PHYLOGENY OF SINGLE FEATURES,

as illustrated by a remarkable new Sapotaceous tree from British Malaya (Madhuca Ridleyi, n. sp.).

By H. J. LAM,

Professor of Botany, and Director National Herbarium, Leiden (Holland).

In older works concerning the field of phylogenetic taxonomy, families and genera were considered as more or less static entities. It was accepted that they wandered both through time and through space, and also that, as they developed, or in general changed by evolutional processes during that journey they helped to form that much-discussed, but ever-mysterious structure, the genealogical tree. Such expressions as : the genus A has probably given rise to the genus B, the genus C is to be derived from the genus D, the genera E and F have common ancestors with the genus G, etc., are characteristic of those days. Although dynamic in the sense of evolution, these taxonomic units were, in fact, static entities, as they were considered to travel and to change as units.

However, taxonomic ideas are not the same nowadays. Genetics arose and developed and, being in some way the branch of science, which covers the phylogeny of living species, greatly influenced the ideas of taxonomical and phytogenetical investigators. Instead of a static treelike structure as the old extreme, we got, as the extreme opposite concept, a sort of dynamic network, comparable with the creeping plasmodium of a slime-mould. No fixed units any more, only a series of ever-changing combinations of a constant number of genetical factors (HAYATA). Although few will agree with an extreme dynamic system like his, the remarkable ideas of this author are certainly both characteristic of, and, to some degree, also responsible for the change of our thoughts. At any rate, the former families, genera, etc., are considerably less solid, not only in a taxonomic, but especially in a phytogenetic sense. Feeling that the old tree is as unsatisfactory as the slime-mould plasmodium to serve as a symbol for our ideas concerning phylogenetical processes, we are nowadays trying to find some "golden mean". We do that, for instance, according to an old and approved recipe, by analysis of the material available; in other words, we are no longer examining the tree and the slime-mould as a whole, but we try to look for what parts they are made of : we study single features. The features, whether determined by a single genetical factor or by a group of such factors, certainly have more right to be called the true taxonomical-genetical units than the individuals. During my investigations on Malaysian Burseraceæ (**5, 6**) I became more and more convinced of the value of this phylogeny of features

("Merkmalsphylogenie"; ZIMMERMANN); next to this my atten-
tion was drawn to the idea that features could, alone or in
combination with others (coupling of factors), travel, fairly
independently, not only through time but also through space for
long periods (Paleogeography of features as *e.g.* practised by
LYMAN B. SMITH, **7**). It seems possible that a middle course
between the tree and the slime-mould may be found by accepting
that all combinations of factors (features) and all grades of
strength or duration of a coupling may occur. Evolution would
mean in that case : a certain, yet undiscovered, trend in the way
in which features cling together or in which certain combinations
succeed each other. Both hybridization (LOTSY) and mutations
(HUGO DE VRIES) find their place in this concept.

As in all phylogenetic studies, paleobotanic data are of
principal importance, but as these are too often wanting we have
to look for what taxonomy (morphology) and geography (distri-
bution) may teach (VON WETTSTEIN). A careful and critical
study of these data may give us an idea of the possible phylogeny
of what we call a taxonomic unit. We shall then see, I expect,
that generalisation is not possible in the way we were used to;
that every genus, etc., has to be investigated quite separately,
and that conclusions of a general nature may only be relative to
the fundamental laws of evolution. These considerations leave
the way open to a process of the origin of genera and families,
which I think has been taken into account only too little up to
now, *viz.* through polyphyletic evolution.[1] On account of our
present knowledge I prefer a phylogenetic symbol in the form of
a network-structure, extremely minute and dynamic at every
point representing the present, and extremely coarse and static,
as viewed from these points, in the farthest past; we have to bear
in mind, however, that this structure is no reality but just a
human attempt to grasp a complicated problem.

