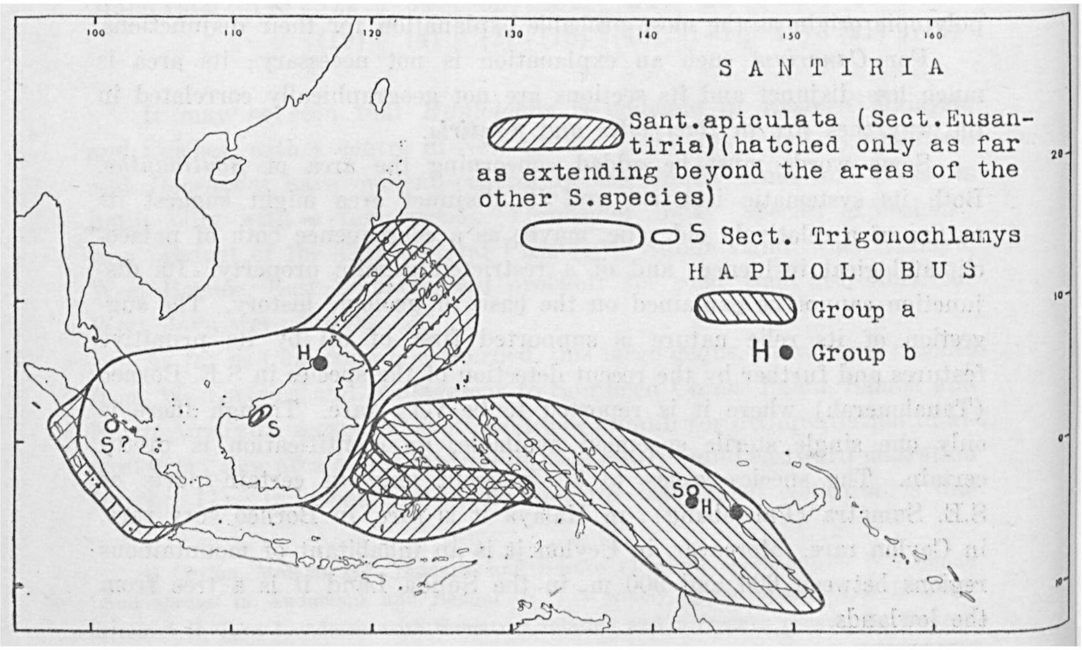
[1]) Probably *Garuga* fruits are also dispersed by birds.


HAPLOBUS
Group a
Group b
1. moluccanus
2. celebicus
3. pachypodus
4. acuminatus
5. furfuraceus
6. maluensis
7. sepikensis
8. leeifolius
9. floribundus
10. borneensis
11. anisander
12. nubigenus
13. Ledermannii
3, 6, 8, 11, 12, 13
110
120
130
140
150
160
20
10
0
10

Map 1.


SANTIRIA
Sant.apiculata (Sect.Eusantiria)(hatched only as far as extending beyond the areas of the other S.species)
S Sect. Trigonochlamys
HAPLOBUS
Group a
H ● Group b
H
S
S?
S
H
100
110
120
130
140
150
160
20
10
0
10

Map 2.

The fact that *Scutinanthe* has retained the primitive character phase of 5-merous flowers (except the gynaeceum which is 3-merous, whilst the fruit is usually 1-seeded), means that the Procanarieae included the potentiality to produce 5-merous flowers. Regarding this feature, they were probably more closely related to the Protieae (*Garuga*, the flowers of which are strongly reminding us of those of *Scutinanthe*) than they are at present.

The primitive Asiatic Procanarieae might therefore have reached the Sunda Land in two closely related groups, which would nowadays perhaps be called genera, viz. one with the primitive characters of the 5-merous *Scutinanthe* (and *Garuga*) and with a tendency towards a canarioid fruit, and one with 4- or 3-merous flowers from which shortly after *Dacryodes, Santiria* and *Canarium* differentiated in the same way as they had done in Africa. From the latter group *Haplolobus* originated; in which way this probably happened, will be discussed later on. On account of both taxonomical and geographical arguments, I would therefore suggest the following order of origin in East Asia:

I a. Scutinanthe
b. Dacryodes, Santiria, Canarium
(I a. and b.: ± simultaneous)
II Haplolobus

4. HAPLOLOBUS (*maps 1* and *2*).

As far as *Haplolobus* is concerned, this genus now comprises about 13 species (cf. *map 1*), 10 of which are endemic in New Guinea, 1 in the Moluccas (Halmahera!, Morotai!, Amboina?), 1 in Celebes (Central Celebes!, North Celebes?, Batjan?) and 1 in North Borneo (Mt. Kinabalu).

Although all of these species are closely related, they seem to form two more or less distinct groups, both of which have disjunct areas. I will indicate these groups with the letters a and b and distinguish them in the following way:

Group a — Leaflets rather large to large (greatest length 17—38 cm), usually thin, glabrous or pubescent, the petiole with usually numerous, rarely less than 5 resiniferous medullary vascular strands. Inflorescences usually large (greatest length 12—32 cm). — 7 Species from New Guinea (5), the Moluccas (1) and Celebes (1).

Group b — Leaflets smaller (greatest length 6—15 cm), often rather rigid, always glabrous, the petioles always with very few (1—5) resiniferous medullary vascular strands. Inflorescences smaller (great-

TABLE VI.

Haplolobus.

	Characters / Species	Leaves		Petioles Number of medullary vascul. strands	Length (in cm) of inflorescences		Distrib.
		Length of leaflets (cm)	Glabrous or pubescent		♂	♀	
Group a	1. moluccanus	24-38	glabr.	∞	23-32	?	Moluccas
	2. celebicus	9-21	glabr.	3-5	10-22	?	Celebes
	3. pachypodus	13-20	pub.	∞	4-12	?	N. Guinea (Sepik)
	4. acuminatus	6-20	pub.	∞	7-12	1-4	N. Guinea
	5. furfuraceus	8-19	pub.	5-10	-28	-28	„ „
	6. maluensis	5-18	glabr.	∞	5-13	3-10	N. Guinea (Sepik)
	7. sepikensis	7-17	glabr.	5-10	6-14	6-14	N. Guinea (Sepik)
Group b	8. leeifolius	6-15	glabr.	1-3	6 8	?	N. Guinea (Sepik)
	9. floribundus	6-12	glabr.	1-4	10-15	?	N. Guinea
	10. borneensis	4-13	glabr.	1-5	6-18	?	North Borneo
	11. anisander	6-11	glabr.	1	1-8	?	N. Guinea (Sepik)
	12. nubigenus	4-11	glabr.	1-3	1-3.5	1-3.5	„ „
	13. Ledermannii	2-6	glabr.	1-2	2-5	2-5	„ „

est length 2—18 cm) — 6 Species from New Guinea (5) and North Borneo (1).

