

The Durian Theory or the Origin of the Modern Tree

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With thirty-six Figures in the Text

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PREFACE

THE value of a theory, as of any organization, is proved by what cannot be done without it. The theory which I offer seems useful because it reveals many insights into the nature of flowering plants, birds, and mammals—the life, that is, *par excellence*, of the tropical forest. It has led me to compare not only the forms of fruits and those of trees, but to think, at the same time, of tapirs, cycads, and brussels sprouts, of colours and monkeys, of fishes' eyes and modern patterns. It has led me to study the chalaza of the ovule as the neuropore of the gastrula, the formation of peltate scales, the lengths of funicles, and the weights of seeds, and to consider, beside the more obvious things, the biological significance of dangling, the origin of poppies, the disappearance of apes and elephants, the clamour of parrots, and that gap in palaeobotany—the beginning of flowering plants.

Hitherto the lead in evolutionary thought has been taken chiefly by zoology. This theory will turn attention, I hope, to tropical trees and, as a proof of the concept of Xerophyton, in a way not visualized by its author, will reawaken interest in that neglected work 'Thalassiphyta' (Church, 1919). There is now in the rain-forests of the equatorial belt a Xerophyton, representing a culmination of plant-evolution still in dynamic equilibrium with its degeneration-products, as the world ages, though the Thalassiphyton has gone for

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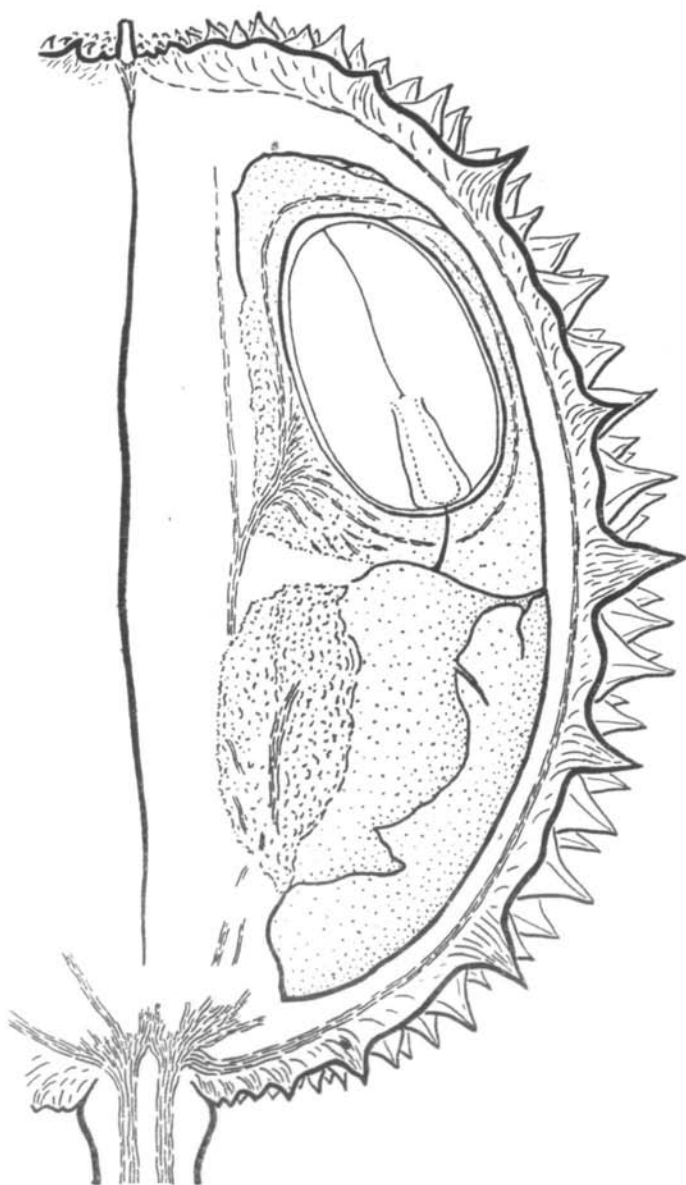


FIG. 1. The ripe fruit of *Durio zibethinus* about to open, in longitudinal section, showing the aril (dotted) round the seeds, the mealy placenta, and the vascular supply to the seed, aril, and spines ($\times 1$).

ever. Unluckily for my present purpose, the life of the tropical rain-forest cannot be compressed on to paper any more than it can be grasped by a foreign expedition. The subject is so vast and the objects so unfamiliar that, at best, I can hope to spur the younger generation to strive after the means of living in the tropics if it would consider evolution. That the seeming oddities of which I have written form a demonstrative whole should prove themselves that, without tropical orientation, biology is lost.

One Sunday in July 1944, when Professor Kwan Koriba was acting director of the Singapore Botanical Garden, we found in a patch of virgin forest on the island the fallen fruits of *Elaeocarpus javanicus* (Tiliaceae). They appeared to us to belong to the Meliaceae, Sapindaceae, Flacourtiaceae, Sterculiaceae, Bombacaceae, and even Connaraceae, until we could correct ourselves in the herbarium, but this very confusion led me to inquire. It seemed that this kind of fruit—a red loculicidal capsule with large black seeds hanging on persistent funicles and enveloped by a red aril (Fig. 6) must have been the ancestral fruit of this group of families. And if of this group, why not of all flowering plants?

I began work on this theory in Singapore during the last year of the war, and I express my gratitude to Professor Koriba for the part which he has played as protector of the scientific research of the Singapore Botanical Garden, as a critical adviser, and, if I may say so, my first convert to durianology.

WHAT IS THE DURIAN?

The durian (*Durio zibethinus*, Bombacaceae) is a lofty forest-tree of the Malayan region, now widely cultivated from India to New Guinea. It has rather small, simple leaves, slender twigs, and bunches of massive pink or white flowers, borne on the branches and giving place to huge, 5-shouldered, spiny, loculicidal capsules which ripen olive to golden-yellow. In each cavity of the fruit are 1-5 large, light-brown seeds covered by the thick, creamy, white or yellow aril. The fruits do not open till they are fully ripe and have crashed to the ground. They then have a powerful and disgusting smell, of garlic and skatol, but the creamy aril is so delicious that the durian is the most popular and famous fruit of the East. Unripe fruits are heavily armoured with stout pyramidal spines, which are driven into the skin by the weight of the fruit when held in the hand, and they can rarely be attacked by animals, not even by squirrels, though the immature and mature seeds are highly nutritious and palatable.

Until recently, durian-trees were not selected. Wild trees in Malaya have as good fruits as those in cultivation which, indeed, is often little other than the protection of sporadic seedlings. In the forest they commonly occur in groves. In the season the smell of the fruits attracts the elephants which congregate for first choice; then come the tigers, pigs, deer, tapir, rhinoceros, monkeys, squirrels, and so on down to ants and beetles which scour the last refuse. The jungle-folk build tree shelters whence they can reach the ground

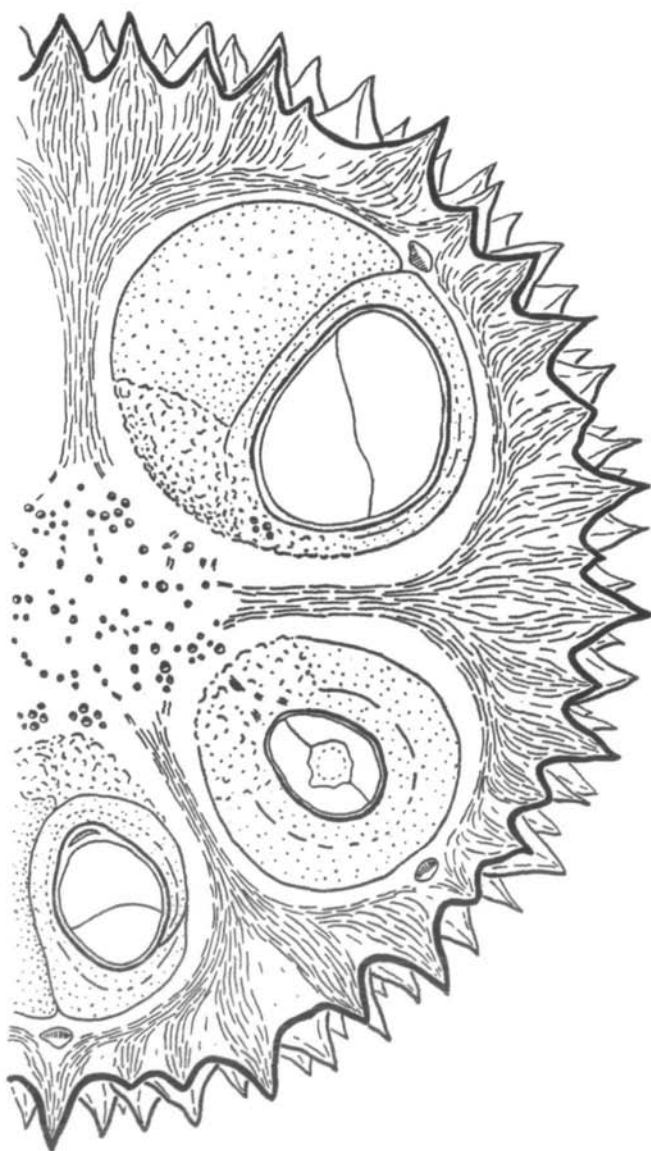


FIG. 2. The ripe fruit of *Durio zibethinus* in transverse section, showing the arils (dotted), the mealy placentas, and the vascular supply (consisting of numerous small axial bundles from which pass the bundles to the fruit-wall and spines, and a main longitudinal bundle on the outside of each loculus) ($\times 1$).

when a fruit drops, and whither they can climb again to safety. Under the big trees are leaning saplings, frayed bark, trampled shrubs, and churned ground, as scenes of elephantine supremacy.

The spines develop only under the initial peltate scales of the ovary, each

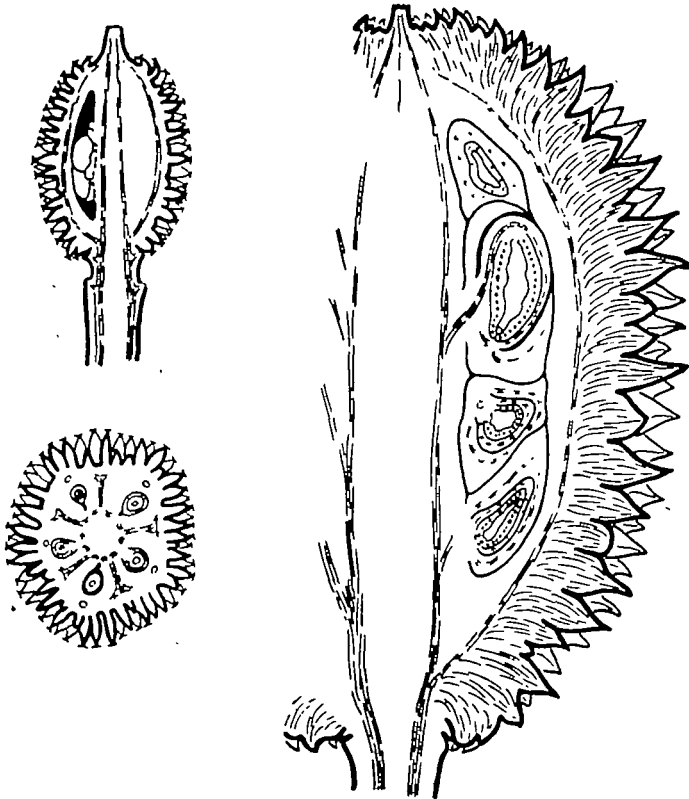


FIG. 3. Developing fruit of *Durio zibethinus*, shortly after pollination (in l.s. and t.s.), and when half-grown, to show the rapid growth of the aril, the development of the spines below peltate scales, and the vascular supply ($\times 1$).

spine bearing, as it were, a primary scale at its tip and secondary peltate scales on the sides.

The aril, as usual, develops only after pollination, but unfertilized ovules may develop the aril as the fruit sets.

There are about fifteen species of *Durio*, distributed through Siam, Burma, Philippine Islands, Malaya, Sumatra, Borneo, and Java. Most have incomplete arils or none at all, and some are cauliflorous rather than ramiflorous.

One species, *D. Griffithii*, has small, red fruits, softening when ripe, and black seeds with short red arils. The fruits are axillary on the leafy twigs and open on the tree so that the black seeds hang on the edges of the star-shaped fruit, as with *Sterculia* and *Sloanea*.

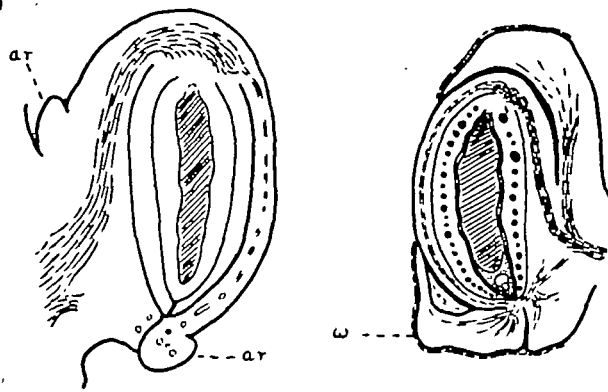


FIG. 4. Developing seeds of *Durio zibethinus*, in the same stages as in Fig. 3; the nucellus containing the embryo-sac fluid, the inner integument developing mucilage sacs (right figure, as black circles), $\times 15$ (left); $\times 2$ (right). *ar*, aril; *w*, waxy secretion of aril.

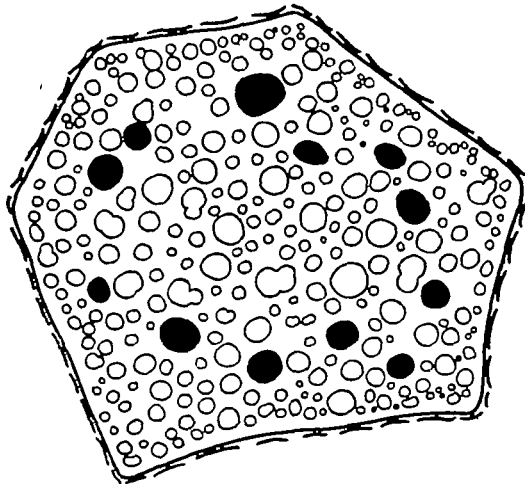


FIG. 5. *Durio zibethinus*; a section of the young fruit (above) with incipient aril and spines ($\times 7$); and a transverse section of a spine from a half-grown fruit, to show its complex vascular supply (the outer smaller bundles being only fibrous), the mucilage canals (black), and the peltate scales ($\times 15$).

Three other genera of the Bombacaceae have arillate seeds, namely, *Coelostegia* (Malaya, 2 spp.), *Neesia* (Malaysia, 10 spp.), and *Cullenia* (Ceylon, 1 sp.).

Only these four genera, all of south-east Asia, in the vast Bombacaceae-Malvaceae of several thousand species, have this type of capsular arillate fruit.

Problem. What is the origin of this huge armoured capsule, so fiercely sought after by wild animals, yet so rare as to occur in a mere sprinkling of tropical trees of this large series? It is, at once, a biological success and a curiosity. Why do durians exist?

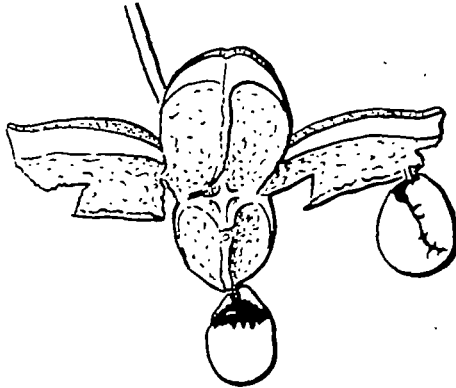


FIG. 6. Dehisced fruit of *Sloanea javanica* (Tiliaceae—Elaeocarpaceae), showing the black seeds with red arils ($\times \frac{1}{4}$).

ARILLATE FAMILIES

The following are the main, if not all, families of flowering plants with arillate seeds.

A. All genera and species arillate

Myristicaceae: Stachyuraceae (1 gen., 2 spp., Japan, Himalayas).

B. Most genera arillate

Dilleniaceae, Connaraceae, Passifloraceae, Scitamineae (Musaceae, Marantaceae, Zingiberaceae).

C. Many genera arillate

Meliaceae, Celastraceae, Sapindaceae, Flacourtiaceae, Melianthaceae, Guttiferae (Clusiaceae).

D. Few genera arillate (number of genera in brackets)

Nymphaeaceae (2), Annonaceae (3), Monimiaceae (1), Berberidaceae (2), Papaveraceae (1), Linaceae, Malvaceae—Bombacaceae (4), Sterculiaceae (3), Tiliaceae (Elaeocarpaceae, 1), Leguminosae (Mimos. 2, Caesalp. 14, Papil. 1, Swartz. 1), Theaceae (1), Samydeae, Rhamnaceae (1), Rhizophoraceae (3), Melastomaceae (4), Aizoaceae, Lecythidaceae (2), Thymelaeaceae (2), Apocynaceae (2), Commelinaceae (2).