At the time that I studied Malaysian Sapotaceæ (**1, 2, 3, 4**),
these ideas had not yet evolved in my mind. However, having
taken up these studies[2] again with the aid of some collaborators,
I have come upon some facts which perfectly fit into the above
considerations, and I am glad to mention here an example of the
probable phylogeny of a single feature, illustrated by a new
species of *Madhuca,* which I am very much pleased to dedicate
to the nestor of Malayan and Malaysian[3] botanists, Mr. H. N.
RIDLEY, on the occasion of his 80th birthday. I have named it
Madhuca Ridleyi; a diagnosis and a picture of the species may
be found at the end of the present paper.

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1 I hope to report on a striking example concerning this before
long.

2 Publication of a revision may be expected next year.

3 Malaya = Malacca = the Malay Peninsula (British Malaya),
which in this paper is considered as forming phytogeographically a
part of Malaysia : Malaysia = the Malay Archipelago ; the word has,
if I am not mistaken, been introduced by E. D. MERRILL.

As appears from may earlier papers (**1,** p. 11, 110–112), *Madhuca* is one of four genera (the others are *Payena, Ganua* and *Burckella,*), together forming the group of the *Palaquiinæ-Madhuceæ-Eumadhuceæ,* well characterized by the possession of two whorls of two sepals each.

Let me begin with some words as to what may be suggested regarding the phylogeny of these four genera. As we know nothing about fossil *Madhuceæ,* we have to look for what data recent representatives have to yield. First of all we have to state, that all of the four genera are very closely related, which is illustrated by the great trouble it took to find a means of sub-division, as all features are very irregularly distributed over the genera. Apparently the *Eumadhuceæ* form a group which is in a state of initial differentiation into four branches; a differentiation, nevertheless, distinct enough to claim different names for the branches.

Valuable data may now be expected in the present distribution of species and features.

Distribution of species. As appears from the accompanying table (Pl. 3) and the map (Pl. 4), the group is restricted to S. Eastern Asia (Western limit : Deccan Peninsula and Ceylon) and Polynesia (as far east as Fiji, Samoa and Tonga) with a very distinct centre of differentiation in Western Malaysia (British Malaya inclusive).

According to orthodox ideas of historical phytogeography, our table (Pl. 3) confirms some well-known facts, obvious also in many other plant families, *e.g.*

1. that the phytogeographic relations between British Malaya and the greater Sunda Islands (especially Sumatra and Borneo) are extraordinarily strong (cf. **2,** p. 384–385, table; and **3**);
2. that next to a line of dispersion from Malaya to Sumatra, a very important line is that from Malaya to Borneo and the Philippines (Palawan !);
3. the hypothesis that this region which in a former period is supposed to have formed one big land mass that split up in postglacial times, has been an important source and centre of dispersion of plant groups, the areas of which are now disjunct.

On account of these considerations I would suggest that the *Eumadhuceæ* have originated in that former land mass, the so-called Sunda-land. From this centre, the group has spread geographically, during its morphological differentiation, both in western direction (continent of Asia) and towards the East, and the isolation of the various islands then gave rise to endemic species (the Philippines—*Madhuca*—and also New Guinea—*Burckella*—have apparently acted as secondary regions of differentiation), while other species remained unchanged everywhere or perhaps evolved in the same way in different places.

Of the three genera *Madhuca, Payena* and *Ganua* (cf. Pl. 3, 4 and 5), *Madhuca* covers the largest area and contains the greatest number of species. The differentiation of these genera mutually is both geologically and morphologically very young; *Ganua* has apparently its centre in Borneo (3 endemic species) with offshoots to British Malaya, Sumatra and Palawan (non-endemics) and, curiously enough, one isolated species in the Moluccas;[1] *Payena,* with greater area than *Ganua,* and also with stronger differentiation, is geographically intermediate between *Madhuca* and *Ganua.* Morphologically *Ganua* is developing in the direction of a peculiar venation of the leaves, of imperfect septa in the ovary and of dry fruits. *Payena* is distinguished by a well-characterized venation and a tendency to form a voluminous endosperm and *Madhuca,* with which *Payena* is connected by many transitional species, shows, besides a type of venation of its own, a tendency to reduce the endosperm. *Burckella* is the only genus that is more distinct morphologically, but especially geographically. In contradistinction to the other genera it does not follow the age-and-area theory, as the number of its species is small and its area large. Yet I see no reason to accept a reduction of the area and to consider the species as relic-endemics, but a biphyletic origin seems to be possible. In its venation it reminds one of eastern *Ganua*-species as well as of a certain type of mostly western *Madhuca*-species (Sect. *Dasyaulus*). It must certainly be remarked that its venation much resembles the type of the two geographically nearest species : *Ganua Bœrlageana* and *Madhuca Burckiana.* It shows, furthermore, a tendency to form very big fruits.