Table VI gives some more details.

As appears from Table III, there is only one *Haplolobus* species, which possesses resiniferous vascular strands in the branchlets, viz. *H. pachypodus*. As the occurrence of such strands is to be considered as an advanced feature phase, *Haplolobus* is in a primitive condition concerning this tendency; next comes *Santiria* and finally *Dacryodes* and *Canarium*. Similar conditions are found in regard to such strands in the petioles. In both tendencies there is, moreover, a pretty distinct geographic correlation, inasfar as Eastern species usually show a more primitive, Western a more advanced phase of the features in question

TABLE VII.

Santiria.

Characters / Species	Leaves		Petioles	Length (in cm) of inflorescences		Distribution
	Length of leaflets (cm)	Glabrous or pubescent	Number of medullary vasc. str.	♂	♀	
§ Eusantiria						
apiculata	6-18	glabr.	1-2	5-22	4-13	Malaya, Malaysia to Phil. & Molucc.
pilosa	7-19	pub.	1-2	7-20	5-14	Borneo
most other species	larger	gl. or pub.	5-10-∞	large	large	Sunda Land except Java
§ Trigonochlamys (all species)						
Griffithii	3-14	pub.	1-5	-20	-20	Sunda Land except Java
rubiginosa	4-12	glabr.	1-2	2-16	2-16	" "
pedicellata	5-11	glabr.	1-2	?	5-13	Borneo
lamprocarpa	5-10	glabr.	1-3	1.5-8	1-6	N. Guinea (Sepik)
nana	2-5.5	pub.	1-2	?	1-1.5	Sumatra
minimiflora	3-5	glabr.	1-3	-6.5	?	Borneo

in either of the genera *Santiria* and *Haplolobus* (Tables VI and VII). It is, however, not apparent in *Canarium*.

It may further be stipulated, that similar conditions as are described for *Haplolobus* seem, *mutatis mutandis,* to be extant also in *Santiria.* In this more Western and probably older genus there are, namely, also two groups, which are ranked as sections and may therefore be accepted to be of older age than the groups of *Haplolobus.* They are, however, partly based upon similar differences and one of them has a distinctly disjunct area in exactly the same way as group b of *Haplolobus* (New Guinea:

Sepik region, and Borneo), as may appear from the following lines and from table VII (see page 139).

Santiria § *Eusantiria* — Anthers basi- to dorsifix; stigma of the fruit of variable position, from near the apex to near the base (*S. apiculata*!); tertiary nerves usually transverse, sometimes longitudinally reticulate (*S. apiculata, S. pilosa* and some others); filaments of the stamens inserted outside or on the disk, always 6 and monodynamous; inflorescences distinctly pedunculate, sometimes branched from the very base (*S. apiculata, pilosa* and some others); no receptacle in the flower.

Santiria § *Trigonochlamys* — Anthers adnate; stigma of the fruit not more than 90° excentric, usually much less; tertiary nerves parallel to the secondary ones, often longitudinally reticulate; filaments of the stamens inserted on the rim of the cupular disk; stamens usually 3, episepalous, rarely with rudiments of the 3 epipetalous stamens (*S. lamprocarpa, S. rubiginosa*), rarely 6 monodynamous stamens (*S. Griffithii*); inflorescences, at least the ♂ ones, branched from the very base; sometimes a receptacle extant (*S. lamprocarpa, S. rubiginosa* and *S. minimiflora*).

Whereas in *Haplolobus* the groups are still vaguely different and therefore probably young (it cannot be said that one of them is distinctly younger than the other), it is possible to say that of the two sections of *Santiria*, the section *Trigonochlamys* is distinctly showing the greater number of advanced character phases and is therefore probably the more recent one, as may follow from table VIII:

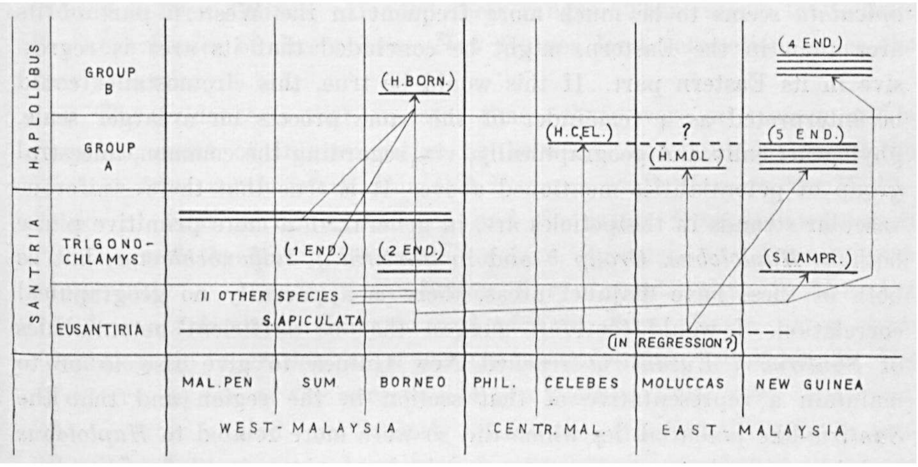
TABLE VIII (cf. table IV).

Santiria.

Sections / Characters	Sect. Eusantiria	Sect. Trigonochlamys
1. Anthers	1	2
2. Excentricity of stigma on fruit . . .	2½	1½
3. Insertion of filaments	1	2½
4. Inflorescences . . .	1½	2
5. Receptacle	1	2
Total	7	10
Average . . .	1.4	2

Regarding the only New Guinea *Santiria*, *S. lamprocarpa*, it may be stipulated that this species shows, to a certain degree, the slight development of a receptacle (♀ flower only), as is occasionally found in certain species of *Dacryodes*, *Santiria* and *Canarium* as a feature recalling *Scutinanthe* and *Garuga*. The excentricity of the stigma in the fruit is, moreover, in a comparatively primitive phase. Both characters suggest that the species was severed from its ancestors at a relatively early date.

I think the congruence of these facts is so striking that an explanation of the phylogeny of *Haplolobus* in connection with that of *Santiria* must be deemed probable about in the following way:



Note. Arrows indicate common ancestors, the point is directed towards the younger group. Present time and geographic area in the plane of the paper; the time as a factor is perpendicular to this plane (see Stud. in Phylog. I).

The above scheme demonstrates that I would accept a bitopic or even polytopic and a birheithric origin of *Haplolobus* on the basis of the older disjunction (and possible bitopy) of *Santiria*. This suggestion is further illustrated by *map 2*.

I hardly need to say that a dispersal of *Haplolobus* from New Guinea to Mt. Kinabalu by means of birds is most improbable, because of its almost dry fruits. Although an inhabitant of the high mountains, which harbours so many Papuan, Australian and even Antarctic elements, *Haplolobus* cannot be classed on the same terms with most of these mountain plants (cf. MERRILL, lit. 20, pp. 92, 98, 99 and 102—103), also because it is not found at a higher altitude than 1500 m in Borneo and 1400 m in New Guinea.