E. Rudimentary aril

Ranunculaceae (Paeonia), Fumariaceae, Polygalaceae, Violaceae, Oxalidaceae, Bixaceae, Turneraceae, Tremandraceae, Euphorbiaceae, Leguminosae (Papiionaceae), Cactaceae, Liliaceae (2).

Only some forty-five families have arils, more or less. Only one large family is wholly arillate: six are mainly arillate. All these families are chiefly,

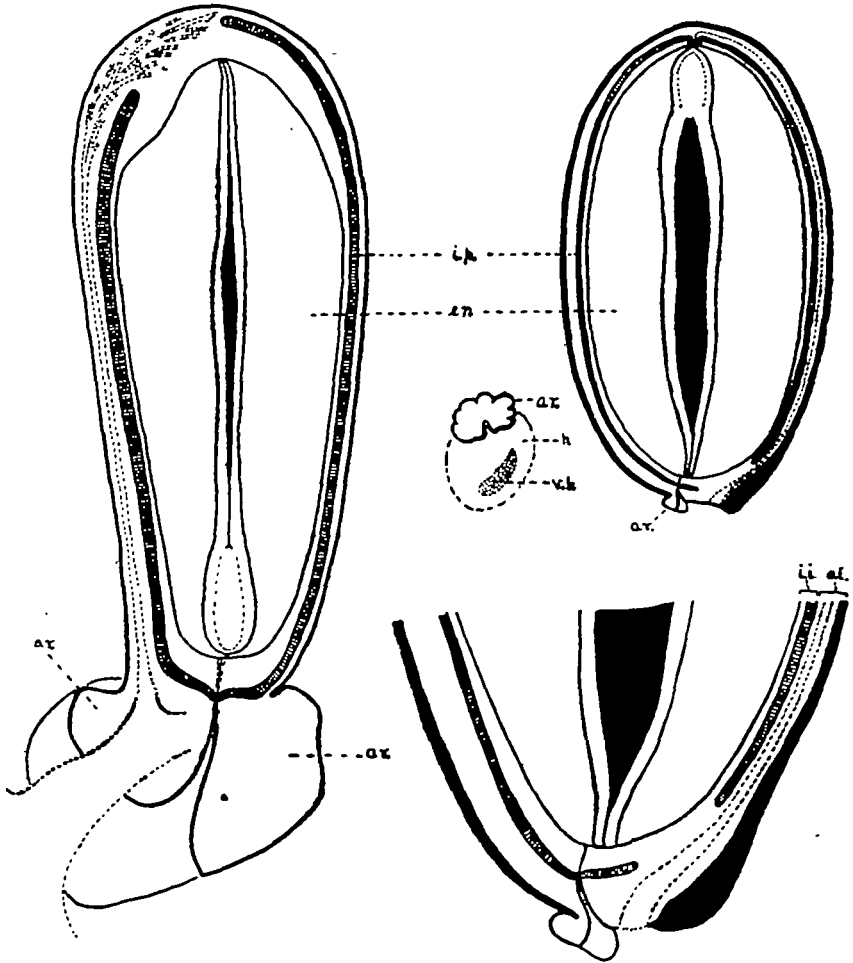


FIG. 7. Longitudinal sections of mature seeds of *Coelostegia Griffithiana* (left, Bombacaceae $\times 3$), and *Sterculia macrophylla* (right, the upper figure $\times 3$, the lower $\times 7$, the hilum $\times 7$). The seed of *Sterculia* has the embryo inverted, with radicle pointing to the chalaza: when the *o.i.* weathers off, the chalazal pore in the palisade of the *i.i.* appears as a false (but effective) micropyle. *ar.*, the aril (much reduced and limited to the micropyle and funicle in *Coelostegia*, entirely rudimentary in *Sterculia*, though bright yellow); *en.*, endosperm; *h.*, hilum; *i.i.*, inner integument; *i.p.*, the palisade of the inner integument; *o.i.*, the outer integument; *v.b.*, vascular bundle (dotted) of the hilum.

if not entirely, tropical. Most of the arillate seeds belong to tropical trees or woody climbers. Extremely few arils of any size occur in small plants, e.g. *Acrotrema* (Dilleniaceae).

Generic examples: *Myristica*, *Xylopia* (Annonaceae), *Wormia* (Dilleniaceae), *Connarus*, *Dysoxylon* (Meliaceae), *Leptonychia* (Sterculiaceae), *Guioa*, *Nephelium*,

Paulinia (Sapindaceae), *Tabernaemontana* (Apocynaceae), *Sloanea* (Tiliaceae), *Ravenala* (Musaceae).

Sterculia provides an example of a rudimentary aril, for several species have a minute yellow arillate cushion 1–2 mm. wide on one side of the micropyle.

Spines. As with the Bombacaceous genera, so in the other cases, these arillate capsules are often spiny (see p. 397).

Problems. Exactly as with *Durio*:

- A. Why are these successful fruits, much eaten by birds, bats, and arboreal mammals, so comparatively rare, even in secondary jungle where animal-distributed plants are common?

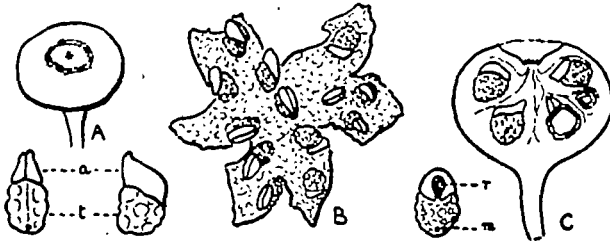


FIG. 8. The epigynous fruit of *Siparuna* sp. (Monimiaceae), irregularly dehiscent, the light-grey tuberculate seeds with dark-red aril (cf. the irregularly dehiscent fruits of some species of *Ficus*). A, the full-grown purple-red indehiscent fruit ($\times 1$); B, the dehiscent fruit with pink, mealy-granulate flesh in which the seeds are embedded ($\times 1$); C, a longitudinal section of the full-grown fruit showing the pulpy, connate carpel-walls ($\times 1\frac{1}{2}$); 3 seeds ($\times 2$). *a*, aril; *m*, micropyle; *r*, vascular bundle of the raphe; *t*, the testa.

- B. Why are there, in many genera, species showing all degrees of development of the aril from none at all to the complete aril, e.g. *Sloanea*, *Xylopia*, *Acacia*, *Dysoxylon*, as with *Durio*?
- C. Why are there, in related genera, so many transitions from this arillate capsule to dry capsules with dry, often winged, seeds (Meliaceae, Apocynaceae), to drupes (Annonaceae) or berries (Dilleniaceae) or nuts (Lecythidaceae)? Even in the one genus *Xylopia* there are arillate follicles, indehiscent berry-like follicles, and 1-seeded drupe-like follicles; and there is almost the same transition in *Pithecellobium* (Mimosaceae).
- D. Are these arillate fruits new and parallel inventions in these different families and genera? Or are they relics showing the ancestral conditions from which modern fruits such as the dry capsules, follicles, nuts, berries, drupes, and so on, have been evolved?

One or other of these two points of view must be correct.

ARGUMENT

A. If these fruits are upgrade and recent, then:

a. Why should all these widely different families, e.g. Apocynaceae and Zingiberaceae, Myristicaceae and Sapindaceae, and even single genera in one

family, have evolved the same mechanism of a third integument developing over the fertilized ovule? I can find no answer to this. There is no means of evolving an aril *de novo*.

b. The early, intermediate, state with a slight beginning of an aril and an undetached seed could have no survival value. Thus an undetached seed in the rain-forest is almost certain to germinate *in situ* and then to dry up and die before the fruit has fallen off the tree (Fig. 9). And yet there are probably more instances of rudimentary, useless, arils than of fully developed arils.

c. Why should *Sloanea* be the only arillate capsule of the Tiliaceae–Elaeocarpaceae, and yet agree in this fruit so closely with the allied Bombacaceae and Sterculiaceae?

d. Why should the Myristicaceae, with very reduced and simplified flowers, have evolved this massive fruit as a universal peculiarity of their peculiarly isolated family? Their big arillate seed is, indeed, a handicap in that it is the chief factor preventing their migration from the tropics, because this seed has no power of dormancy.

B. On the other hand, *if the large arillate fruit is a relic*, then one can easily understand:

a. That most flowering plants have passed on to other kinds of fruits with smaller seeds and better, or more xerophytic, dispersal mechanism in drupes, nuts, achenes, winged seeds, and so on: particularly must this have been necessary for herbaceous plants which cannot possibly reproduce by large arillate fruits. The rarity, then, of the arillate fruit follows from its primitive nature as the unspecialized means of reproduction of tropical rain-forest trees.

b. That there are many useless vestigial arils as relics.

c. That *Sloanea* is a connecting-link between Elaeocarpaceae, Bombacaceae, and Sterculiaceae in its arillate capsule.

d. That only those flowering plants could spread out of the tropical rain-forest which had evolved fruits and seeds better adapted to drought and cold than the large arillate fruits with their exposed, fleshy seeds. Thus the Myristicaceae appear as the one family of tropical trees which have been unable to spread into the monsoon and temperate regions, because they have been unable to evolve a new kind of fruit.

(Compare *Dysoxylon* and *Melia*, Bombacaceae and Malvaceae, Elaeocarpaceae and Tiliaceae, Swartzioideae and Papilionaceae, Dilleniaceae and Ranunculaceae, *Bocchorhia* and *Papaver*, Scitamineae and Liliaceae, &c.)

C. *Conclusion.* The red, fleshy, and often spiny follicle or capsule, with large black seeds covered by a red or yellow aril and hanging from the edges of the fruit-valves, is the primitive fruit of modern flowering plants.

In many families it is easy to see how this fruit has changed into the dry follicle or capsule with small, often winged, easily detached, exarillate seeds, or into the berry, drupe, and nut because there are many intermediates in existence. As an instance I will outline the state in the Leguminosae.

LEGUMINOSAE

Arillate genera. There are in the following four sub-families eighteen genera with the aril more or less covering the seed:

Mimosoideae: 2 genera out of c. 50 (*Acacia*, *Pithecellobium*).

Caesalpinioideae: 14 genera out of 126 (or 70 species out of 2,300).

Swartzioideae: 1 genus out of 9.

Papilionaceae: 1 monotypic genus out of c. 500 genera and 10,000 species.

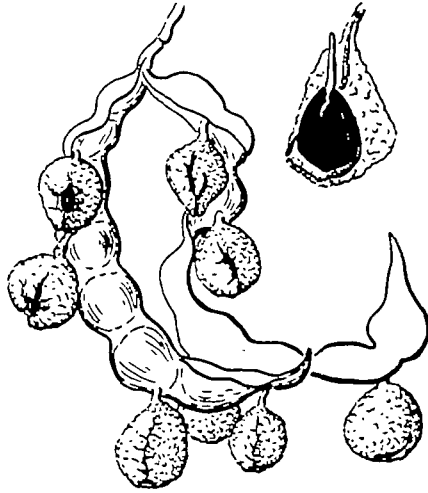


FIG. 9. A dehisced legume of *Pithecellobium dulce*, showing the hanging black seeds covered with the rose-red aril ($\times \frac{1}{2}$): a seed germinating in the aril, undetached from the pod (the aril in section) ($\times 1$).

This is obviously a relic distribution, and nearly every arillate genus shows in different species all stages in reduction or loss of the aril. If the exarillate state were primitive, one would expect to find the inverse proportion, but what is abundant now cannot possibly be primitive (cf. Cycadaceae compared with Abietaceae, Dilleniaceae with Ranunculaceae; or *Amphioxus*, *Peripatus*, and *Monotremata*; or the elephant, tapir, and anthropoid apes, as relics proved by fossil record).

Pithecellobium. *P. dulce* has the black seeds entirely covered by the red aril, and the wall of the pod is pink and somewhat fleshy. Seeds, uneaten from the pod, often germinate *in situ* to wither up through lack of water. *P. ellipticum* has large black seeds which hang from the red pods on long funicles, but they have no aril at all: the seed-coat is thinly pulpy (sarcotesta) and is eaten by birds. In *P. clypeatum* there is no aril or pulpy seed-coat, and the pod opens only in the places where the seeds are, not in the intervals between the seeds, yet it still has the red colour and vivid red inner face (as in *Xylopiä*, *Sloanea*, *Sterculia*; &c.). Other species have indehiscent pods. The genus clearly shows a transition from the rare arillate pod to the common

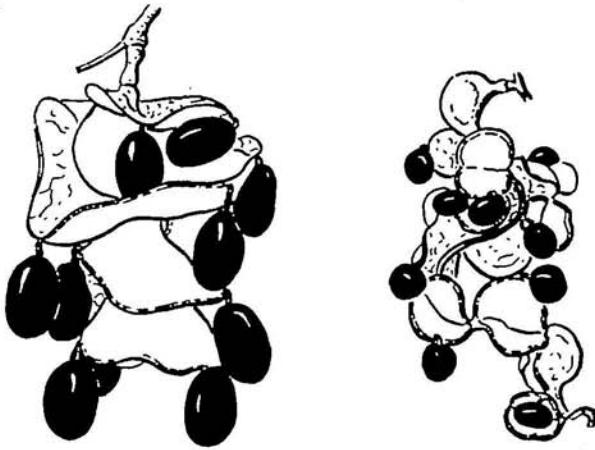


FIG. 10. Dehiscent red legumes of *Pithecellobium ellipticum* (left) and *P. clypeatum* (right), showing the black seeds hanging on persistent funicles (red in *P. ellipticum*) but without arils; the pods of *P. clypeatum* opening only in the parts containing the seeds ($\times \frac{1}{2}$).

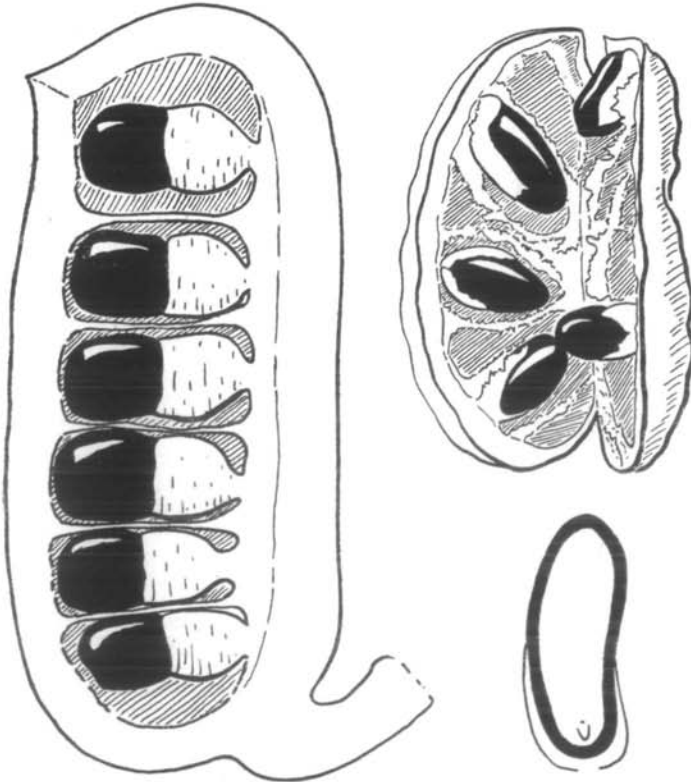


FIG. 11. A mature legume of *Pahudia cochinchinensis* (left, Caesalp.) with one valve removed, showing the red arillode and black seed ($\times \frac{1}{2}$) (from Pierre, Fl. For. Coch. Ch., t. 386); a dehiscent legume of *P. javanica* (right, $\times \frac{1}{2}$), and a seed with red aril in section ($\times 1$) (from Prain, Ann. Roy. Bot. Gdn. Calc., ix, 1901, t. 44).

Mimosa-condition with small dry seeds or the indehiscent state which cannot in any way be considered primitive and upgrade.

Caesalpinioideae. Well-developed arils occur in *Copaifera* and *Pahudia*, but commonly there is no aril and, instead, the funicle becomes fleshy as an arillode, e.g. *Intsia* (allied with *Pahudia*) and *Sindora*. *Tamarindus*, *Hymenaea*, and *Detarium* have woody, indehiscent pods but have distinct arillodes as well developed as in the dehiscent pods of *Intsia* and *Sindora*: but, in so far as

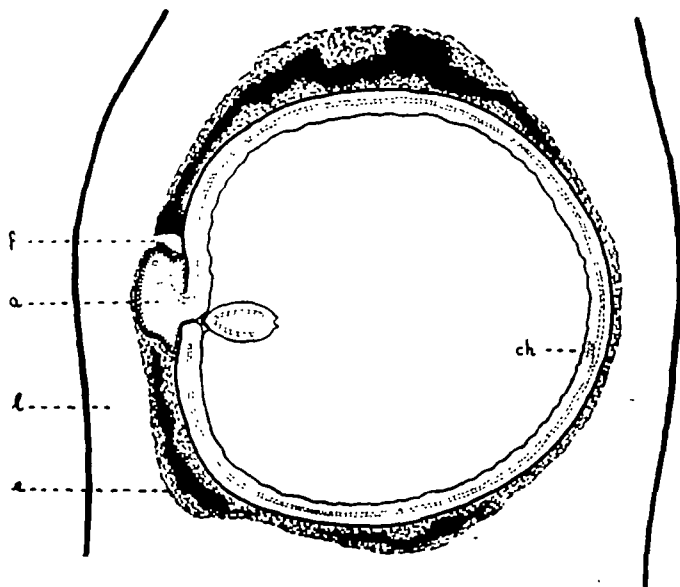


FIG. 12. A mature seed in longitudinal section in the legume of *Intsia bijuga* (Caesalp.), one cotyledon filling the space of the seed ($\times 2$). *a*, arillode; *ch*, chalaza; *e*, the mealy endocarp, partly stuck on to the seed and partly disrupted; *f*, funicle; *l*, the wall of the legume.

these arillodes are never exposed to view, they are functionless as such and cannot be upgrade. Indeed, in *Detarium*, the pod has become a drupe with a stone so hard that it must be cut with an axe, and in a nook on the inside of this stone the arillode is hidden: both pods and arils are clearly down-grade.