These general indications led me to the assumption that *Madhuca* is the basal group in which the other genera are rooting. Further evidence for this supposition may be found in some features, intentionally left unmentioned thus far.

Distribution of features. The characteristics purposely not yet mentioned are the number of parts in the corolla, the andrœceum and the gynæceum. According to what is generally accepted, high numbers may also in this group be considered as representing the more primitive state. In the *Eumadhuceæ* there are two tendencies to be noticed : one to fix the said numbers at P. 8, A. 16, G. 8, and the second (which is, by the way, an extremely general one) to reduce the G. number beyond 8. Now we see that *Madhuca* is the only genus in which all whorls show a great variation *viz.* P. 18–6 (–5 ?), A. 40–12, G. 21–6. In the other genera P. and A. are, to a much higher degree, fixed to 8 and 16 respectively; G., however, shows a further reduction as far down as 3. It is certainly a striking fact that the highest numbers in the last-named whorl occur in or near the geographical

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[1] This may be a case of convergence (polyphyletic origin of the genus).

centre of the group and that the lowest ones occur in the most remote parts of the area (*Burckella* in Polynesia and *Madhuca*, although not exclusively, in India and Ceylon).

Our new species, *Madhuca Ridleyi* is, in this respect, to be considered as a representative of a most primitive state, the numbers of parts in its P. and G. whorls being by far the highest known in the whole group, *viz.* P. 18, A. 37 – 36, G. 21 – 18 !

The following facts may elucidate this somewhat more in detail : —

Madhuca. P. 18–6 (–5?)   A. 40–12   G. 21–6.

Between these extremes there is a very rich variation. Most species show a variability in all whorls, and often a considerable one, also those which cannot be said to be polymorphous in other respects. Some examples are :

		P.	A.	G.
M. lancifolia	...	14–10	28–22	14–10
Kingiana	...	16–12	36–32	10–8
betis	...	10–8	20–16	8
sericea	...	9–8	24–18	10–8
Endertii	...	7–6	13–12	7–6
macrophylla	...	13–10	28–20	18–11
etc.				

M. Ridleyi has the highest numbers for G. As to P. it is only equalled by *M. macrophylla*, as to A. it is only surpassed by *M. Lecomteana* (nom. nov. for *Bassia Thoreliana* Pierre), in which P.=40–35. Only 3 other species, all from the Malay Peninsula show similar P. numbers, except a *Burckella* species, discussed below.

Payena. P. 8–6   A. 20–12   G. 8–6.

These extremes are exceptions. About 12 species out of 16 of which all whorls are completely known, show the 8–16–8 arrangement, many others show little variations and only a few, some of which are polymorphous throughout, are more various, *viz.* P. *lucida* (8–6, 16–13, 8–6), P. *dasyphylla* (8, 20–16, 8), P. *Griffithii* (8-6, 16–12, 8) and P. *truncata* n. sp. (8–7, 16–4, 8?).

Ganua. P. 8–6   A. 24–16   G. (12?–) 9–6.

In this small genus the variability is somewhat more pronounced than in *Payena*. Yet, most of the species are fixed to the 8–16–8 type or almost, and, as in *Payena*, the most striking variability occurs in species that are also polymorphous in other respects, such as G. *Motleyana* (10–8, 20–16, 8–6) and G. *monticola* (8, 24–16, 12 ?–9–8).

Burckella. P. 8–6   A. (40?–) 18–9   G. 6–3.