As has been mentioned earlier, the centre of origin of *Santiria* must be located in the Sunda Land. Therefore, as both *Santiria*- and *Haplolobus*-potentialities have reached New Guinea, as is proved by the occurrence of endemic species of those genera in that island, an ancestral group of common potentialities must have covered an area connecting New Guinea with Western islands, say with the Moluccas and Celebes, although no present species showing such a connection are left. The only living *Santiria*-species with an area extending far beyond the "least common area" (cf. L. B. SMITH, p. 456) of the genus is *S. apiculata.* It is moreover the species of its section that is most closely related to the *Haplolobus* species of Group a. From the fact that *Santiria apiculata* seems to be much more frequent in the Western part of its area than in the Eastern, might be concluded that its area is regressive in its Eastern part. If this would be true, this circumstance could be interpreted as a remainder of the same process on a larger scale, phylogenetically and geographically, viz. regarding the common, ancestral group of potentialities mentioned above. It is true that the resiniferous vascular strands in the petioles are, in general, in a more primitive phase both in *Haplolobus, Group b* and in *Santiria* § *Trigonochlamys,* but as both of these have disjunct areas, there is apparently no geographical correlation. I would therefore suggest that no sufficient potentialities of *Santiria* § *Eusantiria* reached New Guinea to give rise to or to maintain a representative of that section in the region and that the *Santiria*-like potentialities which did so were more related to *Haplolobus* and just enough to give rise to one single species, viz. *S. lamprocarpa.* The large number of *Haplolobus* endemics in New Guinea would then be a "local species explosion", of the same sort as are found in the Sunda land in other genera. The suggestion, pointed out in a previous paper (lit. 12, pp. 305, 405), that *Haplolobus* started as a genus in New Guinea can therefore not be maintained, although it may be that some of its ancestors migrated westward into the Moluccas. The occurrence of *H. moluccanus* and *H. celebicus* may, however, be also very well explained as a polytopy on the basis of the present distribution of *Santiria apiculata.*

5. GENERAL CONSIDERATIONS ON MALAYSIAN PLANT MIGRATIONS (*map 3*).

Nobody is more competent on this matter than E. D. MERRILL, who during more than 35 years gathered materials towards the historic phytogeography of Malaysia (cf. lit. 20, pp. 77—105 and 127—151). In a recent paper (lit. 21) he has given a concise survey of the main results and problems in this field. Though in many of his papers the results of historic geology have been introduced tentatively, botanical arguments are largely prevailing. I cannot do better than quoting here some parts of the paper cited. The following quotation gives a general idea of early conditions (l.c. p. 249):

"The intermigrations of the early angiosperms in what is now trop- "ical Asia and Malaysia doubtless took place at a time when the con- "tinental area extended far to the south, probably in the late Cretaceous "and early Tertiary, and this is the period when the more widely dis- "persed Asiatic types, or the ancestors of certain Asiatic types now "found in New Guinea, extended their ranges. There seems to be little "or no evidence of direct Asia—New Guinea land connections since the "early Tertiary."

"The evidence is that, in later times, there were an eastern and a "western route of intermigration as between Asia and Malaysia, the "former from southeastern Asia and Formosa south through the Philip- "pines at least as far as Celebes, and the latter from India through "Burma and the Malay Peninsula to Java, Sumatra, and Borneo, with "apparently a secondary paralleling line through what is now the "Andaman Islands to Sumatra and perhaps Java. These routes were "doubtless in operation at a relatively early time, probably in the "Tertiary, so far as the ancestors of our modern flora were concerned. "At a later period, particularly from the Pliocene-Pleistocene into "the Recent, there must have been a very active interchange of plants "between Asia and western Malaysia, when the Sunda Islands (Java, "Sumatra, and Borneo) and the Palawan-Calamian group in the Philip- "pines were at times definitely a part of the Asiatic continent."

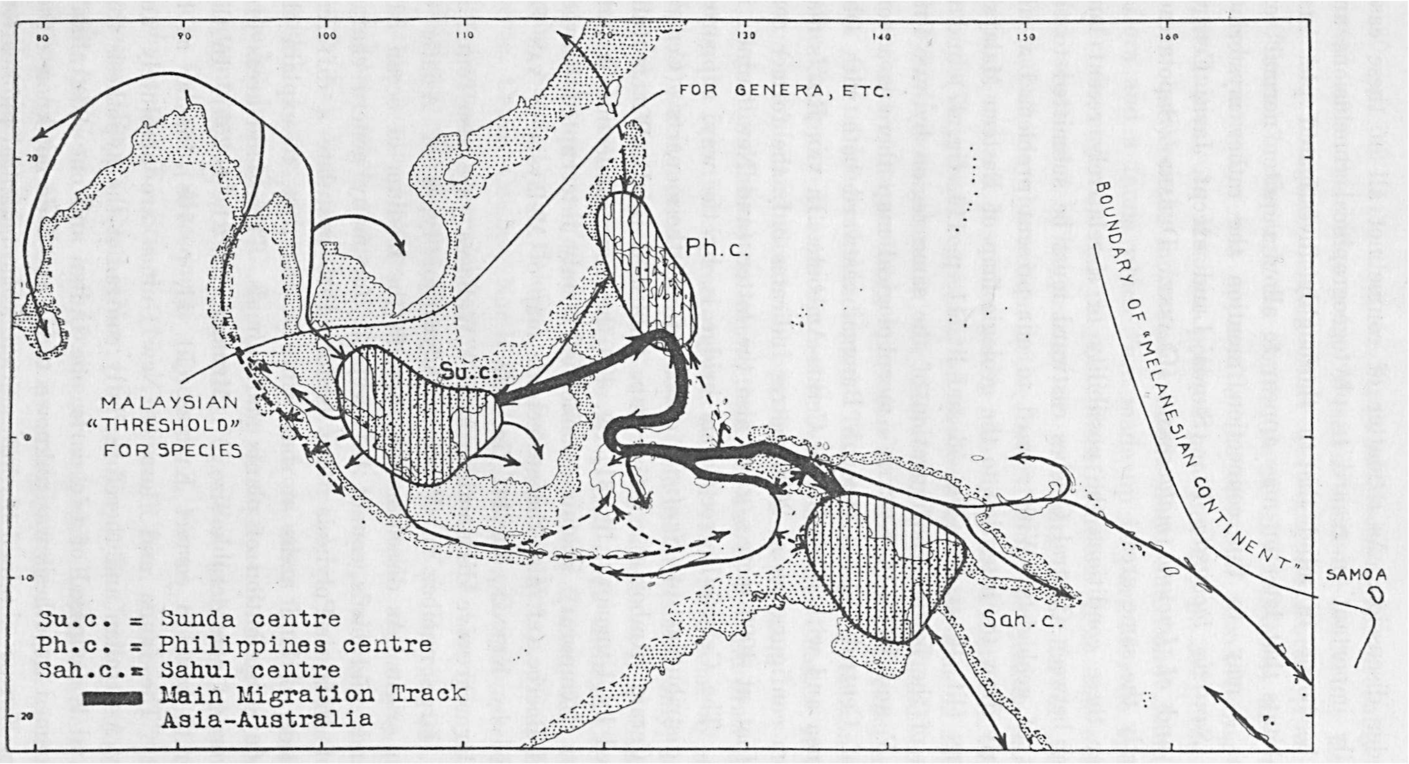
Although climatic conditions have undoubtedly played a certain part, I agree with MERRILL in that their influences were of local rather than of general importance, and that the main "limiting factor seems "to be found in the geologic history of Malaysia" (l.c. p. 251). To which MERRILL adds: "from the Tertiary, a more or less continuous "insular area existed in some part of this region, the straits and arms "of the sea inhibiting the natural dispersal of a great many species "of plants and animals".