Arillaria robusta. This rare monotypic genus of lower Burma and Siam is the only member of the Papilionaceae to have a fleshy pod and a black seed entirely covered by a red pulpy aril. In all other respects the genus resembles the pantropical *Ormosia* with *c.* 50 species. *Arillaria* is, for me, not an oddity but a priceless relic, such as *Amphioxus* or *Ginkgo*, which proves what has been the ancestral fruit of the Papilionaceae. Indeed, *Arillaria* in this respect recalls those other three relic monotypic genera of the Caesalpinioideae, namely, *Tamarindus* (India), *Amherstia* (Burma), and *Lysidice* (South China, Indo-China), which show what an enormous variety of magnificent flowering trees must have become extinct in the evolution of the Caesalpinioideae.

Papilionaceae. Nevertheless, if they lack big red arils, still many *Papilionaceae* have small horny greenish, yellowish, or white arils surrounding the hilum as a rim, e.g. *Mucuna*, *Tephrosia*, *Cytisus*, or *Lathyrus*. Indeed, I have found this rim-aril present, if microscopic, in every *Papilionaceous* seed that

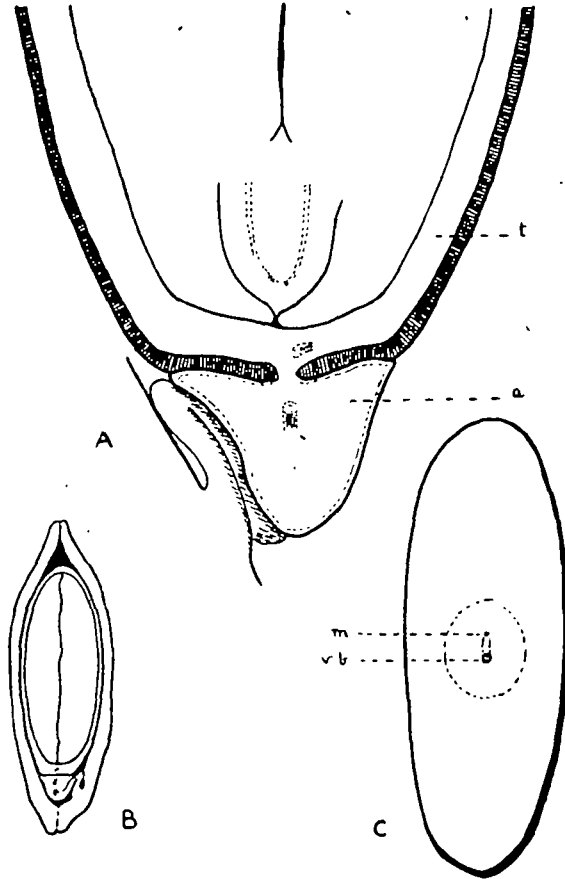


FIG. 13. Details of the seed of *Intra bijuga* (Caesalp.). A, the base of the seed in trans-median longitudinal section, showing the long recurved funicle, the pink, hard, corticated arillode, and the testa with its palisade. ($\times 6$); B, a ripe pod in transverse section, showing the seed *in situ* ($\times 1$); C, a mature, detached seed in hilar view, showing the faint arillode-scar ($\times 2$). *a*, arillode; *m*, micropyle; *t*, testa; *v.b.*, vascular bundle.

I have examined (with the exception of *Inocarpus*), and I conclude that every *Papilionaceous* hilum has, or had, a *rim-aril*, at least, if not a fully developed aril. In other words, the dry rattling pod is the modern shadow (very efficient, no doubt) of the fleshy arillate pod. The arillate seed has no survival-value in the modern *Papilionaceae*.

Adenathera, *Ormosia*, *Erythrina*, *Abrus*. These four genera, the first being Mimosoid, the others *Papilionaceous*, have hard red seeds which hang on the dry opened pods with persistent funicles, but no aril. Why? As with the

durian, so with these beautiful objects, there is an evolutionary history to account for their oddity. What is it?

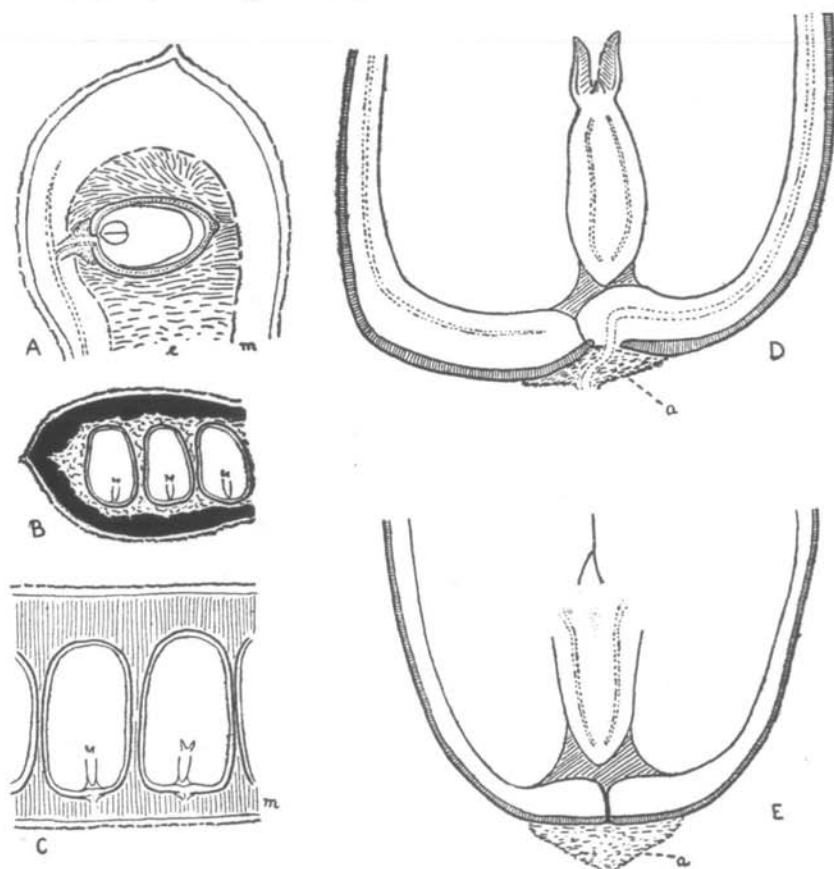


FIG. 14. Details of the seed and indehiscent legume of *Tamarindus indicus* (Caesalp.) showing the functionless white powdery aril at the base of the massive seed. A, the apex of a young legume with immature seed (the endosperm encroaching upon the nucellus), but with the aril developed, the cavity of the legume filled with the cottony-pulpy hairs of the endocarp e ($\times 2$); B, the apex of a ripe legume, showing the shell-like exocarp and the pulpy mesocarp contracted into a sticky brown mass on the seeds, leaving a gap (black) between them and the epicarp ($\times 1$); C, part of full-grown, but unripened, legume (in l.s.) showing the pulpy mesocarp m ($\times 1\frac{1}{2}$); D, E, the bases of full-grown seeds in median and transmedian longitudinal section, and the thick testa with external palisade ($\times 6$). a , aril; e , endocarp; m , mesocarp.

In *Adenanthera bicolor* and some species of *Ormosia* and *Erythrina* the seeds are partly black and partly red. The red part is that near the hilum and micropyle, the black being at the chalazal end. It seems that there has been a *transference of function* (see Corner, 1949): the aril has been lost (*Adenanthera*) or reduced to a rim-aril (Papilionaceae), but its redness has been transferred to the seed by invasion from the funicular end where the aril normally develops. Thus, these half-and-half seeds are a step between the black seed

with red aril and the red seed without aril. Black-and-red seeds, few and comparatively rare, are relics. But, in *Abrus*, an inversion seems to have occurred, perhaps as a mutation on a normal sequence, for the red part of the seed is chalazal and the black part is round the hilum. In *Erythrina*, too, there

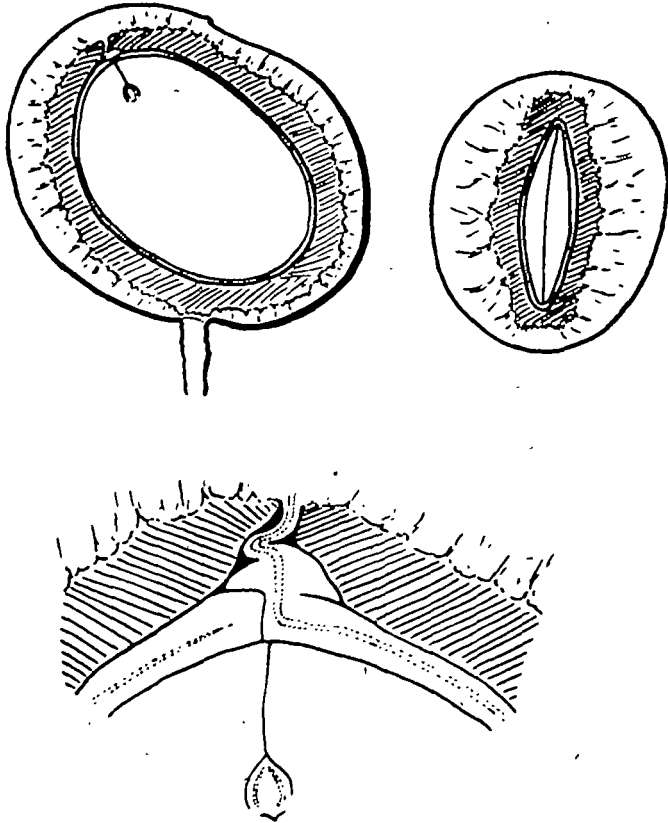


FIG. 15. The ripe drupe-like follicle of *Detarium senegalense* (Caesalp.) in median and transmedian longitudinal section, showing the hard stone (endocarp) with fibres entering the pulpy mesocarp, and the minute, pale-pink functionless aril inside the indehiscent endocarp (upper figures $\times 1$; lower figure $\times 5$).

are some anomalies. However, there is clearly something to be learnt even from bi-coloured seeds.

The red seeds, hard though they are, are eaten plentifully by strong-beaked birds—they catch the parrot's eye and, unless he cracks them, their seed-coat is so hard they will not germinate.

A parallel example is *Guarea* (Meliaceae) with red seeds but no aril, superficially exactly like the seeds of *Dysoxylon* (Meliaceae) which are wholly covered by a red aril. In each case the red colour is in the cuticle.

Arillodes. The fleshy red, pink, yellow, or white funicle is called an *arillode* (see Pfeiffer, 1891). It represents clearly the long Mimosoid and Caesalpinoid

funicle which has had transferred to it the function of the aril, while the aril has disappeared. Fig. 20 shows how easily the characters of the aril may be displaced and transferred. Thus, the aril develops in the Leguminous seeds

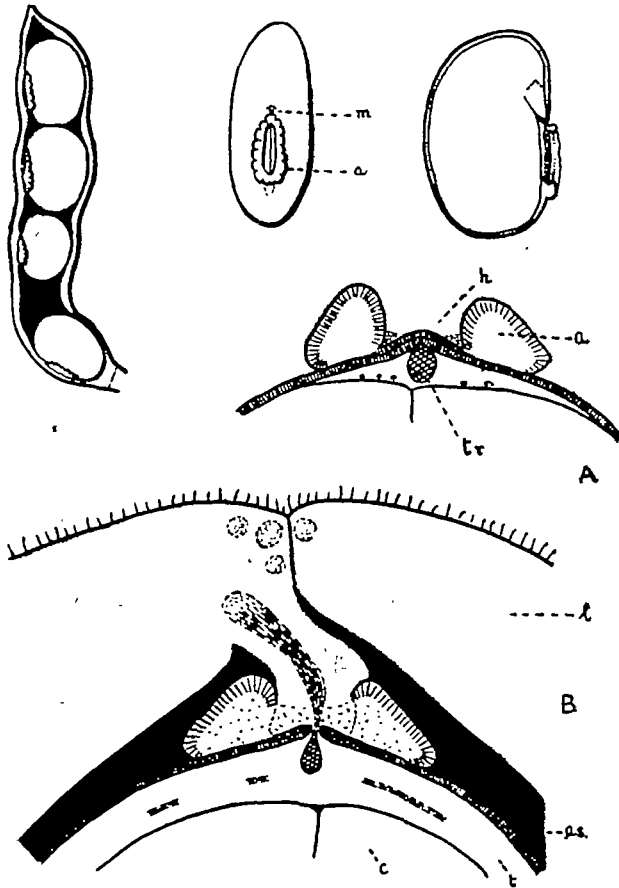


FIG. 16. A mature legume (one valve removed, $\times \frac{1}{2}$) and seeds (one in section, $\times 1$) of *Mucuna utilis* (Papilion.) showing the rim-aril surrounding the hilum (an oblong socket). A, a transverse section of the hilum of a ripe dried seed showing the rim-aril attached to the palisade of the testa by the counter-palisade of the hilum ($\times 7$); B, a transverse section of the hilum and funicle of a full-grown, but unripened, seed, showing the aril as the dilated head of the funicle, the vascular bundle of the funicle contacting the tracheide rod of the hilum, and the funicle breaking off in the aerenchymatous tissue in its head ($\times 7$). a, aril; a.s., air-space; c, cotyledon; h, hilum; l, the legume-wall; m, micropyle; t, testa; tr., tracheide rod of the subhilum.

from the region marked A. A slip in time or place of differentiation of the aril-characters may transfer them to C, which is the funicle, and then the arillode is formed. Thus, in *Acacia*, there are numerous transitions from arillate seeds with long funicles to seeds with arillodes (Fig. 21). Further displacement to the placenta (D) will produce the red pseudo-arillate placental sacs which

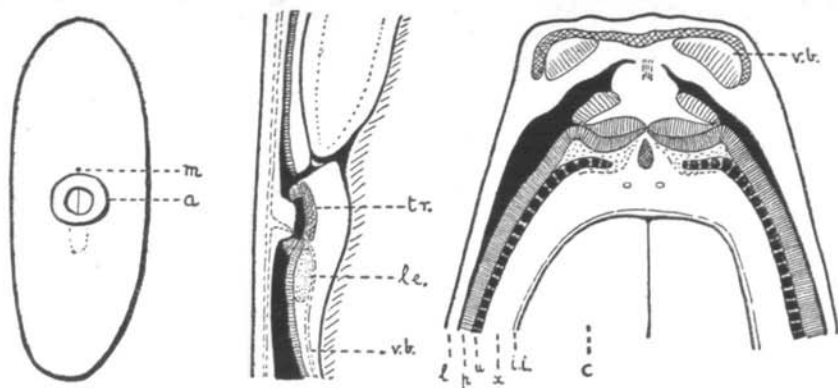


FIG. 17. Seed and hilar structure of *Desmodium triflorum* (Papilion.), showing a seed in hilar view ($\times 25$), and a longitudinal ($\times 25$) and a transverse section ($\times 50$) of the hilum of the seed still attached to the fruit-wall, the air-spaces being shown in black. The seed breaks from the funicle by rupture of the aerenchymatous tissue in the head of the funicle, the counter palisade of which remains fixed to the palisade of the testa in the hilum (see Fig. 18). *a*, rim-aril; *c*, cotyledon; *i.i.*, the inner integument; *l*, the wall of the legume; *le.*, the lens of thick-walled cells in the testa; *m*, micropyle; *p*, the external palisade of the testa; *tr.*, the tracheide rod of the subhilar tissue; *u*, the hour-glass cells of the testa; *v.b.*, vascular bundles; *x*, the cortex, or body, of the testa.