There is hardly any variability in the corolla; only one species is said to possess 6 petals. In the andrœceum three species have 18–16 stamens, one has 16–9 and one (*B. Thurstonii* [HEMSL.] H. J. LAM, from Fiji) is said to have as many as 40 (p. 8, G. 4).

This fact gives me an opportunity to say a few words on the phylogenetic value of the three whorls mentioned. As may appear also from the following statement, the corolla and the andrœceum seem, in general, not to yield valuable and trustworthy data for phylogenetic conclusions. There is only a slight indication as to a reduction of the P and A. numbers in three Ceylon species of *Madhuca* (6–12–6). For the rest, it may even be that these whorls are not always subject to a reduction but may, on the contrary, in some cases, attain higher numbers by progression. This not uncommon phenomenon is *e.g.* illustrated by the figure of the andrœceum of *Burckella (Bassia) Thurstonii* in HOOKER'S Icones Plantarum t. 2569 (XXVI, 1899), in which a petaloid stamen is figured and also by the fact that stamens with halfway split anthers are not rare in the group of the *Palaquiinæ*. This made me refrain from laying any particular stress upon the phylogenetic value of the characters of these two whorls.

The gynæceum, however, being an organ of much less phylogenetic plasticity as a rule, is more reliable in this respect, and shows a distinct reduction in the more remote parts of the area. It does so in all of the four genera; in *Payena* this reduction is hardly conspicuous (down to 6 in 3 out of the 19 species in which this feature is known); in *Ganua,* being also in other features more isolated (ovary, fruit, venation) it become more apparent (down to 6 in 3, to 7 in another of 9 species); in *Madhuca* the genus with the highest G. numbers this reduction is occasionally found (*viz.* down to 6 in 2, 7 in 1 W. Malaysian, down to 5 in 1, to 6 in 7 and to 7 in 1 Continental species). It is also a striking fact that in *M. mindanænsis* the Philippine specimens possess 8, the North Borneo ones (living in a place which is probably colonized from the main area in the Philippines) 6 cells in their ovaries. None of these genera, however, have a G. number below 6. This is only reached in *Burckella* where there are 6, 5, 4 or 3 cells, however, wihout more detailed geographic correlation with the accepted general migration from West to East.

The following table gives the average numbers in the whorls in question in order to show any geographic importance :

—	P.	A.	G.	% of species in which G=							
				>9	9	8	7	6	5	4	3
MADHUCA											
W. Malaysia ..	9·1 (33 sp.)	20·6 (33 sp.)	9·3 (32 sp.)	46	52	66	13	6	..	..	..
C. & E. Malaysia ..	8·4 (4 sp.)	21·2 (4 sp.)	8·1 (4 sp.)	..	25	75	25	25	..	..	..
Cont. of Asia—											
E. Peninsula ..	9·5 (8 sp.)	20·4 (9 sp.)	8·1 (10 sp.)	30	20	80	50	40	..	..	..
W. Peninsula ..	8·8 (4 sp.)	20·5 (4 sp.)	7·5 (3 sp.)	33	33	67	67	33	33	..	..
Ceylon	6 (2 sp.)	12 (2 sp·)	6 (2 sp.)	..	..	..	..	100	..	..	..
PAYENA											
West Malaysia, Cont. of Asia (E. Penins.) (no difference)	7·8 (18 sp.)	15·7 (20 sp.)	7·8 (19 sp.)	..	..	100	16	16	..	..	..
GANUA											
West Malaysia, 1 species in Moluccas (no difference)	8·1 (8 sp)	16·8 (8 sp)	7·7 (9 sp.)	11?	22	77	44	44	..	..	..
BURCKELLA											
Moluccas, N. Guinea, Polynesia (no difference) ..	7·6 (7 sp)	16 (*6 sp.)	4·6 (8 sp.)	..	..	..	..	25	63	63	13

* *Note:*—Including *B. Thurstonii* (*see* note above), the A. average (of 7 sp.) would be 21.