As is indicated both by biogeographical and by geological arguments, this insular area is particularly what has been called by DICKERSON "Wallacea" (lit. 6a, pp. 382—383), viz. the region between WALLACE's and WEBER's Lines. It has been repeatedly pointed out (e.g. MERRILL, lit. 20, pp. 142—143) that the Strait of Macassar has probably not been crossed since the Palaeogene. Western elements occurring East of it, must have reached Celebes either through the North (Philippines—N. Celebes) or through the South (Java—S.W. Celebes) and the first-named connection was apparently the one that was offering the best opportunities. As MERRILL pointed out (lit. 21, p. 254), the unstable portion between the more stable Sunda Land and Sahul Land, possess a flora and a fauna which "are made up in part of relic species and "their descendents, and in part of infiltrations from the west, north "and southeast." The process of increasing isolation of islands in "Wallacea" may have been active both during the greater part of the Tertiary and, on a smaller scale, also since the Pleistocene. If this is true, the supposed regression of *Santiria apiculata* and of the *Haplolobus-Santiria*-ancestors in the Moluccas, would be found confirmed. On account of its probably regression in "Wallacea", its exact migration track can no longer be indicated. The species is still common in many of the Philippine Islands but not known from North Celebes; it is known from Central- and South-Celebes, but not from Java.

Regarding the eastern connections of Celebes, I would draw the attention to the fact that in recent years several cases have come to my knowledge, in which species, thusfar known from eastern islands only, have been collected in Central Celebes, such as: *Gmelina palawensis* H. J. LAM (Palau, Centr. Celebes), *Premna sessilifolia* H. J. LAM (New Guinea, Centr. Celebes), *Canarium acutifolium* (DC.) MERRILL (New Guinea, Kai, Amboina, Ceram, Soela, Centr. Celebes), *C. balsamiferum* WILLD. (Kai, Amboina, Boeroe, Centr. Celebes, North Celebes, Talaud), *C. maluense* LAUTERB. (New Guinea, Centr. Celebes), *C. multijugum* H. J. LAM (Centr. Celebes, Halmahera), *C. oleosum* ENGL. (New Guinea, Kai, Boeroe, Obi, Batjan, Ternate, North Celebes, Timor); *Planchonella moluccana* (BURCK) H. J. LAM (Gebeh, Batjan, Centr. Celebes, Flores), *Palaquium amboinense* BURCK (Kai, Misoöl, Amboina, Soela, North Celebes, several Lesser Sunda Islands). I may add some other cases from other families, which I owe to the kindness of Dr C. G. G. J. VAN STEENIS at Buitenzorg, who called my attention to the following cases: *Grevillea* (Australia, New Guinea, Centr. Celebes), *Macadamia* (Queensland, Centr. Celebes), *Litsea* aff. *calophyllantha* K. SCHUM. (New Guinea, Centr. Celebes), *Tylecarpus papuanus* (BECC.) ENGL. (New Guinea, Kai, Obi, Centr. Celebes), *Neuburgia tubiflora* BL. (= *Couthovia celebica* KOORD.) (New Guinea, Amboina, Centr. Celebes). This is certainly only a small choice of the examples that could be brought together in support to the migration track under discussion. As a matter of course not all of these cases are equally important in regard to phytogeographical conclusions and it must be borne in mind that a thoroughly investigated plot may reveal habitats that later on may appear to allow a quite "normal" explanation. I may, in this connection, mention the rather mysterious areas of *Santiria laevigata* BL. (Sunda Land except Java, Central Celebes) and of *Lucuma malaccensis* (CLARKE) DUBARD (Sapotaceae) with exactly the same area.

Under these conditions the possibility of a relatively recent land connection between Central Celebes eastward must be submitted to the judgment of geologists. With regard to our present problem I would particularly draw the attention to the geologic map of Eastern Malaysia by KUENEN (lit. 10, p. 192, fig. 53 and lit. 11, p. 114, fig. 47) and to the maps of the bottom configuration of the same region by VAN RIEL (l.c., Pl. V and VI). In KUENEN's morphological map there is a connection of Central Celebes through Banggai eastward both with Obi-New Guinea and with Soela-Boeroe-Ceram-Amboina. In VAN RIEL's map the bottom configuration at 2000 metres indicates only the former connection, that at 4000 metres gives also the latter (and New Guinea in addition). The Celebes-Boeroe-Ceram bridge is, by the way, supported by the distribution of *Santiria apiculata* in those parts (Central Celebes, Ceram, Amboina). On a map, published by B. WILLIS (and reproduced by UMBGROVE, lit. 31, fig. 43) the same connection is indicated as a "temporary isthmian connection", only interrupted between Soela and Boeroe (cf. also the geotectonic map of Malaysia by VAN ES, reproduced by KUENEN, lit. 11, fig. 40).

Similar regressive disjunctions as in "Wallacea" are also found in a pretty large number in Western Polynesian types of Asiatic or Malaysian origin. As dissemination through the medium of ocean currents, winds and birds cannot be accepted, for many genera characteristic of Malaysia-Polynesia "one is forced to postulate a different "distribution of land areas at some time in the past, to explain the "present-day distribution of plants and animals. These land areas pro-"bably were of considerable size..." (MERRILL, lit. 21, p. 255). In this connection I have to correct KUENEN (lit. 11, p. 108) inasfar as he says that "The fauna and flora of New Guinea are absolutely and "typically Australian and therefore flatly contradict the hypothesis that "this island is composed of two parts, one Indian and one Australian". The last-named hypothesis was unknown to me and I do not know either wherefrom KUENEN obtained his information, as no botanical publications



Map 3. — Supposed centres of dispersal and migration tracks in Malaysia (see § 5).
Dotted areas represent epicontinental seas.

are quoted by him; but it is sufficiently know that New Guinea and even North Queensland and Polynesia have a flora of a predominant Malaysian type (cf. MERRILL, lit. 20, pp. 97—105, and 21, p. 247).