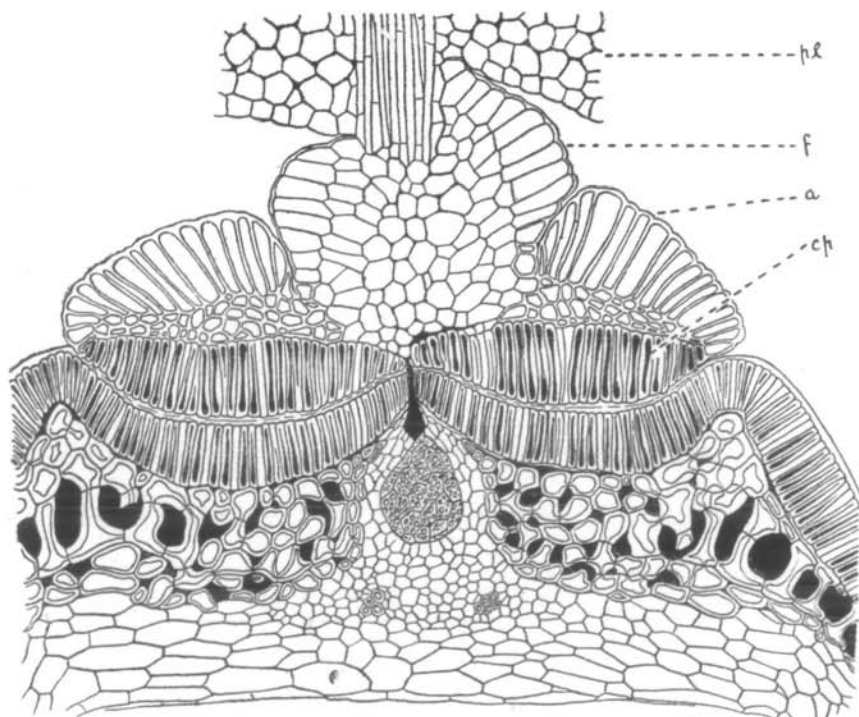


FIG. 18. A transverse section of the hilum of the seed of *Desmodium triflorum*, still attached to the funicle, as typical (in miniature) of the Papilionaceous seed with rim-aril ($\times 225$). *a*, aril (a single layer of elongate epidermal cells); *c.p.*, the counter palisade of the head of the funicle, stuck to the palisade of the testa; *f*, the funicle; *pl.*, the placenta; the subhilar tissue with tracheide bar and two recurrent vascular bundles; the air-spaces of the aerenchyma in black.

envelop the seeds of *Momordica* (Cucurbitaceae) or the red placental mush which covers the seeds of *Randia* spp. (Rubiaceae) and, possibly, *Pittosporum*: and finally, on displacement to the endocarp (E) the red pulp of berries or, changing red for yellow, the pulpy papaya which often has abnormal arillode-funicles, and, eventually, the tomato and the orange.

Red fleshy seeds. If the time or place of appearance of the characters of the aril is delayed, on the other hand, and deferred to region B (Fig. 20), they will become the functions of the seed-coat. Hence may well be explained the hard red and the pulpy red seed-coats in genera and families with arillate allies.

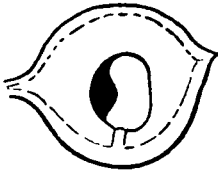


FIG. 19.

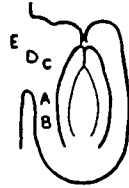


FIG. 20.

FIG. 19. A black and red seed of *Ormosia* sp. (Papilion., collection Black 48-2668, Inst. Agronomico do Norte, Brazil), with black chalazal part: the legume 1-seeded. ($\times 1$.)

FIG. 20. A diagram of an anatropous ovule. A, the region of the aril, B of the testa, C of the arillode (funicle), D of the placenta, and E of the endocarp.

As the red seeds of *Adenantha* follow, as it were, from the black seeds with red arils of *Acacia* and *Pithecellobium*, so the red seeds of *Iris foetidissima* and *Gloriosa superba*, on persistent funicles in dry loculicidal capsules, indicate that the Liliaceae had an arillate ancestor, as do also the red berries of *Dracaena*; and the proof is given by the relic-arils in *Colchicum* and *Asphodelus*. Similarly the red pulpy seeds of Magnoliaceae relate to the arillate seeds of Annonaceae, Dilleniaceae, and Myristicaceae, and the red pulpy seeds of many genera of Euphorbiaceae (*Sapium*, *Glochidion*, *Aporosa*, *Cheilosa*, *Baccaurea*) relate to the rare arillate seeds of the family, exactly as *Garcinia* (pulpy seed-coat) does to *Clusia* (arillate) in the Guttiferae. *Bixa* has both a red pulpy seed-coat and a rudimentary aril.

Three more relics. The genus *Delonix* (Caesalpinioideae) consists of two species of east Africa and peninsular India. This is a well-known relic, or Lemurian, distribution. *D. regia*, the Flame of the Forest, is limited to Madagascar and was nearly extinct when it was discovered in 1830. Now it survives widely, as an ornamental, because its brilliant red flowers present in their symmetry a primitive grandeur. The fruit has not yet been adequately described. It is a massive, dirty-brownish, sabre-like, dry pod, 40-60 cm. long, gaping slightly but enough to allow some 60 dull grey seeds, *c.* 2 cm. long, to hang out on persistent funicles for weeks until these have decayed. This sordid object, revived durianologically, becomes a scarlet sabre, 2 feet long, of black seeds with red arils, and shows what has disappeared from the face of the earth. If not, why does *Delonix* have this fruit?

The genus *Archidendron* consists of some twenty species in Austro-Malaysia. It is a Mimosoid genus characterized by having 5–15 carpels in the flower. It appears, therefore, to have the most primitive gynoeceum of the

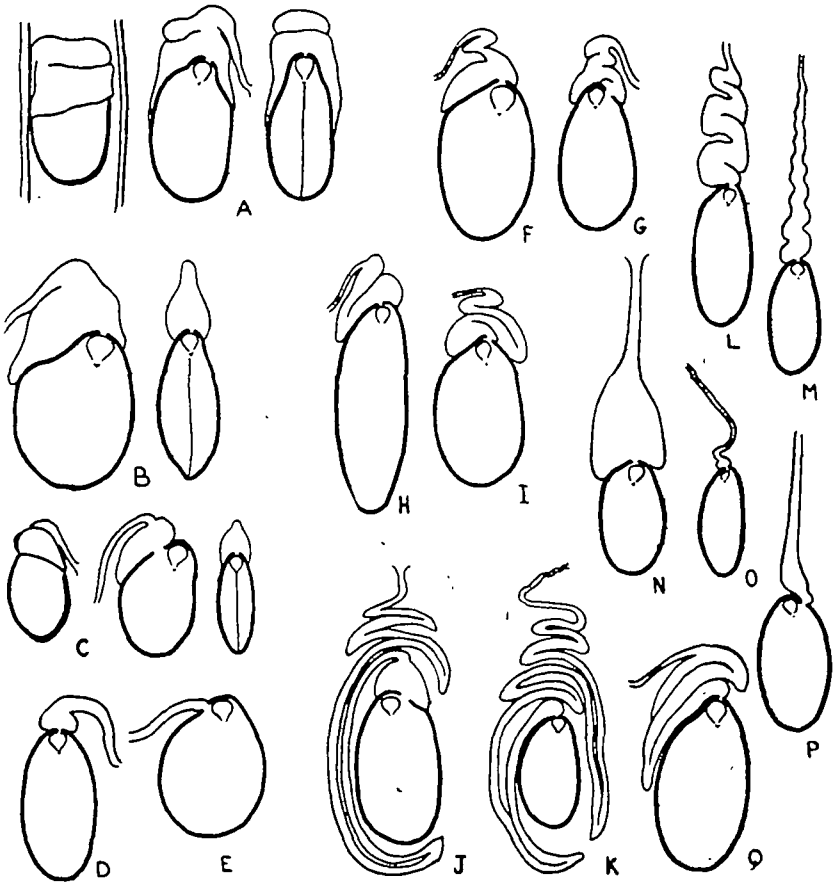


FIG. 21. Seeds of *Acacia* (copied from Mueller, Ic. Austral. Sp. Acac., 1888), mostly in median longitudinal section, to show the reduction of the aril or its modification into the arillode ($\times 1$). A, *A. colletioides*, 3 seeds (one in the pod), showing the well-developed aril, disappearing in B–E; B, *A. sessiliceps*; C, *A. coriacea*; D, *A. latifolia*; E, *A. praelongata* (with simple funicle); F–K, showing the elongation of the funicle and loss of aril; F, *A. phlebocarpa*; G, *A. Wallachiana*; H, *A. Luehmannii*; I, *A. lyriphloia*; J, *A. anceps*; K, *A. cincinnata*; L–Q, showing the development of the arillode, or fleshy funicle, with loss of aril; L, *A. stipuligera*; M, *A. aulacocarpa*; N, *A. retivenea*; O, *A. gonoclada*; P, *A. delibrata*; Q, *A. montana*.

Leguminosae. What kind of fruit does it have? From each flower, at least in the Australian species, develops a bunch of large, red, fleshy pods with yellow interiors and many large, black, shiny seeds hanging on long funicles (see the illustration, Bailey, 1916). There seems to be no aril, but, from the examples of *Sloanea*, *Durio*, *Sterculia*, *Acacia*, &c., I have no doubt that at least one species will be found with an aril. The fruit of *Archidendron*, as well

as the gynoeceium, is thus extremely primitive and is the living proof of the pathetic decadence in the beautiful *Delonix*.

The long funicle (1-6 cm.) for the dangling seed is characteristic of the Mimosoideae, especially, the Caesalpinioideae and the Swartzioideae, in contrast with the Papilionaceae. The Asiatic species of *Parkia* (Mimosoideae)

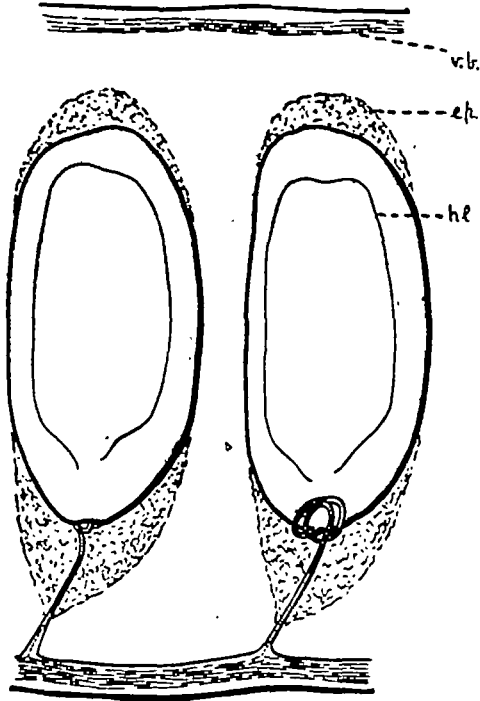


FIG. 22. Two ripe seeds of *Parkia javanica* (Mimos.) in the indehiscent legume, showing the long but functionless funicles ($\times 2$). *ep.*, the endocarp-pith; *hl.*, the heart-line of the testa (characteristic of many Mimosaceous seeds); *v.b.*, the vascular bundle on the dorsal side of the legume.

have indehiscent pods containing rows of large seeds with long, slender, coiled funicles. Why? The length of the fine funicle is useless and clearly a cause of the long delay in ripening of the pods by reducing the food-channel to the seeds. But, as a characteristic of the dangling arillate seed of *Acacia*, *Pithecellobium*, and *Swartzia*, it is readily understandable as a relic. The pods are dehiscent in some of the tropical American species of *Parkia* and the hanging seeds are eaten by parrots. Indeed, the red macaw appears to feed largely on a red-flowered *Parkia* of the Amazon valley.

The bunch of *Parkia*-pods at the end of the swollen clavate head of a long stalk resembles an elongate head of *Archidendron*: but, instead of being the production of a single flower, it is the multiple product of the unicarpellary flowers in the centre of the *Parkia*-capitulum. Thus *Parkia* represents the

state of *Archidendron* in the second degree, as a Composite-capitulum is a second-degree flower. Both are caused by intricate transference of function in embryonic structures. But it is interesting to see how this isolated genus of tropical trees with capitulate inflorescences of highly reduced flowers (the lower, even, sterile and 'attractive' as in the Compositae) retains the essential characters of the cluster of arillate pods, as a primitive determination.

Conclusion. The primitive Leguminous fruit was a cluster of large, many-seeded, red fleshy pods with black seeds, each covered by a red aril and hanging out on a long funicle. Perhaps the pods were spiny, a half to one metre long, with some 50 seeds, and may even have been held erect (cf. *Pentaclethra*).

Corroboration. The only family which is at all nearly related with the Leguminosae is the Connaraceae. Many Connaraceous genera have red pods and black seeds with red or yellow arils (mostly covering the lower part of the seed). Some genera, as *Cnestis*, have 5 carpels thus developed from the flower, and their fruits resemble those of *Sloanea* and *Sterculia*. Perhaps the Annonaceae are related: at least, in *Xylopia* one finds the same apocarpous polycarpellary ovary developing a cluster of arillate follicles. But the evidence goes to show that the Leguminosae are one of the most isolated series of flowering plants and should constitute by themselves one of the main subdivisions of the Dicotyledons.

OTHER EXAMPLES

Bocconia. I saw near Bogotá, in 1947, across a valley some pinnate leafed treelets resembling palms. Dr. Enrique Perez-Arbelaez, the Colombian botanist, told me that they were saplings of the Papaveraceous genus *Bocconia*, the two species of which develop into trees up to 10 or 15 m. high. I said on reflection, at first hearing of a tree-poppy, that it must have rather large black seeds with red arils, though I was acquainted only with the minute seeds of *Papaver* and its allies. Dr. Perez-Arbelaez remembered that it had; and, shortly, we found the fruits. They are rather small, yellowish, fleshy, loculicidal capsules, c. 12×7 mm., containing 1 (rarely 2) black seeds, 7×3 mm., with a red aril round the base: the seed hangs from the persistent hoop-like replum (Fig. 23). The deduction was proved, and affords one of the most striking evidences of the Durian theory that I have met. One could have argued back from the minute arils, or strophiolles, in the seeds of *Chelidonium* and Fumariaceae, but *Bocconia* is the living relic.

Aesculus. The spiny, loculicidal, fruits of the Horse-chestnut (*Aesculus*), with large brown seeds and thick white endocarp, resemble in so many ways a small durian that, in 1946, I carefully studied developing fruits to see if there was a trace of an aril. I found none, but Dr. Dugan, Professor of Botany in the University of Bogotá, informed me that the Colombian and Central American genus *Billia* had arillate seeds, though its fruits were spineless.

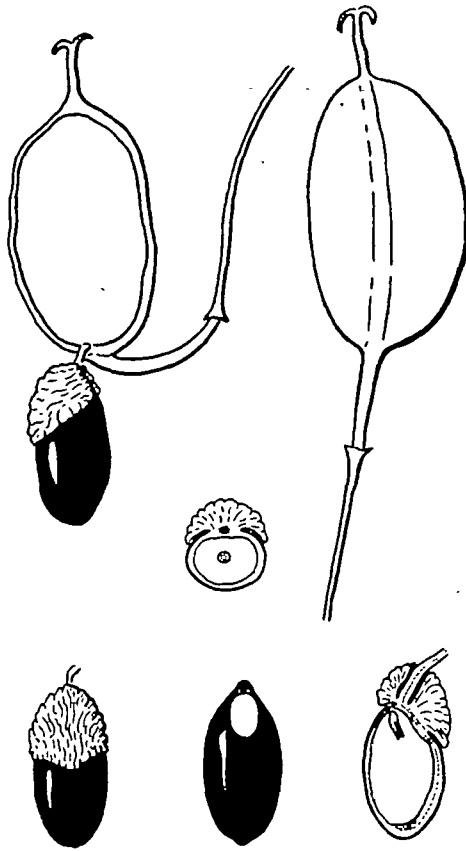


FIG. 23. Fruits and seeds of *Bocconia frutescens* (Papaveraceae) ($\times 3$): an indehiscent and a dehiscent fruit with the valves fallen from the replum and the single seed dropped out on the funicle: the black seeds with red aril, the central lower figure showing the white patch where the aril is attached.

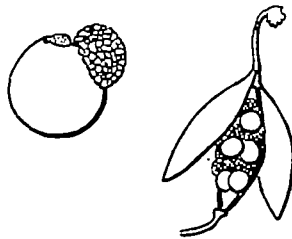


FIG. 24. Fruit and seed of *Corydalis lutea* (Fumariaceae), showing the rudimentary aril, mag. (from Payer, *Traité d'Organogénie*, 1857, t. 50, f. 14 and 15).

PRIMITIVE ANGIOSPERMS

For the immediate ancestors of modern flowering plants, I postulate, therefore, massive red follicles or capsules with many large black seeds with red arils. It is possible from this startling premiss to make the following deductions:

1. *Trees*. Such fruits must have been borne on massive twigs. No herb could produce a durian, a nutmeg, or an Annonaceous fruit, far less the Leguminous cluster of arillate pods. Therefore it must be inferred that these ancestral flowering plants were *trees*.

2. *Tropical*. Large arillate seeds have no power of dormancy or of withstanding desiccation and cannot survive outside tropical and sub-tropical rain-forests. Therefore the ancestors must have been *tropical trees*.

3. *Compound leaves*. Tropical trees with massive twigs are typically those with massive, compound spirally arranged leaves, whether pinnate or palmate, and in such trees there are always transitions to simple leaves. Therefore these ancestral tropical trees must have had *compound leaves* (pinnate in the first place, for the palmate is the pinnate with reduced axis).