It appears, I think, especially from the percentage data, that there is a tendency to be traced to reduce the number of carpels as the distance from the centre of dispersion is greater, both to the West (India, Ceylon) and the East (Polynesia). That this reduction is more distinct in the East may readily be ascribed to the preponderant insular character of those parts. In the other whorls, there is no correlation, possibly partly due to an eventual tendency to raise the number of petals and stamens *e.g.* by what · has sometimes been called a reduplication ("dédoublement").

The above facts have been combined with my general ideas on the dispersion of the whole group in a tentative "genealogical branch" (Pl. 6) which may speak for itself, but concerning which I must state that, of course, complicated processes as the phylogeny of a group of plants can never be symbolized in a thoroughly satisfactory way on a sheet of paper; furthermore I have to emphasize that the "branches" are not meant to be "solid", but should be imagined as sponge-like tissues of extremely complicated structure. For the rest, I am quite aware of the very problematic value of such considerations and ideas.

A description and analysis of the new species may follow here :

Madhuca Ridleyi (Sect. *Dasyaulus*), nova species, Pl. 7— Arbor mediocris, ramuli crassi; internodiis brevibus bulboso-inflatis, 1.5–2 cm. longis et latis rugosis; folia ad eorum apices dense conferta; stipulæ deciduæ 0.3–1.2 cm. longæ pubescentes; folia coriacea glabra, obovata vel oblongo-obovata, 14–25 cm. longa, 5–10.5 cm. lata, basi in petiolum glabrum 1.5–3.5 cm. longum, 0.2–0.3 cm. crassum attenuata, apice acuta vel subrotundata; costa media i.s. supra canaliculata, subtus valde prominens; nervi secundarii subtus prominentes, 18–25, angulo 60°–70° de costa adscendentes, recti, prope marginem curvati, diminuti, haud conjuncti, 0.7–1 cm. distantes; nervi tertiarii transversi, angulo circ. 120° de costa descendentes, subtus conspicui, reticulatione perminuta, interdum nervo brevi secondariis parallelo a costa media usque ad ⅓–½ adscendente; *inflorescentiæ* ex foliorum delapsorum axillis ortæ, nonnullæ ad ramulorum longorum rectorum apices dense confertæ, 15–25–floræ, pedicelli minute tomentosi, graciles, 2–2.5 cm. longi; alabastra acute ovoidea; *calyx* 1–1.3 cm. longus, sepala extus dense minute fulvo-ferrugineo-tomentosa, intus glabra, angula apicale circ. 90°, exteriora 1.25 cm. longa, 1 cm. lata, interiora 1.3 × 1.1 cm.; *corolla* in alabastris vix exserta (flores novellos tantum vidi) 1.1– 1.2 cm. longa, extus glabra vel subglabra, intus glabra; petala 18 uniserialia dextrorsum tegentia 0.95–1 cm. longa, 0.4 cm. lata, margine plus minusve irregulariter minute denticulata; *stamina* glabra 36–37, plerumque uniserialia, interdum nonnulli serie imperfecta addita, 0.5–0.6 cm. longa, nova filamenta usque ad 0.2 cm. longa, antheræ 0.2–0.35 cm. longæ, 0.15 cm. latæ, apice

acumine acuto 0.075–0.15–0.25 cm. longo ornatæ; *ovarium* gla-
brum depressi-globosum extus paulo sulcatum, 18–21- loculatum;
loculi 1-ovulati; stylus solidus in alabastro 0.9 cm. longo; *infrutes-*
centiæ ramulorum apicibus subumbellatim confertæ, pedicelli
2.5 cm. longi, 0.25–0.3 cm. crassi, apice vix dilatati; calyx
persistens, sepala 1–1.8 cm. longa, extus tomentosa; *fructus*
globosi, apice sæpe stylo 3 cm. longo persistente ornatus, dense
ferrugineo-pubescentes, pericarpio crasso subduro; 4–6 semina
oblonga, testa tenuis, extus nitida; cetera ignota.

Malay Peninsula: Pahang, Bukit Serdam, Raub, 1300 ft.,
on dry limestone rocks (HENDERSON 25055, flowers, on 6 Oct.
1931, *type specimen*)—Upper Perak, Gunong Runto, Lenggong,
500 ft., on limestone (HENDERSON 23834, fruits on 11 June, 1930).