Concluding this paragraph, I am giving a tentative map of centres of origin and of migration-tracks in the region under discusion (*map 3*; cf. also § 6). It is based upon evidence contributed by botanists in the last decennia, and though it is, as far as I can see, not in contradiction with the results of geologic history, it does not suggest land connections in any definite time, except that no older periods are regarded than Tertiary ones. The Sunda centre of origin is undoubtedly more distinct than the two other centres. It is of Tertiary age and has been active during a long time. The Sahul centre is probably younger. Both are of more or less continental nature. The Philippine centre, however, though possibly also pretty old, is different by its continuous insular character. I am inclined to consider it more as a definite centre, particularly for species, than Celebes and the Moluccas, although both groups of islands are forming a part of "Wallacea". The "Malaysian threshold" is introduced to elucidate the remarkable specific endemism ¹) of Malaysia towards the Continent of Asia. It is certainly much younger and of specific importance in its southern part, and older along the China-Formosa-Luzon track and there probably also of generic importance. There is no evidence of such a threshold between Australia and Malaysia. Problematic or weak tracks have been indicated by interrupted lines. In Northeast Australia and in New Caledonia infiltrations of Antarctic types are suggested.

6. GEOLOGICAL EVIDENCE.

As it may be of some use to compile briefly the conclusions geologists have independently arrived at by their own methods, I submitted the general lines of Malaysian phytogeography, as far as land-connections are concerned, to the opinion of Prof. J. H. F. UMBGROVE, Delft, who has for several years been a student of Malaysian geology and who has repeatedly given a survey of the geological history of these parts (lit. 32 and 33, recently recapitulated in 35). I am pleased to tender him my best thanks for his kind cooperation.

As a matter of course, a "palaeoflorist" is a man who does not care much about the theoretical side of geological history, however interesting it may be also for the layman. It does matter very little to him, whether a sea arm has been shallow or deep, except insofar a shallow

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¹) Cf. H. N. RIDLEY in Blumea, Suppl. I, 1937, 183.

one is perhaps more liable to turn into a land connection than a deep one. It does not matter to him either whether or not WEGENER's hypothesis of continental drift is to be applied to Malaysia or not (cf. KUENEN, lit. 11, pp. 98—109). The only thing which interests him is: where and in which period did land connections exist?, or rather: how was the relation of land and sea in all former times? The phytogeographer thus asks much more than the geologist can possibly tell him, as large stretches of sea remain terra incognita.

In the following lines I have endeavoured to give a concise survey of those points of the geologic history of Malaysia, which are of interest for palaeofloristics. The sources were mainly the publications of BADINGS, DICKERSON, KUENEN, VAN RIEL, and UMBGROVE, and the survey was kindly checked by the last-named author. This does, of course, not mean that I take part with or against any investigator or school concerning any structural theory, as a botanist is not competent to do so.

As the primitive Angiosperms probably came into existence during the early or middle Cretaceous and the Burseraceae are certainly not a very primitive order; as furthermore the supposed eastward migration from Tropical America to Tropical Asia must have taken a considerable time, it is probably sufficient to consider, in the present case, geological conditions in East Asia and Polynesia from the end of the Mesozoicum onward.

a. Malaysia as a whole — UMBGROVE (lit. 31) and KUENEN (lit. 11) have published surveys of theories on the origin of Malaysia. The last-named author concludes (l.c., p. 115) that "the Asiatic and the "Australian continents at one time formed a more or less continuous "mass". The greatest land area was probably at the end of Mesozoic and the beginning of Tertiary times. From this period onward there was a clearly increasing extent of the several Palaeogene and Neogene transgressions, until the Pleistocene regressions.

An intensive folding during the Young Miocene in a part of the region probably as far East as Fiji, may have enabled migrations along geanticlines, as far as not submerged (cf. UMBGROVE, lit. 35, fig. 11, p. 38). A younger, Plio-Pleistocene folding affected other parts of the present archipelago (lit. 35, fig. 18, pp. 50—53).

b. Sunda Land — This region was forming a more or less broad peninsula to the East-Asiatic Continent from the Cretaceous through almost the whole of the Tertiary (lit. 35, fig. 5, 8—10, 14). Its size may have been subject to certain changes, but there was probably enough continuous land during the whole period to harbour a rich flora in close contact with that of the continent. It is probable that the land had its greatest extent during the oldest Eocene, and that since then its area diminished more and more on account of proceeding transgressions. For the greater part of the Tertiary, however, parts of Malaya, East Sumatra and West Borneo were part of this peninsula, or at least enough remained of what is now inundated by the Southern part of the South China Sea to enable the floristic recovery of adjacent regions. Only Java may have been apart for long times. There has probably been a connection with the Sunda Land in the Oldest Eocene, maybe another one in the Pliocene (?) and undoubtedly several times connections during the Pleistocene. These conditions are distinctly reflected by the relatively poor Java flora and especially by the fact that generic areas are often connecting the island with other parts of the Sunda Land, while specific areas find either their boundary in the Java Sea and the Sunda Strait or do, in some cases, not extend further eastward than a small Western portion of Java. On account of the last-named fact it is probable that this portion was in a more favourable condition regarding a land connection with the Northwest than the other parts of Java.

The present configuration is very recent, as it is postglacial. During the Pleistocene several transgressions and regressions took place on the Sunda Land; during some of the former, narrow isthmi may have maintained themselves, e.g. between S.E. Sumatra-Bangka-Billiton-Karimata and S.W. Borneo and between S.E. Sumatra and S. Malaya.

c. The Strait of Macassar — The biogeographic conclusion that the Strait of Macassar forms an important floristic demarcation line and that it has existed for a long time, is substantiated by geological evidence. As early as Miocene, or even Eocene, an area of land in the West (Borneo, etc.) was separated from land areas in the east by a shallow sea of much greater extent than that which separates at present Celebes from Borneo (lit. 35, p. 60, figs. 9 and 10).

d. Borneo-Philippines-Celebes — There are at present three rows of islands, two from Borneo to the Philippines (one to Luzon and the other to Mindanao) and one from Mindanao to North-Celebes. A fourth row, though with more gaps, is connecting Mindanao and the Northern Moluccas. As far as the three first connections are concerned, they may have formed land connections during the whole Tertiary, although, of course, not always in the same way (cf. DICKERSON, l.c.).

e. Sunda Land-South Celebes — There is a very slight possibility of a land connection of some Southern part of the Sunda Land with Southwest-Celebes at the end of Mesozoic and the beginning of Tertiary times.

f. Islands West of Sumatra — No definite data are available concerning eventual land connections of these islands, either with Sumatra or with Burma [1].