Such is the present-day condition of many trees with arillate fruits borne laterally on the current shoots, that is, in the leaf-axils, e.g. Meliaceae, Sapindaceae, Leguminosae, Connaraceae, *Sterculia*, *Bocconia* (*Aesculus*).

4. *Monocauly*. The following two complementary principles occur with such regularity in the construction of flowering plants as to appear susceptible of mathematical treatment:

a. *Axial conformity*. The stouter, or more massive, the axis in a given species, the larger and more complicated are its appendages. Thus the stouter the main stem, the bigger the leaves and the more complicated their form, e.g. saplings of trees (some with compound leaves while the branches have simple leaves, as in *Artocarpus*, *Scaphium*, and some Proteaceae), or the stems of herbaceous plants as *Nicotiana* and *Helianthus*, or rosette Umbelliferae and Compositae with the large basal leaves diminishing in size and form to bracts.

b. *Diminution on ramification*. The greater the ramification, the smaller become the branches and their appendages, e.g. in *Solanum*, the leaves, inflorescences, flowers, fruits, and twigs become smaller as the ramification increases; and, in *Carica papaya*, the scarcely branched female inflorescences have a few large flowers whereas the highly branched male inflorescences have many small flowers.

These principles are needed to understand what form a primitive angiosperm must have taken in order to produce the enormous fruiting mass which must be postulated, and to understand how the modern angiosperms, highly ramified with slender appendages, have thence been evolved. The two principles, it may be noted, do not apply to algae, having more or less wholly assimilatory surfaces, but are new principles of Xerophyton giving to land-plants their regular diminishing, not expanding and thallus-like, appearance.

Now, reduce a pinnate-leaved flowering tree to an undivided stem, that is, its sapling stage, and turn the apical bud into a single terminal flower. The result will be clearly a Cycad-like tree with a rosette of sterile and fertile floral leaves, and such must have been the appearance of the proto-Leguminosae with the terminal rosette of gigantic arillate follicles. Indeed, this proto-Leguminous follicle so closely resembles the Cycad megasporophyll that it is necessary merely to regard the red pulpy seed of *Cycas* as a transformed arillate seed (as of *Taxus*) and to incurve the sporophylls to form a follicle (as by the common process of precocious maturity) in order to arrive at once at the proto-Leguminous follicle.

Now, reverse this procedure. Make the flower axillary and it will become smaller, though still massive (e.g. the flowers of *Magnolia*, or the female flowers of *Carica*). Then ramify the axillary buds to produce highly branched inflorescences, and the flowers will be yet smaller (as in the cymes of Annonaceae, or the male inflorescences of *Carica*, some of which still retain a single massive terminal female flower). Finally, ramify the stem and produce ultimately the very small flowers of the panicles of Sapindaceae, Meliaceae, Mimosoideae, and other modern trees with twigs which are slender compared with their sapling stems. The modern solitary Leguminous carpel is, thus, the still more precociously matured proto-Leguminous carpel fitting the bud-character of the relatively small modern Leguminous flower borne on an ultimate ramification of high degree: and the modern solitary Leguminous follicle represents the Cycad megasporophyll developed *post*, instead of *pre*-, fertilization (see Corner, 1949), as all that the relatively slender axis can bear in the way of fruit. As the Cycad megasporophyll unfolds, the Leguminous follicle ultimately dehisces, and, as the Cycad megasporophyll must be borne on a massive stem; so too the peduncle of the Leguminous flower thickens and matures *post*-fertilization. Thus, it can be understood that, to fulfil their hereditary requirements, fertilized ovules had to enlarge into seeds and fruits had to enlarge and dehisce: and so, too, at the other extreme, it can be understood how the modern Compositae, for example, have escaped this hereditary yoke, the achene showing practically none of the features of the follicle and capsule. Seed-structure and seed-demands will be found more and more important in the study of flowering plants.

By arguing back to the single stem, or monocaulous state, with huge open terminal flower, as the necessary progenitor of the huge fructification demanded by the Durian theory, one arrives not at a figment but at a reality, the well-known *Cycas*, which has so often posed as the angiospermous prototype. Now, it can be seen how, without entering into particular detail, the modern Dicotyledonous tree may well have been evolved from this prototype by ramification in all parts, leading to the diminution in the size and the complexity of structure of branches, leaves, flowers, fruits, and seeds, and by relegation of flowers to axillary buds: but the fruit tends to revert to the ancestral form of the Cycad megasporophyll because the seed, as the dispersal organ, is the conservative and overruling factor in reproduction.

Typically the Cycad is devoid of internodes. The large leaves dominate the stem-apex and the stem itself, as in the tree-ferns. It would seem that the tendency to produce internodes is a new process of juvenescence running through the evolution of angiosperms and ending in the appearance of the herb, that is, the tendency to prolong the seedling phase and so to produce elongated stems at the expense of the development of the leaf-base, rather than the leaf-rachis. The Cycad-phase of angiosperm-evolution, however, is clearly shown with the addition of incipient internodes in the growth-form of *Carica papaya*, palms, pandans, and the saplings of trees with compound leaves in general (Araliaceae, Caesalpinioideae, Bignoniaceae, and even by such Euphorbiaceae and Annonaceae as *Phyllanthus* and *Drepananthus* the phyllomorphic ramuli of which retain this ancestral trait to the second degree of branch-systems with simple leaves, the whole resembling compound leaves). The terminal inflorescence of pandans and of Bignoniaceous trees, enforcing sympodial growth, appears as a primitive character, in that the axillary inflorescence has not been evolved. Similarly, the massive rosette of *Agave* with its terminal inflorescence and monocarpic habit appears as an immediate derivative of the Cycad form and more primitive than the ramified trees of *Dracaena*. Among palms, the sequence can be read from monocarpic palms, with huge terminal inflorescences (*Corypha*, *Metroxylon*) and immense leaves, to highly branched palmllets (*Bactris*, *Geonoma*, *Pinanga*) with slender stems, small leaves, and lateral inflorescences. It can be seen, therefore, that neither has the ramification of the stem proceeded *pari passu* with that of the inflorescence, nor have these factors been linked necessarily with the transference of the terminal inflorescence or flower to the lateral position: thus, no Monocotyledon really corresponds with *Magnolia* or *Nymphaea* in having massive, solitary, axillary flowers, although there are many higher analogues such as sympodial trees or unbranched rosettes with terminal inflorescences (*Agave*, *Lobelia*).

Monocauly, therefore, and monocarpy appear not as newly acquired peculiarities of modern plants but as relics of the normal features of the early angiosperms. Conversely, the highly branched tree with slender twigs, simple leaves, and highly branched inflorescences of very small flowers, typical of the Amentiferae, appears in its true light as a modern derivative. Furthermore, the apparent oddities of flower-size, inflorescence, and sex in *Carica* are seen to represent a phase in the evolution of the axillary inflorescence which most other Angiosperms have undergone.

Note. Can *Carica papaya* be induced to form a terminal flower? Its naked bud is open for experiment, and its massive stem offers the possibility of producing a proto-angiospermous flower, by reversion, at its apex. It is a very generalized plant of primitive habit, surviving, no doubt, by its chemical virtues rather than its structural.

5. *Leptocauly*. I use this name to indicate the modern tree with relative slender primary axis and branches in contrast with the *pachycaulous* Cycad. Increasing ramification, the evolution of the simple leaf, and the development

of internodes are the basic features of the modern tree. The slender twig, with long internodes, provides length, or height, with less weight, and leads not only to the rapid overtopping of the old, clumsy pachycaul with massive and slow-growing branches, but outstrips it also geographically by providing the leptocaul with better powers of resisting drought or cold, if only because the small buds are more numerous and more easily made and the damaged twigs more easily substituted. The leptocaul, or modern tree, thus comes to dominate in height and spread and distribution the ancient pachycaul, forming the modern forests, while the palms, pandans, *Carica*-like trees, and so on, just as the Cycads and tree-ferns, are relegated to subordinate and, as their constitutions still require, mainly tropical stations.

6. *Cauliflory*. If a highly advanced leptocaul retains the old massive flower and fruit, as the Durian theory demands, then its flowering and fruiting must be postponed for dormant buds on matured wood, the slender leafy twig being too precocious. Thus are introduced ramiflory and cauliflory according to the degree of ramification and relative physiological immaturity of the twigs and branches. Most species of *Durio*, *Xylophia*, and *Myristica*, for example, with slender twigs and simple leaves in appanate sprays, but with massive arillate fruits, are ramiflorous and cauliflorous: and, even, pinnate-leaved trees with slender twigs and appanate foliage, as *Swartzia* or *Lansium*, but with massive arillate fruits, become ramiflorous or cauliflorous.

The *tropical* phenomenon of cauliflory receives, therefore, a simple and natural explanation as the instance of trees which have evolved the modern twig but have retained the old habit of the arillate fruit. This massive fruit implies, however, a massive flower or inflorescence or, at least, a physiological massiveness as an advanced state of maturity of the tissues before the reproductive organs can be developed: and, while the arillate fruit may have passed on to the indehiscent drupe, berry, or nut, either the massive flower or inflorescence or the physiological requirements remain to enforce cauliflory, as in *Annona*, *Polyalthia* (Annonaceae), *Averrhoa* (Oxalidaceae), *Diospyros* (Ebenaceae), or *Theobroma*.

An instructive example is afforded by *Artocarpus*. *A. amisophyllus* has the largest, spirally arranged, pinnate leaves and the most massive twigs of the genus, and its large fruits are axillary. *A. incisus* (Breadfruit) has almost as massive, pinnatifid leaves and twigs, but the fruits tend to mature on the bare parts of the twigs from which the leaves have fallen. *A. heterophyllus* (the Jack-fruit), however, has slender twigs with simple leaves tending to the modern horizontal spray and is cauliflorous.

Averrhoa, on the other hand, seems exceptional. *A. bilimbi* has massive twigs and is cauliflorous, while *A. carambola* has slender twigs and more or less axillary fruits. As a rule, however, it is not difficult to decide *a priori* from the twig and the flower and fruit whether a tree is cauliflorous.

7. *Megaspermy*. Even the ramiflorous trees of modern form cannot escape from the rain-forests because of their large, quick-germinating seeds. For the colonization of the drier tropics and the temperate regions one must expect

clear that a study of the physiological thresholds for flowering and fruiting in tropical trees should be undertaken and, being cognate with bud-grafting for early fruiting, it is a matter of practical importance (a search of tropical agricultural-horticultural literature may reveal some published information already). It should be borne in mind, too, that the leptocaul twig, necessary for the microspermous fruit, is essentially a precocious organ developed at the expense of previous assimilation and, thus far, resembles the seedling; and that the herb is also little more than a seedling matured at low threshold.

9. *Conclusion.* The immediate ancestors of modern flowering plants must have been sparingly and sympodially branched, soft-wooded, tropical trees of low or medium height, with massive twigs bearing spirally arranged compound leaves without distinct internodes, and reproduced by large arillate seeds borne on massive red follicles, succeeding terminal flowers or inflorescences. The more remote ancestors appear to have been monocarpic and monocaulous, with the Cycad-habit.

No such plants now exist, but many carry traces of this ancestry. The primitive form is shown, I think, in the habit of palms, pandans, tree-Senecios, tree-Lobeliaceae, tree-Euphorbias, tree-Paeonies, bottle-trees (*Adansonia*, *Brachychiton*), Cacti, *Carica*, Araliaceae, and so on, even to brussels sprouts, which owe their curious appearance to this primitive form: in fact, almost any 'funny tree' is funny because its form is primitive and, now, unusual. As a corollary, woody parenchyma appears, not as a modern feature as maintained by many wood-anatomists, but primitive in accordance with the habit of the early angiosperm (e.g. *Cecropia*, *Macaranga*, *Carica*, &c.).

EFFECT ON ANIMALS

In modern tropical forests, perhaps 50 per cent. of the trees and woody climbers have edible fruits. Of this portion, perhaps 90 per cent. have berries and drupes and only 10 per cent. have arillate seeds or pulpy seed-coats. But these 10 per cent. are certainly the most nutritious because the aril or pulpy testa is rich in oils, carotinoids, and other complex substances.

In the ancestral forests of early flowering plants, as the Durian theory implies, all the trees must have been hung with red lanterns of arillate black seeds, contrasting vividly with the green foliage, and there must have been much more food for animals in the trees. Imagine timeless forests consisting wholly of durians, instead of less than 1 per cent. as in Malaya now: imagine forests filled with red chestnuts and pulpy seeds: and the effect that the modernization of forests must have had on forest herbivores can be seen. In the beginning of the forests of flowering plants there was every inducement to climb, jump, and fly among the low stout branches after the fruits, and the roughly simultaneous origin, therefore, of flowering plants, birds, and mammals does not appear extraordinary. But, as the microspermous trees evolved and heightened and complicated the forests, there was less to eat both quantitatively and qualitatively. Modern monkeys, so isolatedly various, are only relics, as the fossil record is proving, of those which feasted in the early

forests. Mammoths grew extinct, no wonder, with herbs instead of durians to feed upon: and elephants, too, in the declining orchards. Parrots and squirrels, on the other hand, have the means of dealing with the modern nuts and seeds. Sloths hang on with leaves: monkeys become omnivorous: but fruit-eating birds and bats survive on the remaining arils and pulpy derivatives. These arils, so chemically rich, may have been an important speciating factor, for the converse effect can be seen in the poverty of variety of fruit-eating animals in the vast forests of oak, beech, pine, and hazel in the north temperate region.

Note. This heightening of the forest by the modern tree gave the Primate-environment. The development of the microspermous habit gave the optimum herbivorous environment, which brought the Primate back to ground.

EFFECT OF ANIMALS ON FRUITS

Armour. High pressure of animals leads to the eating of immature fruits and consequent waste of immature seeds. More loss is suffered to-day by tropical trees from attacks of squirrels, bats, honey-bears, and monkeys, which strip the immature fruits, than from insect-borers or disease. One can be sure that, from an early state in the evolution of flowering plants, the immature fruit must have been protected. There are three general means.

Firstly, there is camouflage by greenness among the foliage: that is to say, the reproductive mechanism of the flowering plant has two attractive stages, one for pollination and the other for seed-dispersal, and between them comes an inconspicuous stage. Large fruits, however, cannot be concealed, though the early arboreal vertebrates may have been short-sighted, and other means must be found.

Secondly, there is mechanical protection such as can be provided by a woody fruit-wall (which cannot become effective until the fruit has stopped enlarging), by persistent sepals, by a dense coating of hairs, and, particularly, by an armour of spines which can become effective by the hardening of the spine-tips as soon as the fruit begins to be conspicuous in size.

Thirdly, there is the chemical method of unpalatability by acidity, astringency, and poison. Nowadays this method is clearly the most effective, as it is the most universal: in fact, if they were not so protected, most modern fruits could not survive in the tropical forest.

There is much evidence, however, which suggests that the armour of spines has been an important and primitive factor. Just as the aril is comparatively rare among modern flowering plants, so are spiny fruits: and the association of spines and arils is so close as to imply that the armour of the durian is as characteristic as its aril. Where spiny fruits occur, arils may be expected in the same genus or in related genera and vice versa.

Examples: *Victoria*, *Rheedia* (Guttiferae), *Sloanea* spp. (Tiliaceae and other non-arillate genera), *Cnestis* (Connaraceae): *Nephelium*, *Xerospermum*, *Paullinia* (sect. *Castanella*), *Schleichera*, *Lepisanthes* (Sapindaceae, with the non-arillate *Paranephelium* of Malaya resembling a small durian); *Aglaia* with rudimentary spines (Meliaceae, but *Flindersia* with muriculate fruits and winged seeds as the transition

between the durian-type and *Swietenia*); *Sindora* (Leguminosae): *Carpotroche*, *Mayna* (Flacourtiaceae); *Rinorea*, *Alsodeia* (Violaceae, ? non-arillate); *Monordia*, *Cucumis*, *Sechium*, and *Echinocystis* (Cucurbitaceae, with pseudo-arillate seeds); *Tabernaemontana* spp. (Apocynaceae); *Ricinus*, *Mallotus* (Euphorbiaceae): *Geanthus*, *Amomum*, *Globba* (Zingiberaceae): *Canna*.

