THE INFLORESCENCE OF DILLENIA

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ABSTRACT. The species of *Dillenia* (Dilleniaceae) have been compared with regard to the size of the flower, the number of its parts, the number of flowers in the inflorescence and the mechanism of the fruit, whether dehiscent and arillate or indehiscent and exarillate. It is concluded that the branched inflorescence with many relatively small flowers has evolved from the single terminal flower; that the branched inflorescence has also reverted to the simple; that fruit-evolution has been independent; and that both inflorescence and fruit have thus progressed in different specific alliances of the genus.

When studying Malayan trees, I came upon the evolutionary problem set by the massive, solitary and terminal flower of *Dillenia indica* in comparison with the smaller, axillary flowers of *D. albiflos*, which are arranged in a branching terminal raceme as the most complicated inflorescence of the genus. The first has indehiscent and exarillate fruits; the second has dehiscent and arillate. Among the Malayan species it appeared that this distinction in fruit went along with the size and number of flowers in the inflorescence; and I inclined to the view that the many-flowered, branching inflorescence with arillate fruit had become reduced to the single large flower with baccate fruit. The evidence was far from satisfactory; the conclusion did not agree with the generally accepted hypothesis of a primitively terminal flower for Magnoliales; and the large tree, *D. pulchella*, with the smallest flowers did not fit because the flowers were solitary, though axillary, while the fruit was dehiscent and arillate.

Since then, there has appeared the thorough revision of *Dillenia* by Hoogland (1951, 1952, 1976). He recognises about 60 species, distributed from Madagascar and the Seychelles to Fiji, excepting New Caledonia and Australia other than Queensland. From the ample descriptions I extracted the relevant facts, tabulated them, re-arranged them, and came to the conclusion that I had been mistaken. The evidence supports the contrary hypothesis that from single, massive, terminal flowers leptocauly has introduced smaller flowers, then branching from its bracts, and finally the small-flowered and branching raceme. Thus, in inflorescence, *D. albiflos*, which is endemic to the south of the Malay Peninsula, is the most advanced while retaining the primitive fruit-mechanism, and the widespread *D. indica* is one of the more primitive, while advanced to the baccate fruit. It became clear that the ten Malayan species were no fair sample of *Dillenia*, and that its modern species were the scattered fragments of many extinct lines of progress and reversion in inflorescence and fruit independently; some have close geographical proximity but others, as bits of former alliances, are now widely separate. Thus *Dillenia* becomes an intriguing challenge to students of evolution, just as the whole family is in its primitive status among dicotyledons (Dickison 1970; Corner 1976).

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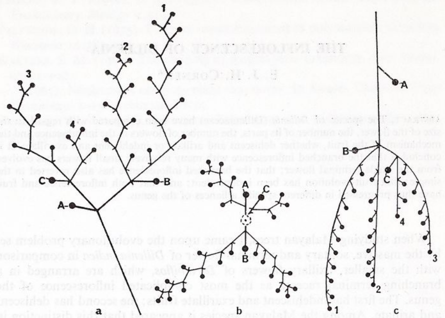

Fig. 1. *Dillenia albiflos*, diagrams of the inflorescence: a, the plan of a large inflorescence with 30 flowers, the first three indicated as A, B, and C, and the successive branches as 1, 2, 3, and 4; b, the ground-plan of this inflorescence to show the direction of the branches; c, the hanging inflorescence, with a variation in the position of branches 3 and 4 from flower C without a bract.

I record here a summary of my notes on *D. albiflos* and *D. suffruticosa*. They are far from perfect and call for the study of the inflorescence in many other species, particularly for its early stages in development. As trees and shrubs in the lowland forest, the species are recognised from the reddish orange flaky bark as well as from the large flowers. It is to be hoped that somewhere in Malesia an arboretum of these remarkable relics will be established; then, with hybridisation, there may be progress scientifically and horticulturally.