g. Java and the Lesser Sunda Islands — No positive data are available concerning possible land connections in this region.

h. Celebes-Moluccas — It is very probable that West-Celebes has had a geologic history that is much different from that of East- and Southeast-Celebes. It is not impossible that Central- and East-Celebes were in connection with Boeroe-Ceram-Tenimbar-Timor (and Ceram possibly with New Guinea) in the Oldest Eocene; another possible connection, though less distinct, may have existed after the Miocene folding of these areas.

i. Philippines (Mindanao)-Northern Moluccas — This connection which is suggested by certain plant areas, can as yet not be confirmed or dated on the basis of geology.

j. Moluccas-New Guinea — Connections in the Oldest Eocene are not improbable, possibly some other connections may have existed after the Miocene folding. The Central Moluccas (Soela, Boeroe, Ceram) are better known concerning this point than the Northern Moluccas (Halmaheira, etc.).

k. New Guinea-North Australia — There has possibly been a connection in the Oldest Eocene, and very probably other ones in the Pleistocene.

l. New Guinea-Melanesia — The Melanesian continent (cf. UMBGROVE, lit. 34, pp. 502—509) shows several subsequent folding systems, the most recent and for our present purpose most important of which being of Miocene age; it affects some groups of islands East of New Guinea, possibly as far East as Fiji. Samoa has never formed a part of this Continent, as it has always been an oceanic island. This confirms our suggestion that both *Garuga* and *Canarium* are probably passively though not intensively dispersed by birds, as the areas of both genera are including Samoa but are, for the rest, congruent with the

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[1] BADINGS (l.c., p. 240, maps II—V) suggests possible land connections between Sumatra and the islands of Nias, Simaloer and Siberoet during the Eocene and the Oligocene. MOLENGRAAFF (De Zeeën van Ned. Indië, 1922, p. 309) says that these islands may have obtained floristic and faunistic elements from Burma through the Andamans and the Nicobars, and from Sumatra. With reference to the last-named connection the Pleistocene regressions are mentioned — H. J. LAM.

boundary of the Northern Part of the supposed continent (cf. lit. 12, p. 299, figs. 1—2). UMBGROVE considers — in accordance with the opinion of many "Melanesian" geologists — the present conditions in this region as comparable to those in "Wallacea"; the deep sea basins should be of comparatively recent date (Plio-Pleistocene), but parts of the continent may already have become submerged earlier by epicontinental seas.

In conclusion, it may be said that Asiatic genorheithra, migrating in an eastward direction some time from the Old Tertiary onward, encountered three different regions, viz.

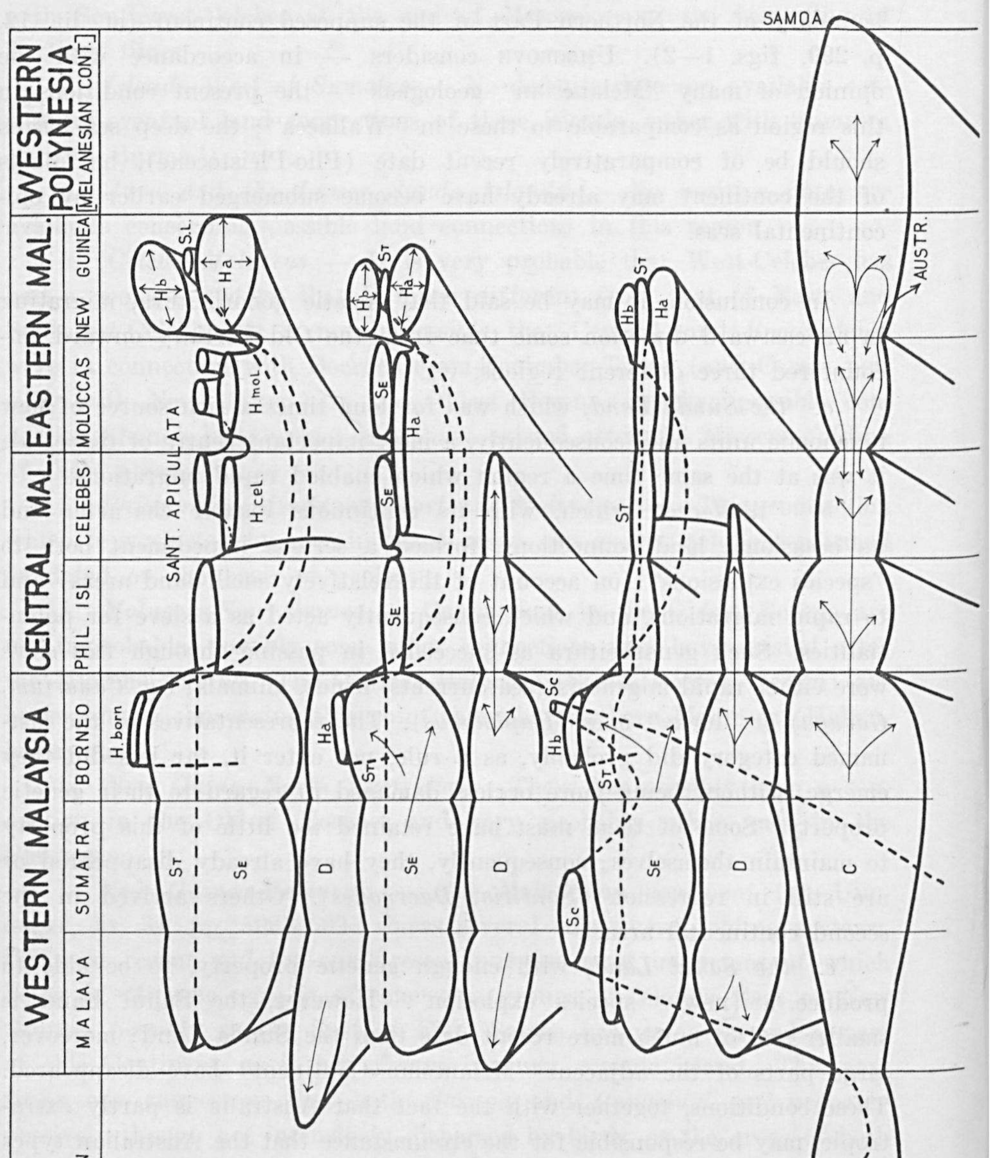
a. the Sunda Land, which was for long times a rich source of new taxonomic units and, consequently, a most important centre of dispersal; it was at the same time a region which enabled rapid migrations.

b. "Wallacea" which, with its continuous insular character and its occasional land connections, formed a serious impediment both to "species explosions" (on account of the relatively small land areas) and to rapid migrations, and which consequently acted as a sieve for potentialities. Such genorheithra as succeeded in passing through this sieve were either rapid migrators (sea currents, winds, animals; e.g. *Canarium, Garuga*) or "lucky" ones (*Haplolobus*). The representatives of the last-named category did probably, as a rule, not enter it, far less did they emerge, without being more or less damaged in regard to their genetic property. Some of them must have retained too little of this property to maintain themselves; consequently, they have already disappeared or are still in regression (*Santiria, Dacryodes*). Others arrived in the second continental area,

c. the Sahul Land, with enough genetic property, to be able to produce a (new) "species explosion". However, the Sahul Land is smaller and of much more recent date than the Sunda Land; moreover, large parts of the adjacent "Melanesian Continent" have disappeared. These conditions, together with the fact that Australia is partly extratropic, may be responsible for the circumstance that the Australian types that have reached Asia are considerably fewer than the Asiatic types that have reached Australia and Polynesia; for the difficulties encoun-

Legenda to fig. 1.