The presence of spines on the fruits of *Allamanda* (Apocynaceae), *Datura*, some Bignoniaceae, *Melastoma*, *Galium*, *Ranunculus*, and *Dichaea* (Orchida-

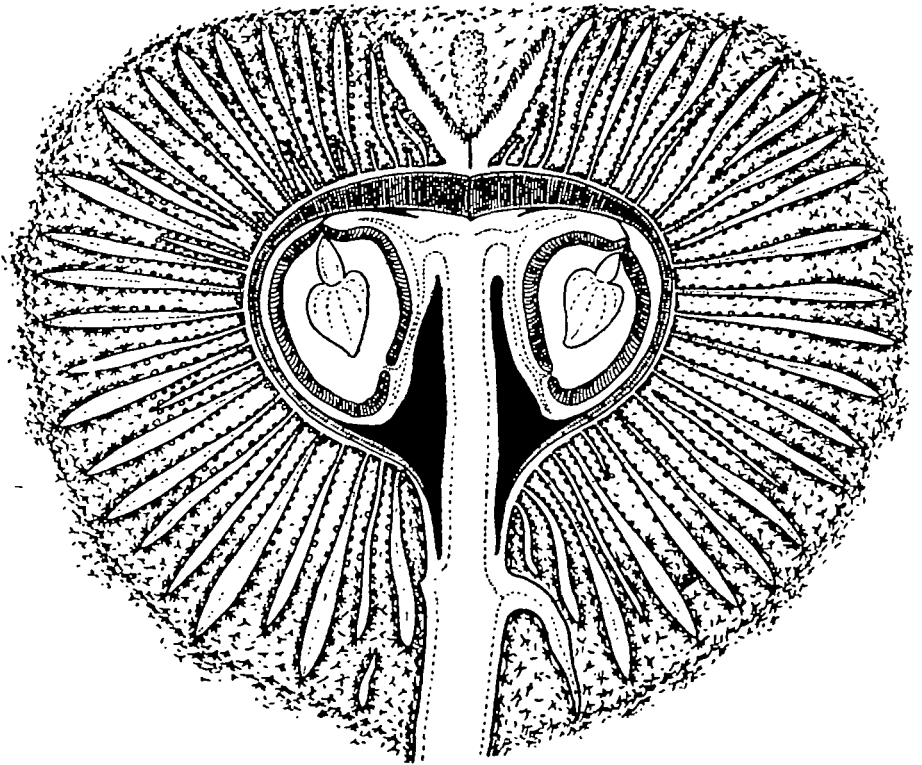


FIG. 25. The ripe, as yet indehiscent, fruit of *Mallotus barbatus* (Euphorb.) in longitudinal section, showing the rather stiff, irritant, stellate-hairy, spines and the seeds with pulpy sarcotesta (outer integument), hard palisade layer of the inner integument, and a rudimentary aril on the micropylar side of the funicle: illustrating the complexity of spinous fruits ($\times 6$).

ceae) are, therefore, suggestive as relics, exactly as with *Bixa*, which has a rudimentary aril and pulpy testa.

The absence of spines from the Dilleniaceae and their development of the persistent sepals instead, suggests that this family may have had from a very early stage a different mechanism for protecting the arillate fruits.

Now, as far as I have discovered, the spines on fruits are definite outgrowths developing immediately under the primary and larger peltate or glandular hairs of the ovary (glandular hairs being juvenile modifications of the peltate). Peltate scales are a Pteridophyte-feature, and thus spininess is related with yet another archaic character. Spininess, indeed, typifies the petioles of many tree-ferns (*Cyathea*).

The imbricating, backward-pointing scales of the Lepidocaryoid palms develop from the peltate scales of the young ovary and appear as the modern

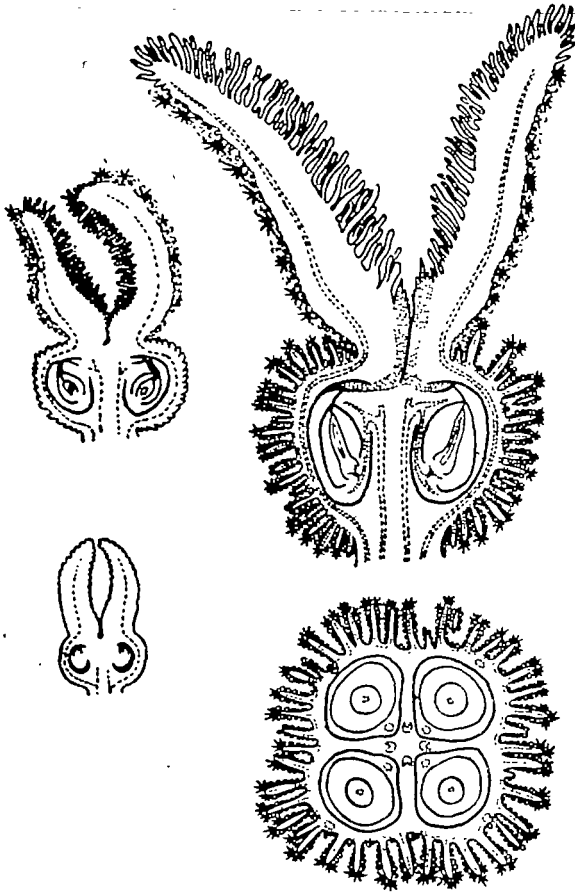


FIG. 26. Developing flowers of *Mallotus barbatus* (Euphorb.) to show the early origin of the spines of the ovary beneath stellate hairs, the basipetal development of the styles and ovary, and the oleaginous conducting tissue (dotted) of the stigmas leading to the aril-flap over the micropyle (in the right-hand mature flower): the spines of the ovary with both glandular hairs (on their stalks) and stellate hairs (at their tips) ($\times 15$).

armour of their modern drupe, adapted from the spiny arillate capsule of the proto-Palmaceae.

The spines of *Annona muricata* and *Rollinia* (Annonaceae) appear in the same light, as transferred to the carpel-points. In the case of *Artocarpus*, the function of the aril is transferred to the ovary-wall and that of the spines to the perianths of the minute flowers, thus developing a durian-fruit from an inflorescence. *Pandanus* is comparable. In the case of *Castanea*, the protective function has been transferred to the spiny bracts, and the Spanish-chestnuts

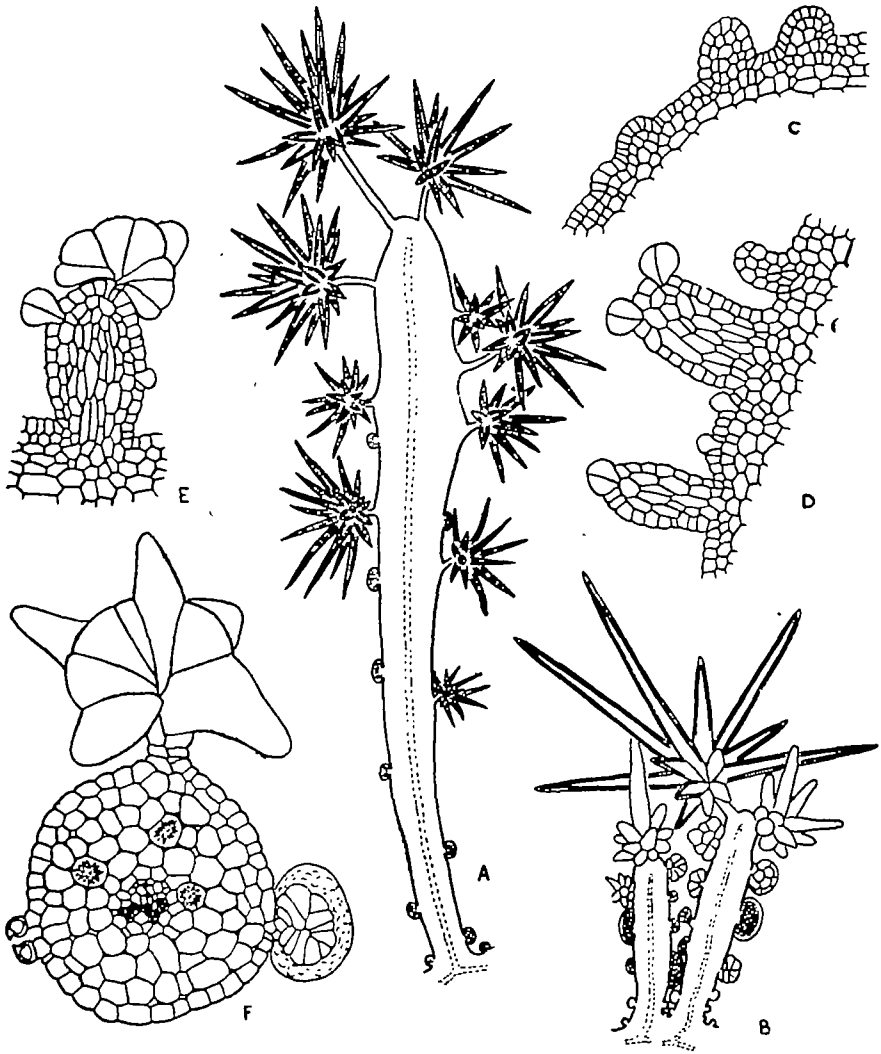


FIG. 27. The spines of the ovary (B) and fruit (A) of *Mallotus barbatus* (Euphorb.), showing the stellate hairs at the apex and upper part of the spine and the glandular sessile hairs in the lower part (developed basipetally after fertilization) (A $\times 25$; B $\times 40$). C-E, stages in the basipetal growth of the spines on the ovary, developing stellate hairs at their apices ($\times 225$). F, a transverse section of a spine of a half-grown fruit, showing a young stellate hair, a glandular hair, a stoma, and the central vascular bundle ($\times 225$).

appear as Horse-chestnuts in the second degree, from inflorescences instead of individual flowers. Certainly *Artocarpus* and *Castanea*, when correctly interpreted, will prove to be the key-genera to the evolution of the Moraceae-Urticaceae and the Cupuliferae, just as *Durio* is to the Bombacaceae-Malvaceae.

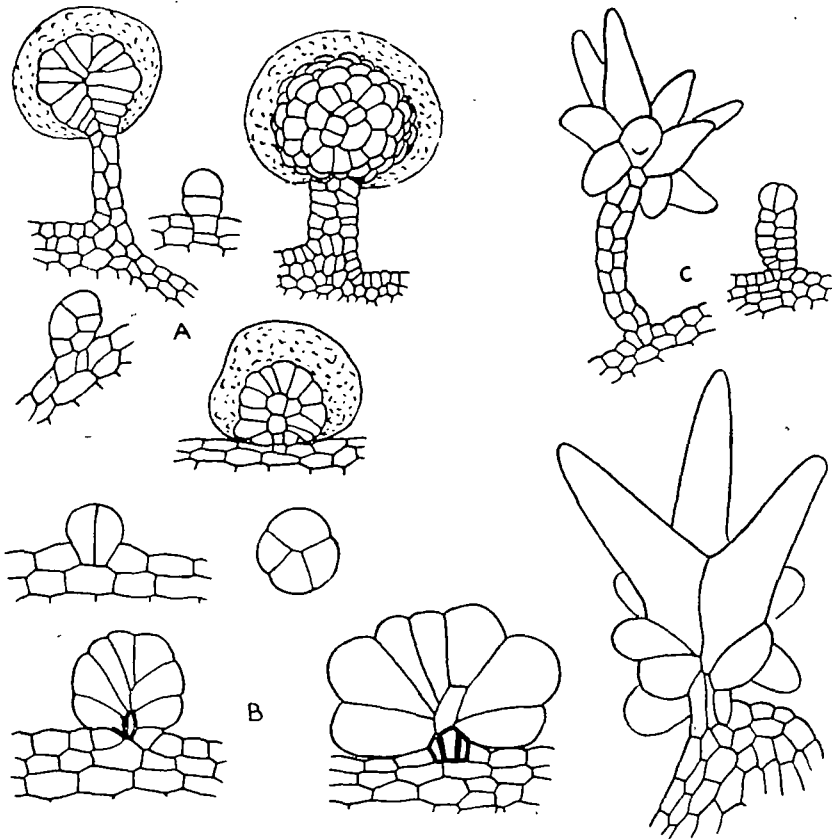


FIG. 28. Developing hairs on the spines of *Mallotus barbatus* (Euphorb.), showing how stellate, glandular, and, by simplification, all other hairs can be derived from peltate hairs initiated by 4 longitudinal cell-walls in an enlarged epidermal cell: A, sessile and stalked glandular hairs ($\times 225$); B, sessile and sub-sessile, young stellate hairs ($\times 400$); C, stalked, stellate hairs ($\times 225$).

In its arillate spiny capsule, large seeds, and peltate scales *Durio* appears as the most typical modern representative of the primitive angiosperm-fruit. *Durio* is modern, however, in its tree-habit with slender twigs and sprays of simple leaves: hence, its ramiflory. In contrast, the well-known Horse-chestnut (*Aesculus*) appears as the best temperate outlier of the tropical proto-angiosperms. Its massive, spiny capsules with large, but non-arillate, seeds are terminal on massive shoots with compound leaves, the massiveness of the shoot (well known in botanical classes because of the large bud) preventing

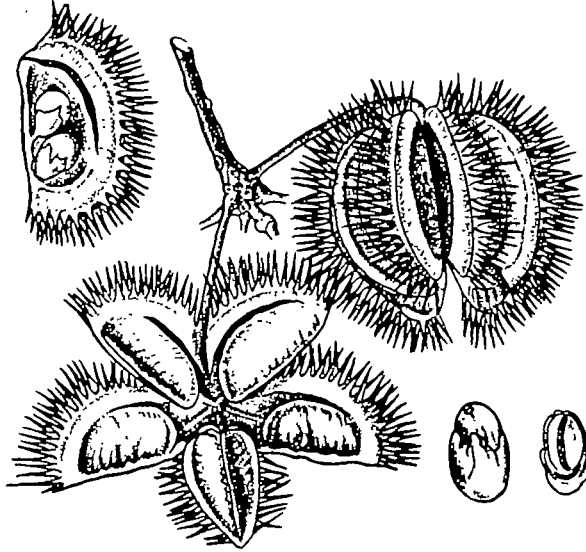


FIG. 29.

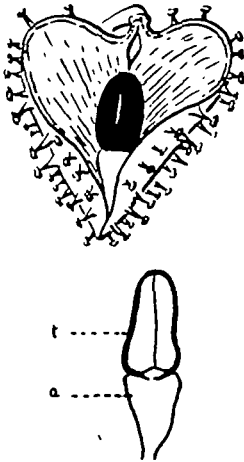


FIG. 30.



FIG. 31.

FIG. 29. The spiny fruit of *Sloanea hongkongensis* (Tiliaceae—Elaeocarp.), with arillate seed ($\times \frac{1}{2}$) (from Hooker's Ic. 11. No. 2628, Ser. IV, vol. vii, pt. ii, 1900).

FIG. 30. The spiny 1-seeded legume of *Sindora* sp. (Caesalp.), with black testa (*t*) and red arillode (*a*), the spines resin-tipped ($\times \frac{1}{2}$).

FIG. 31. The dehiscent, spirally coiled, brownish legume of *Acacia auriculaeformis*, with black seeds dropping down on yellow waxy funicles ($\times 1$).

ramiflory. *Aesculus* is a key-genus to the Sapindaceae–Aceraceae, and shows the utmost geographical possibilities of the mechanism of the primitive angiosperm.

To the attributes of the primitive angiosperm there must, therefore, be added peltate scales and spiny fruits, and both characters open further vistas of inquiry among the families of modern flowering plants, e.g. the stellate hairs as relics of peltate scales (as in *Solanum*, where the hairs help to distinguish modern, glabrous or simply hairy, slender species as *S. dulcamara*, *S. nigrum*, and *S. parasiticum* from massive *Carica*-like species as *S. quitoense*

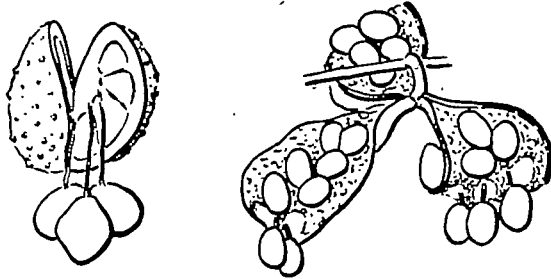


FIG. 32. A dehiscent follicle of *Michelia champaca* (left, Magnoliaceae) with pink seeds (sarcotesta) and the dorsally dehiscent follicles of *Xylopiya fusca* (right, Annonaceae) with bluish testa (sarcotesta), neither with aril but both with pseudo-funcicles (see text) ($\times \frac{1}{2}$).

and *S. grandiflorum* with dense coatings of stellate hairs), and the hydathodes of Bromeliaceae.

Dangling seeds. Only the small-fruited *Durio Griffithii* shows the hanging arillate seed which is so conspicuous in *Sloanea*, Meliaceae, and Leguminosae, or in *Sterculia*, *Gloriosa*, and *Erythrina* which lack the aril. Nevertheless, dangling is a character of the arillate or pseudo-arillate seed as shown also by the following four examples:

- a. Magnoliaceae. There is no aril, the pink or red testa being pulpy; and there is practically no funicle (as in Annonaceae), but the seeds hang down on slender threads which are the uncoiled spiral thickenings of the protoxylem-vessels of the raphe.
- b. *Xylopiya fusca* (Annonaceae). The blue-grey seed has a pulpy testa but no aril: it hangs on a stalk which is the vascular bundle of the placenta after the friable pink endocarp has broken away from it in the open fruit.
- c. *Guioa* (Sapindaceae). The seeds are arillate but sessile: when the fruit opens they drop out and hang on a long thread developed from the aril at the micropyle.
- d. *Gyrocarpus* (Thymelaeaceae). The seeds appear to have a very astonishing brown furry aril (I have not been able to examine its morphological character) and, when the dry capsule opens, the one or two seeds, which it contains, drop down on slender threads which strip from the septum and dangle like spiders.