A small but rather stout tree, both specimens known growing
on limestone; bark pale, horizontally and longitudinally fissured;
fruits rusty brown.

I have to thank Mr. K. GRIFFIOEN for his assistance in pre-
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BAAS BECKING for kindly looking over the English.

Summary.

After some theoretical considerations on modern phylogene-
tical Taxonomy as a discipline, dealing with morphological as
well as geographical evolution and newly influenced by Genetics,
it is stated that next to Paleobotany two categories of data may
be considered important for our ideas on Phylogeny, *viz.* the
present distribution of species and that of features. This is
illustrated by examples taken from the *Eumadhuceæ,* a group of
East-Asiatic to Polynesian Sapotaceæ. It is shown that the
former Sunda-land is the most probable place of origin of this
group and that the species have migrated both westward (India,
Ceylon, Indochina) and eastward (Polynesia). Evidence for this
suggestion is found in the distribution and evolution of certain
features, especially in the reduction of the number of carpels in
both directions mentioned. The paper was stimulated by the dis-
covery of a new *Madhuca*-species, *M. Ridleyi,* from British
Malaya, the gynæceum of which shows the highest number of
carpels known in the whole group. A description of this species
is added.

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Explanation of Plates 3-7.

Plate 3

Present Distribution of the Eumadhuceæ.

Well known species only; numbers between brackets under genera indicate total number of species, in the other columns they indicate the number of endemic species in the region concerned; however, it must be borne in mind that amongst these are a number of new and more recent species.

Plate 4

Areas of *Madhuca* (M), *Payena* (P), *Ganua* (G) and *Burckella* (B) and total number of species (*Eumadhuceæ*) in the separate regions.

Plate 5

Probable lines of migration.

Plate 6

Probable phylogeny of *Eumadhuceæ*.

Plate 7

MADHUCA RIDLEYI, n. sp.—a. branch with leaves; b. shoot with inflorescences; c. id. with fruits; (d) flowerbuds; e. outer sepal, in- and outside; f. id. inner sepal; g. corolla inside; h. petals; k. stamens; m. pistillum; n. ovary, cross-section—after HENDERSON 25055, except c. which is taken from HENDERSON 23834.

Plate 3

	INDIA PROPER (W. PENINS.)	CEYLON	BURMA, ASAM, ANDAMANS	SIAM, FR. INDO-CHINA	MALAY PENINSULA	SUMATRA	BORNEO	JAVA	PHIL. ISL	CELEBES	LESSER SUNDA ISL.	MOLUCCAS	NEW GUINEA, BISMARCK ARCHIPELAGO	POLYNESIA (N HEBR., FIJI, TONGA, SAMOA)
BURCKELLA (13)	—	—	—	—	—	—	—	—	—	—	—	2 (2)	7 (7)	4 (4)
GANUA (12)	—	—	—	—	4 (0)	5 (0)	10 (3)	—	2 (0)	—	—	1 (1)	—	—
PAYENA (26)	—	—	1 (1)	3 (2)	13 (6)	12 (4)	12 (3)	1+2? (0)	1 (0)	—	—		—	—
MADHUCA (65)	4 (4)	3 (3)	1 (1)	10 (10)	22 (14)	11 (3)	21 (10)	2 (1)	10 (5)	3 (0)	1 (0)	1 (0)	—	—
TOTAL: 116	4 (4)	3 (3)	2 (2)	13 (12)	39 (20)	28 (7)	43 (16)	3+2? (1)	13 (5)	3 (0)	1 (0)	4 (3)	7 (7)	4 (4)
		CONT. OF ASIA: 22 (21)			BR. MAL. & W MALAYSIA: 74 (57)				CENTR. MALAYSIA: 13 (5)			E. MALAYSIA: 11 (10)		POLYNESIA 4 (4)

(A) PALAWAN
(B) S PHIL ISL

SAMOA FIJI TONGA

Plate 7

Gardens Bulletin, S.S.