C. Canarium; G. Garuga; P. Protium; Sc. Scutinanthe; D. Dacryodes; S. Santiria; SE. Santiria, sect. Eusantiria; ST. Santiria, sect. Trigonochlamys; Ha. Haplolobus, group a; Hb. Haplolobus, group b; S. l. Santiria lamprocarpa.


ASIA
CEYLON & CONTIN
WESTERN MALAYSIA
MALAYA
SUMATRA
BORNEO
CENTRAL MAL.
PHIL. ISL.
CELEBES
EASTERN MAL.
MOLUCCAS
NEW GUINEA
WESTERN POLYNESIA
[MELANESIAN CONT.]
IX
RECENT
TO
PLEISTOCENE ?
VIII
PLIOCENE ?
VII
YOUNG MIOCENE ?
ST
SE
D
C
Sc
H.born
Ha
Hb
H cel
H mol
S.L.
SANT. APICULATA
SAMOA
AUSTR.

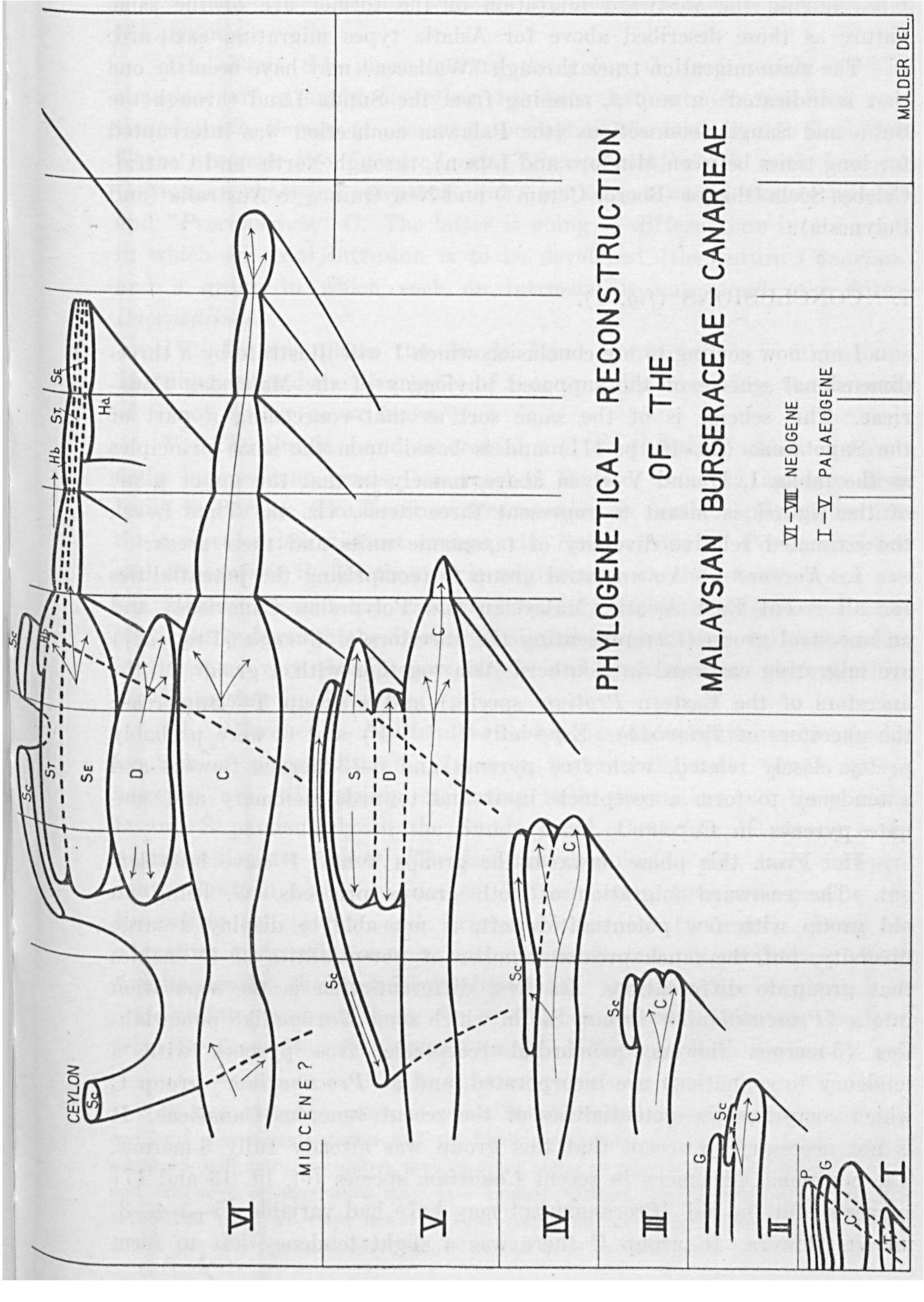

PHYLOGENETICAL RECONSTRUCTION
OF THE
MALAYSIAN BURSERACEAE-CANARIEAE
VI–VIII NEOGENE
I–V PALAEOGENE
MULDER DEL.
CEYLON
MIOCENE?
I
II
III
IV
V
VI
VII
Sc
SE
ST
D
C
S
G
P
Hb
Ha

Fig. 1.

tered during the westward migration of the former are of the same nature as those described above for Asiatic types migrating eastward.

The main migration track through "Wallacea" may have been the one that is indicated on *map 3*, running from the Sunda Land through the Sulu- and Sangihe-connections (the Palawan connection was interrupted for long times between Mindoro and Luzon), through North- and Central-Celebes-Soela-Obi (or -Boeroe-Ceram?) and New Guinea to Australia (and Polynesia).