When one considers also that seeds, more or less arillate, hanging on funicles 1–4 cm. long, are characteristic of the huge genus *Acacia* and that the large, more or less arillate seeds of the big genus *Swartzia* (Leguminosae)

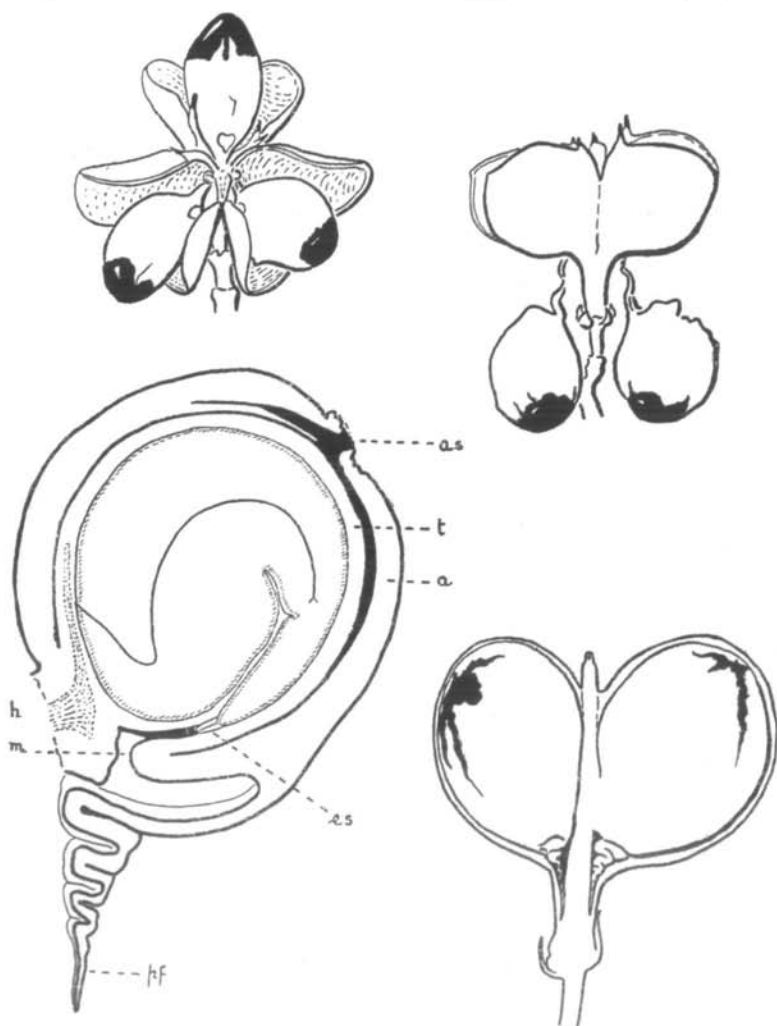


FIG. 33. Fruits and seed of *Guioa pubescens* (Sapindaceae), with black seeds and yellow aril developing a pseudo-funicle (*pf*) from its micropylar outgrowth. (The two upper fruits $\times 2$; the section of the unopened fruit $\times 3$; the longitudinal section of the seed $\times 7$.) *a*, aril; *as*, arilostome; *es*, endostome of inner integument; *h*, hilum; *m*, micropyle; *pf*, pseudo-funicle; *t*, testa.

behave in the same way (having even longer funicles in some cases), it is clear from all these varied examples that dangling edible seeds must have a biological significance. As movement helps the unsophisticated vision it seems that they catch the eye of birds which peck off the pulp. Possibly, in the

dry Australian forest, the waxy aril of the small seeds of *Acacia* supply considerable food and, even, liquid to the birds to which they may appear as spiders or caterpillars on threads. Certainly a dangling seed, pecked and

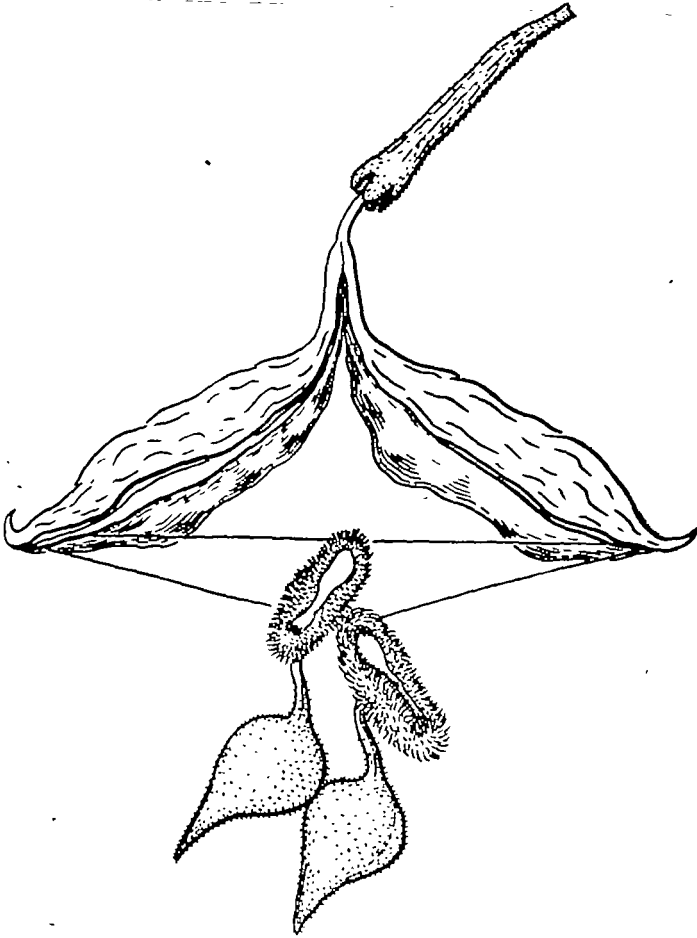


FIG. 34. The dehiscent, two-valved, dry, brownish capsule of *Gyrinopsis* sp. (aff. *G. Cumingiana*, Corner, Singapore Field, No. 29195: Thymelaeaceae), showing the two seeds (one from each loculus) with brown furry appendages (? arils) and pseudo-funicles derived from the split central portion of the septum on dehiscence ($\times 2$).

dropped, has more chance of survival than a durian-seed which may be crushed before being swallowed, though one such seed indigested will start with a favourable supply of manure.

So another feature of the flowering plant, namely, the length of the funicle, gains importance. Why should seeds have funicles? Why do the Acanthaceae have specially modified funicles? The only answer, or thought, that can yet be supplied is that they possess these features by inheritance from the

primitive arillate fruit, just as such funicles are retained as useless relics in the indehiscent pods of *Parkia* and *Cassia*. In fact, the problem is, rather, how seeds came to be detached from their funicles.

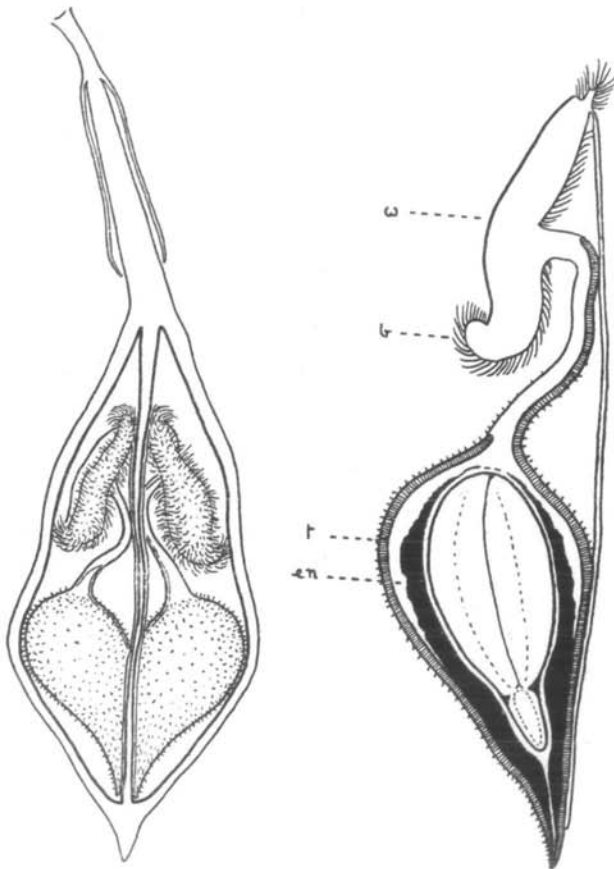


FIG. 35. A full-grown capsule in section ($\times 2$) and a mature seed in section ($\times 4$) of *Gyrinopsis* sp. (Corner 29195, Thymelaeaceae), showing the blackish, carbonaceous, shortly hairy, bomb-like body of the seed with rigid, curved neck and brown hairy appendage with white disc (*w*): the pseudo-funicle, joining the appendage to the bomb of the seed, being part of the septum of the capsule and splitting longitudinally into two threads on dehiscence of the capsule. Note how the embryo is suspended in the bomb of the seed with an air-cushion (black) around it. *b*, brown hairs of the appendage; *en*, the remains of the inner part of the testa; *t*, the black carbonaceous layer of the testa; *w*, the smooth white disk of the appendage.

Colour. No more vivid contrast can be imagined than a red fruit with hanging black seeds and scarlet arils against green foliage. The very blackness of the seed emphasizes the aril. Modifications into yellow fruits and yellow arils seem not to affect the result. But the problem raises the question of the colour-blindness—whatever that may mean—of animals. In my own experience, I have found that red is so appealing to the Coco-nut Monkey (*Macaca*

nemestrina) that, even when too sick to stand or eat or swallow, yet he will start with joy at the sight of a red fruit. I consider it to be no coincidence that bird-flowers are red, that parrots are red, that nutmegs have red mace or pulp, that the primitive angiosperm fruit should appear to have been red, that savages should paint their faces, monkeys their buttocks, and women their nails red, that holly-berries and red crackers should decorate Christmas, that flags should be red, that warning signals should be red, and 'On the whole it seems that bony fishes are more attracted by the red end of the spectrum than by the violet end. This accords with the evidence of anglers who find red baits very effective' (Pincher, 1947). What is redness to attract and gladden life?

Smell. The final characteristic of the durian is its smell. An even stronger smell is that of the Chempedak (*Artocarpus integer*), which has modified durian-fruits, or the Horse-mango (*Mangifera foetida*). Ducke records a similar smell for a species of *Swartzia* (Leguminosae), the pods of which are eaten by tapirs and pigs in Brazil, as durians are in Malaya. There is certainly more to be learnt about the significance of this factor as the ultimate appetizer, as there is with the chemical protection of the immature fruit. There must have been many more smells to attract the early elephants and tapirs and the short-sighted beasts; and it would seem that to them we owe the selection and survival of the durian.

RECAPITULATION

As any of the foregoing passages could furnish material for a book I will recapitulate for the sake of clarity, in the sequence in which I believe their evolution has generally occurred, the main steps in the development of the modern tree, bearing in mind that it is the fruit and seed, as the dispersal mechanism, which are the more significant reproductive parts of the flowering plant.

A. *Pachycaul Stage*

Stems massive, sappy, soft-wooded, not or sparingly branched, with little or no internodal development: megaphyllous: megaspermous.

1. *Monocaul or Cycad phase.* Low, stout, unbranched monocarpic trees without internodes, with peltate scales; leaves multipinnate, probably with a spiny rachis (flowers primitively terminal, gigantic, uncondensed, of pinnate stamens, and large, peltate-scaly carpels: fruit as a cluster of large spiny follicles, perhaps 0.5–1 m. long, ripening red and dehiscing with many large black seeds, perhaps 2 cm. long, covered with a red aril and hanging on persistent funicles).

This phase is largely hypothetical. It may have been truly monocaulous and monocarpic or sympodial, polycarpic, and pseudomonocaulous as *Cycas* itself: the resemblance to the tree-fern suggests, however, lack of branching in the first place. As a tree-form, this phase persists not only in Cycads but, with some modification in the development of internodes, in palms and the

saplings of many dicotyledonous trees with compound leaves (*Carica*, *Cecropia*, *Schizolobium*, *Bombax*, *Aralia*, &c.), the sapling stage recapitulating, in fact, this ancestral phase in the evolutionary history of modern trees.

Reduction of the leaf to an entire blade introduces most of the remainder of modern saplings and, as an instructive instance, the monocarpic *Agave* which, having become microspermous, shows that the massive rosette plant, without internodes, may have originated directly from the Cycad-form of tree. At least, *Agave* indicates the necessity for re-examining the massive growth-forms of tropical and subtropical Monocotyledons.

The primitive spiny fruiting carpel clearly represents the pinnate megasporophyll reduced to a bud-scale or basipetal phyllode, and is thus homologous with the spiny petioles of *Cyathea* and *Cycas*. But, in the evolution of the angiosperm, the full development of the megasporophyll or carpel is postponed until after fertilization. This early basipetal or phylloidal tendency not only continued to characterize the monocotyledonous leaf but the flower in general, leading eventually to the gamophyllous floral whorls and the inferior ovary. (The most extreme reduction is seen in *Welwitschia*.)

2. *Monocotyledonous phase*. Suckering must have entered sooner or later in the Cycad-phase, as a result of excess photosynthesis in the monocarpic tree, especially without secondary thickening. Thus in the palms, Gramineae and Scitamineae, tufted tree-forms have arisen (*Metroxylon*, *Bambusa*, *Ravenala*, *Musa*) and, with microspermy and internodes, these forms have produced the characteristically tufted monocotyledonous herbs as the grasses, sedges, Zingiberaceae, and Marantaceae, in which the rhizome is a secondary development of the sucker. Such herbaceous forms do not occur in Dicotyledons where the herb has evolved from trees with secondary thickening which obviates suckering, and where the seedling does not go through the stage of the *Agave*-rosette without internodes.

Ravenala is usually mistaken as a genus with two species, *R. guyanensis* and *R. madagascariensis*, evidencing discontinuous distribution. Actually they are generically distinct. *R. madagascariensis* has the lateral inflorescences, flowers, seeds, and pollen of the South African *Strelitzia*, and *R. guyanensis* has those characters which distinguish the South American *Heliconia*. Thus, geographically, the two natural groups are coherent and, phyletically, they indicate the ancient and relic character of this tree-form.

3. *Carica-phase*, resembling the Cycad-phase but with incipient internodes and sparse branching of the less massive stem: in Dicotyledons, not suckering owing to the elongation of the seedling and the presence of secondary thickening.

Typical of this form is *Pandanus*, as well as *Carica*: perhaps, also, *Hyphaene*, the Cactaceae and Nymphaeaceae (as aquatic sub-herbaceous derivatives). But, at the same level of tree-form, though with more or less hard-wooded and much less massive trunks, occur also many tropical trees scattered among such families as Simarubaceae (*Eurycoma*), Campanulaceae, Solanaceae, Compositae, Bignoniaceae (*Oroxylon*, *Pajanelia*), Araliaceae, &c. It is impossible to draw a sharp line between them and the following two stages, cf.

Artocarpus, *Cecropia*, *Macaranga*, but it is interesting to observe that they may also give rise to herbaceous derivatives through introduction of micro-spermy before the true modern tree-form has been reached. *Cecropia* and *Macaranga*, it may be noted, with their low height are restricted mainly to secondary forest or priseres of the tropics, thus evidencing the ecological evolution of the tree-form.

The chief variation in this phase seems to be the position of the inflorescence, whether terminal (Bignoniaceae, *Pandanus*) or lateral (*Carica*, *Nymphaea*, as *Cecropia*, *Macaranga*, and the Araliaceae).

The bottle trees, as *Adansonia* and *Brachychiton*, appear to come between the *Carica*-phase and the *Dysoxylon*-phase.

B. *Leptocaul Stage*

Twigs more or less slender, much branched, more or less hard-wooded: with internodes more or less well developed: megaphyllous or microphyllous: megaspermous or microspermous.

Megaspermous

4. *Dysoxylon-phase*. *Dysoxylon* (Meliaceae) is typical of this important kind of tropical tree with megaphyllous compound foliage, spirally or decussately arranged on rather massive ascending twigs. *Dysoxylon*, also, retains characteristically the arillate fruit as a fleshy loculicidal capsule. Many Leguminosae, Sapindaceae, Burseraceae, Anacardiaceae, Bombacaceae, Sterculiaceae, &c., belong here, as well as *Bocconia*, *Hevea*, and *Artocarpus* pr.p.

Again, both lateral and terminal inflorescences occur, as in the *Carica*-phase, but, as in the following two groups, there are no herbaceous derivatives, this being the megaspermous tropical tree *par excellence*.

5. *Magnolia-phase*. This resembles the preceding phase but has simple leaves, representing either terminal leaflets (*Mangifera*, *Lucuma*, *Persea*) or webbed compound leaves (*Dillenia*, and, perhaps, *Magnolia*), and less massive twigs. Typical are Magnoliaceae, Dilleniaceae, Sapotaceae, *Barringtonia*, *Persea*, *Quercus*, &c., but there are many transitions to the foregoing (as in Sterculiaceae) or the following (as in Myrtaceae, Melastomaceae, and Elaeocarpaceae). The pagoda-trees of *Terminalia*, *Achras*, *Palaquium*, *Elaeocarpus*, *Sloanea*, and *Cerbera* are characteristic of this phase (see Corner, 1940). The leaves may be large or small.