7. CONCLUSIONS (*fig. 1*).

I am now coming to my conclusion which I will illustrate by a three-dimensional scheme of the supposed phylogeny of the Malaysian Canarieae. This scheme is of the same sort as that concerning a part of the Sapotaceae (lit. 15, p. 111) and is based upon the same principles as the tables I, II and V given above, namely in that the upper plane of the figures is meant to represent three items, viz. the Time Level, the estimated relative diversity of taxonomic units and their areas:

I. *Eocene?* — An ancestral group C (comprising the potentialities for all recent East Asiatic, Malaysian and Polynesian Canarieae) and an ancestral group G (representing the ancestors of *Garuga* [Protieae]) are migrating eastward in Southern Asia together with a group P (the ancestors of the Eastern *Protium* species) and a group T (Bursereae; the ancestors of *Triomma*). Especially G (+ P) and C were probably pretty closely related, with free pyrenes and 5—3-merous flowers and a tendency to form a receptacle in G and towards meiomery and connate pyrenes in C.

II. From this phase onwards the groups T and P have been left out. The eastward migration of both groups proceeds. G, being an old group with few potentialities left, is not able to display a large diversity, but the much greater number of potentialities of C enables that group to differentiate. Its first differentiation is the separation into a "*Proscutinanthe*" group Sc, in which some *Garuga*-like potentialities (5-merous flowers, primordial receptacle, free pyrenes with a tendency to connation) are incorporated, and a "*Procanarium*" group C which comprises the potentialities of the recent 3-merous Canarieae. It is not necessary to accept that this group was already fully 3-merous. The occasional pleiomery in recent *Canarium* species (cf. lit. 13 and 17) suggests that the old "*Procanarium*" may have had variable (5—) 4—3-merous flowers. In group C there was a slight tendency left to form a receptacle but a strong tendency to meiomery and to connation of the pyrenes.

III. From this phase onward the group G, from which the Procanarieae are strongly diverging, has been left out. As has been mentioned above, *Garuga* at present covers almost the same area as *Canarium.* There are now two "genera", viz. *"Proscutinanthe"* Sc with 5-merous flowers, a primordial receptacle and a tendency towards connate pyrenes, and *"Procanarium"* C. The latter is going to differentiate into a group in which an axial intrusion is to be developed (the future *Canarium*) and a group in which such an intrusion is not found (the future *Dacryodiinae*).

IV. In this phase the Sunda Land is reached by both groups. The diversity and the divergence of C are rapidly increasing, the diversity of G not, as far as we know[1].

V. The Sunda Land is crossed and *Scutinanthe,* which is now a fully independent genus, has reached Borneo, covering an area from India to Borneo. The 3-merous *Procanarium* is further splitting up into three more or less distinct groups, viz. *Procanarium* C, *Prodacryodes* D and *Prosantiria* S. Of these C is migrating with the greater speed and has already crossed the Eastern boundary of Sunda Land (probably particularly through the Borneo-Philippines connection), S is proceeding in the same way though more slowly and D is slowest. But all three are increasing in diversity.

VI. *Miocene?* — *Scutinanthe* Sc has passed its optimum (regression by lack of potentialities?). Its area becomes disjunct. C, D and S, however, are still rapidly increasing their diversities and their areas, D and S particularly in the Sunda Land, *Canarium* in almost every separate floristic region. The last-named genus is now fully independent. *Santiria* shows a further differentiation into two groups viz. *Eusantiria* SE (older) and *Trigonochlamys* ST (younger). Both are migrating eastward, however, with relatively few potentialities. Almost simultaneously the primitive *Haplolobus* ancestors are beginning to differentiate, group a from SE in Celebes and the Moluccas, group b from ST from Borneo eastward to the Moluccas. Both *Canarium* and

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[1] As a matter of course, of genera like *Scutinanthe* and *Garuga,* of which only one or a few recent species and no fossil remainders are known, a phylogenetical scheme is still more speculative than in other cases, as rapid and short-lasting increases and decreases of diversities may have existed without leaving any traces. From a theoretical point of view, however, such events are not very probable and we may accept the interpretation given above as the more probable one.

Santiria are migrating eastward into the Philippines, Celebes and the Moluccas, and *Canarium*, as the more rapid migrator, has reached New Guinea.

VII. *Young Miocene or Pliocene?* — The regression of *Scutinanthe* Sc is proceeding; it has disappeared from India and becomes rare in Ceylon and Borneo. Of the other genera not only *Canarium* but also *Dacryodes* and *Santiria* are independent now. In which way this may have been accomplished may be taken from Table III. All genera are still increasing in diversity. *Canarium* is rapidly proceeding into the Melanesian Continent or its remainders. Some of its Papuan products are migrating backwards into the Moluccas and Celebes. *Dacryodes* has proceeded as far as Celebes. *Santiria* has reached New Guinea but only the *Haplolobus*-potentialities were apparently numerous enough to maintain and to diversify the species there. Its group a was still connected with the Moluccas; group b however, became disjunct as its representatives in the Moluccas and Celebes (and the Philippines?) either never were materialized from their potentialities or disappeared. Se did probably not reach New Guinea at all or could not maintain itself. St, however, did and is still represented by a single species.

VIII. *Pliocene?* — From this phase onward *Scutinanthe* and *Canarium* have been left out. *Dacryodes* has still more proceeded into Celebes. *Santiria*, however, could increase its diversity only in the Sunda Land. As far as *Haplolobus* is concerned, this genus is not yet fully independent taxonomically, but its area is already in regression in the Moluccas and in both group a and group b. In New Guinea, however, both groups are increasing their diversity.

IX. This symbolizes the period from the *Pleistocene* onward. *Dacryodes*, of which only the western part of the area has been drawn, has passed the Malaysian Threshold in a westward migration through which it has reached Cochin China. *D. rostrata* is the only species of the Malaysian section *Curtisina* that is known from outside Malaysia. It is not known whether its area is continuous through the isthmus of Kra. The above interpretation is, of course, not the only possible one. Another one is that the species originated more towards the continent, in which case the species must be a relatively old one. Finally also bitopy could be suggested as an explanation. *D. rugosa* has probably reached West-Java during one of the Pleistocene regressions. *Haplolobus* is fully independent and the area of both groups is still more disjunct than in VIII. Both, however, are strongly increasing their diversity in New Guinea and it may be expected that some of these will migrate westward (as some *Canarium* species did in an earlier phase, cf. VII) as soon as a land connection gives them the opportunity to do so. Of ST only one species is left in New Guinea (*S. lamprocarpa*); the others are restricted to Borneo and apparently still increasing in diversity there. The only recent representative of SE East of Celebes, viz. *S. apiculata,* is also in regression in the eastern part of its area, as is indicated by its rarity in those parts. The Burseraceae of North Queensland (1 *Protium,* 1 *Garuga* and 2 *Canarium* species) probably reached the Australian Continent during the Pleistocene regressions.

It hardly needs to be said that the indications of the geological periods are arbitrary to a high degree (especially in regard to *Scutinanthe*). The only periods for which some probability could be accepted in connection with migration, are the Early Eocene, the Young Miocene and the Pleistocene. Perhaps only a few of the youngest endemics might be of postglacial age.

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