6. *Myristica-phase*. This agrees with the *Magnolia*-phase in the simple leaves, but they are arranged alternately or decussately in one plane to give the applanate foliage, or horizontal spray, as the most advanced foliage-display of trees, and the twigs are, typically, slender. The trees are usually more or less microphyllous. Characteristic are Myristicaceae, Annonaceae, and many modern genera of tropical and temperate trees as *Fagus*, *Carpinus*, *Durio*, *Symplocos*, pr.p., *Diospyros*, *Lecythis*, *Memecylon*, *Eugenia*, pr.p., &c.

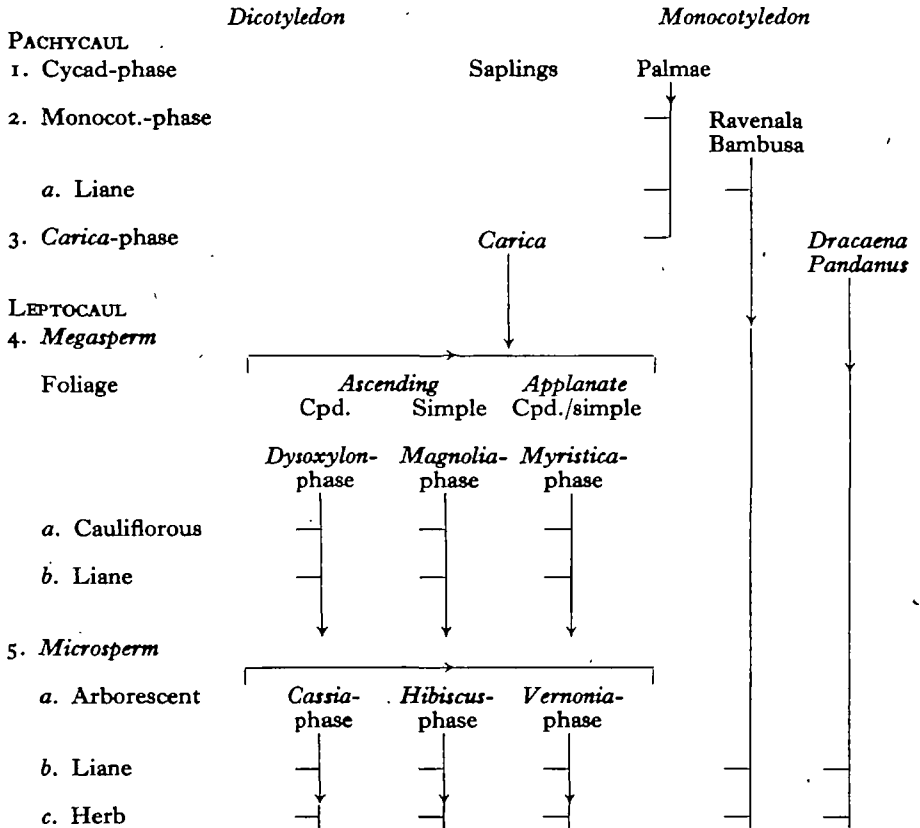
7. *Cauliflorous phase*. This phase may be imposed on any of the three preceding phases with slender twigs and massive flowers or fruits, but is more

characteristic in the *Myristica*-phase, cf. *Myristica*, *Polyalthia*, *Diospyros*, *Eugenia*, *Durio*, &c.

Microspermous

This most modern kind of tree may repeat any of the preceding phases 4, 5, and 6, which may be represented typically by *Cassia*, *Hibiscus*, and *Vernonia*, all of which give, characteristically, herbaceous derivatives, though there are examples as *Weinmannia*, *Populus*, and *Salix* which are entirely woody.

Diagram of Angiosperm Tree-forms



When the theory is represented diagrammatically, one can see:

a. That the gap between the Cycad-phase and the Leptocaul is filled largely by Monocotyledons which may be taken as representing the proto-Dicotyledons, just as Conifers and Gnetales are modern representatives of the protogymnosperms. While the Dicotyledons have produced the succeeding stages in forest-evolution, the monocotyledonous tree-habit seems to have represented the early ones. Thus, the tropical tree-fern, pteridosperm-, and cycad-forests seem to have given place to palm-forests before the broad-leaved

dicotyledonous forests were established, and the absence of normal secondary thickening in Monocotyledons, as well as the absence of a tap-root and inter-nodal development in the seedling, may be a primitive tree-fern character. The problem may, in fact, be not why the Monocotyledons diverged from the Dicotyledons, but why the dicotyledonous seedling diverged from the Monocotyledons.

b. That there is a strong difference between the woody and herbaceous habits in the first group of dicotyledonous trees (*Leptocaul-megasperm*), but not in the second (any more than in the two monocotyledonous series giving herbaceous derivatives). Failure to distinguish these two classes of tree is the cause of the confusion existing at present in attempts to classify Dicotyledons into woody and herbaceous groups. The *Meliaceae* and *Sapotaceae* are not equivalent to the woody *Malvaceae* and *Rubiaceae*.

c. That the herbaceous form has been derived along two main lines, from the pachycaul and from the microspermous leptocaul (which may or may not be secondarily soft-wooded), and that this analysis will help to explain some of the misunderstandings which exist, also, in reference to the herbaceous habit.

d. That the liane is a special case derivative from all phases of the leptocaul tree (as well as from the Monocotyledon).

e. That all the phases are well and fully represented by tropical plants, but only the microspermous and the monocotyledonous herbs are well represented in the temperate floras, thus illustrating the conviction, which most botanists studying tropical forests must have formed, that no flowering plant could have emerged from the tropical rain-forests to the monsoon and temperate regions until it was fit, structurally and physiologically, to meet the rigorous conditions.

f. That (i) the microspermous and microphyllous arborescent *Casuarinaceae*, *Salicaceae*, *Cunoniaceae*, &c., and (ii) the megaspermous but temperate *Quercus*, *Fagus*, *Juglans*, *Aesculus*, &c., stand out as blind alleys in evolution, and require special consideration.

g. That the early angiosperms, being soft-wooded with large, compound, mesophytic leaves and large, non-dormant seeds, are unlikely to have left fossil evidence. The *Rhizophora* seedling, germinating *in situ*, may be the modern representation of an archaic, estuarine, proto-angiosperm habit.

h. That reduction in size, after a zenith in an optimum locality, always takes place, cf. *Lepidodendron* and *Calamites*; so the forests of the tropics are giving place to pasture through human interference, e.g. bamboo to grass.

i. That there is an enormous field of research opened to analyse the relative position of every family and genus of angiosperm in this evolutionary diagram. Every small specific group of tropical plants will need renewed investigation, for the majority cannot be placed by consulting published information, cf. the confusion over *Ravenala*.

CONCLUSION

I have avoided nearly all reference to the flower. As recently as 1930 it was written that 'the fruit contributes little or no evidence of value concerning

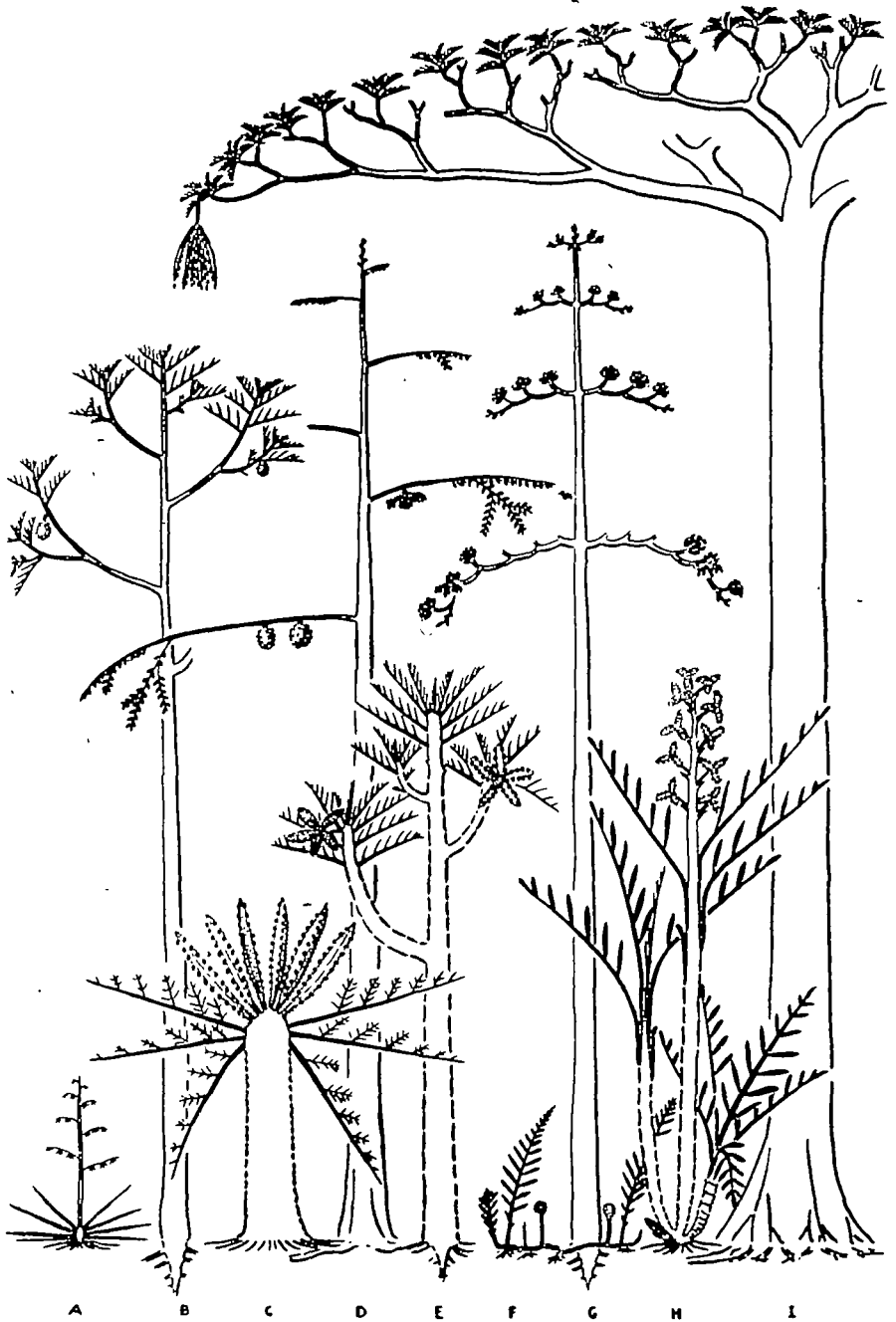


FIG. 36. Diagrams of the main tree-forms and of two sub-herbaceous derivatives (A, F). A, the *Agave*-rosette, as a direct reduction-form of C; B, the megaspermous leptocaul tree with spirally arranged pinnate leaves, giving ascending foliage; C, the hypothetical Cycad-form, monocaulous and monocarpic with a terminal cluster of spinous follicles with arillate

the primitive habit of Angiosperms'. The Durian-theory, as I have been advised to call it by Dr. H. Godwin, F.R.S. (Cambridge Botany School), shows that it is possible, from the study of tropical fruits, to arrive at a far-reaching understanding of the evolution of the modern tree and, perhaps, of most living accompaniments to the origin and dispersal of flowering plants.

The theory shows that from mesophytic Cycad-like trees, possibly monocarpic, with terminal flowers or inflorescences and large red spiny follicles disclosing black seeds with red arils, the tropical forests have gradually evolved the modern microspermous tree, as the antecedent to the dicotyledonous herb, and in so doing have both heightened the forest, thereby increasing its complexity particularly with regard to climbers and epiphytes, and also reduced its food-content for animal life. The theory directs attention to one of the most neglected aspects of biology, namely, the real life of the tropical forests, not only with regard to the dependence of the animals upon the plants, but particularly with regard to the enormous variety of tree-forms representing all sorts of combinations of evolutionary processes in varying response to the main trend. Thus the cauliflorous tree, the palm, and the pagoda-tree, as well as the berry, the drupe, the nut, and the size of the seed, find a natural explanation; *Aesculus* and *Artocarpus*, *Castanea* and *Pandanus* fall into place with *Sloanea* and *Durio*. But any hypothesis, shedding light on so large a field, must be continually readjusted as its new aspects are seen: and every case of genus or family will need its own particular consideration. Tree-habit, wood, leaf, bud, flower, fruit, seed, and root all supply independent criteria which must be analysed and estimated.

Now, the antecedents of *Archidendron*, *Delomix*, *Durio*, *Sterculia*, *Sloanea*, *Dysoxylon*, and so on, which had massive twigs of compound leaves, large flowers, and red arillate fruits, clearly represented a climax of tree-form in the optimum conditions for terrestrial plants in the tropical rain-belt, and were, thus, an expression of Xerophyton, or the land-plant. But the culmination of plant-growth on land, expressed in size and survival, is shown now not only by these very genera but by such families as Papilionaceae, Dipterocarpaceae, Anacardiaceae, Lecythidaceae, Cupuliferae, and so on, which tend to a reduction in size and complexity of the twig, leaf, flower, and fruit, though retaining the big seed, as the forest-factor. It is these modern families of megaspermous tropical trees that I consider to represent, in their homoplastic diversity, the idea of Xerophyton. They are the modern tropical forests,

seeds; D, the cauliflorous tree with simple alternate leaves giving applanate foliage, leptocaul (cf. *Durio*); E, the *Carica*-form, pachycaul, with few branches, compound leaves, incipient internodes and arillate follicles (axillary); F, the cauliflorous Monocotyledon, as a rhizomatous sub-herbaceous plant, with aerial sprays of applanate, simple foliage, analogous with the cauliflorous dicotyledonous tree, but derivative from H (cf. Zingiberaceae); G, the pagoda-tree with arillate capsules (cf. *Sloanea*) and simple leaves in rosettes; H, the monocotyledonous pachycaul with suckers, monocarpic with arillate, spinous follicles and compound leaves (cf. *Ravenala*); I, the megaspermous leptocaul ancestor of Leguminosae with dehiscent arillate legumes and spirally arranged, compound leaves (cf. *Parkia*). (The picture needs primitive birds and mammals for completion.)

from which most of the temperate floras have been derived. They will last, apart from human interference, so long as the climate of the rain-forests persists, but, as this deteriorates, they will give place to the microspermous trees and, eventually, savannahs, as the golden age will always pass.

SUMMARY

Taking the Durian (*Durio zibethinus*) as the type of fruit, and using the Leguminosae, particularly, for exemplification, as well as *Carica*, *Artocarpus*, *Aesculus*, and *Castanea*, it is argued that the primitive angiosperm fruit must have been a red fleshy follicle, probably spiny, with large black seeds hanging on persistent funicles and covered with a red aril.

From this precept, it is argued further that the primitive angiosperm must have been a mesophytic, tropical, Cycad-like monocaulous tree with large pinnate leaves and peltate scales, probably monocarpic, and producing a terminal cluster of large arillate follicles.

Ramification with consequent reduction in size and complexity of the branches, leaves, flowers, and fruits, and the evolution of axillary inflorescences, have led to the modern tree-form with many slender twigs, simple leaves in horizontal sprays, small flowers, and greatly increased height.

Among modern tropical rain-forest trees a distinction is drawn between the more primitive *pachycaul* trees with massive unbranched, sparingly branched, or suckered (monocotyledonous) trunk, soft wood, and large leaves, and the orthodox *leptocaul* trees with relatively slender twigs and hard wood. A further distinction is made among leptocaul trees between the *megaspermous* and non-herbaceous and the *microspermous* from which the dicotyledonous herbaceous plants have been derived: transitions between these two kinds of trees appear to be rare. Cauliflory is a condition forced upon leptocaul trees with, usually, appanate foliage by the retention of the old massive forms of flower and fruit.

The principles of *axial conformity* (or the correspondence in size and complexity between appendages and the parent axis) and *diminution on ramification* are indicated as fundamental to the construction of land-plants.

Modern fruits as capsules, nuts, winged indehiscent fruits, and so on have been evolved from the primitive arillate fruit with consequent great loss in food-supply to forest birds and mammals.

The significance of the spiny armour, the colour, the dangling seeds, and the smell of the arillate fruit is discussed.

LITERATURE CITED

- BAILEY, F. M., 1916: Catalogue of Queensland Plants.
 CHURCH, A. H., 1919: Thalasssiophyta. . . Oxford Botanical Memoirs, No. 3.
 CORNER, E. J. H., 1940: Wayside Trees of Malaya. Singapore.
 ——— 1946: Suggestions for Botanical Progress. New Phytol., xlv. 185.
 ——— 1949: The Annonaceous Seed and its Four Integuments. Ibid. xlviii (in the press).
 PFEIFFER, A., 1891: Die Arillargebilde der Pflanzensamen. Engl. Bot. Jahrb., xiii. 492-540, t. 6.
 PINCHER, CHAPMAN, 1947: Vision in Fishes. Discovery, July, p. 215.