THE INFLORESCENCE OF DILLENIA ALBIFLOS

This small tree used to be fairly common in central and east Johore. It has not been found in the west and does not occur in Singapore, but it may extend into south Pahang. Its nearest ally is *D. beccariana* of Sarawak. This limited alliance suggests that the two are either relics on the two sides of the Riouw Pocket (Corner 1958) or of recent evolution. Yet I am not convinced that they are specifically distinct. *D. beccariana* was said to have yellow flowers but Dr P. S. Ashton enquired into this for me and reported *in litt.* that the flowers were white. Perhaps *D. albiflos* is merely a subspecies with smaller flower, branched inflorescence, and less hairy gynoecium.

Figure 1 shows diagrammatically the largest form of the inflorescence. It reaches 50 cm long, hangs down, has four branches, and bears up to 30 flowers in all, each 4–5 cm wide and every one setting fruit. The flowers open before dawn, one at a time along the branches from base to apex, perhaps on successive days, and the white petals drop off soon after noon. In the immature inflorescence the flower-buds are distichous along the zig-zag branches of the compound raceme (fig. 1a), but as the inflorescence begins to work the internodes of the branches are twisted and the flower-pedicels are curved to set the flowers facing each other and downwards (fig. 1c); branch 2 becomes the mirror-image of branch 1, and branch 4 that of branch 3. The branches have been numbered according to the sequence in which they arose; they are also successively shorter, but branch 3 may arise before branch 2 in which case it is longer. Variations arise from failure of branches to develop. In the commonest state of the inflorescence branch 4 does not develop; in other cases there are only branches 1 and 2 or branches 1 and 3, or indeed only branch 1 (which appears to be the state in *D. beccariana*).

The first flower has been labelled A; it terminates the stalk of the inflorescence. The first flower on branch 1 is labelled B, and that on branch 3 is labelled C. Flower A never has a bract and appears to be truly terminal in correspondence with the big terminal flower of *D. indica*; its pedicel is the longest. All the other flowers have bracts but that of flower C may be displaced down the first internode of branch 3 (fig. 2a) or it may be absent, in which case the bract of the second flower on branch 3 is displaced (fig. 2b). The detail suggests that flower A may have lost its bract and, really, be lateral, or if terminal that it may have lost the bracts which should subtend branches 1 and 3; no branches, however, are subtended by bracts and their morphological status is enigmatic. Branch 1 opposes flower A; branch 2 opposes flower B; branch 4 opposes flower C; and branch 3 opposes branch 1,

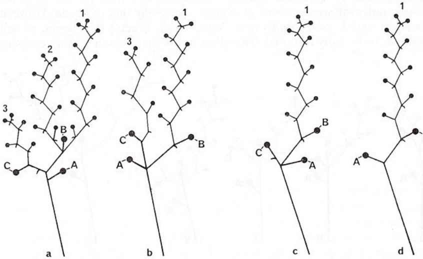

Fig. 2. *Dillenia albiflos*, variations in the inflorescence: a, without branch 4, flower B without a bract, that of flower C displaced; b, without branches 2 and 4, flower C without a bract; c, with branch 3 reduced to one flower; d, the apparently unbranched inflorescence.

but it may be displaced along the first internode of branch 1, even to a position opposite flower B (fig. 2a) so as to give a cluster of branches suggestive of the inflorescence of *D. grandifolia* and its allies, details of which are not known. Flowers A and B lie in a vertical plane to which the pairs of branches are set roughly at right angles (fig. 1b). Then, as the inflorescence opens, the twisting and curving set all in roughly the original plane. In addition to these variations I noticed that branch 3 may be reduced to the single flower C (fig. 2c).

I preserved many developmental stages of these inflorescences in alcohol with the object of studying them at leisure but, when the opportunity came some years later, I found that the alcohol had turned to vinegar, as it had become diluted with continual 'topping up', and that the material had in consequence fragmented.

THE INFLORESCENCE OF DILLENIA SUFFRUTICOSA

This common shrub or small tree of swampy ground in west Malesia was often used as an introductory flower in school-classes. I studied it in considerable detail because, as with all efforts to find a tropical flower suitable for teaching, there were awkward discrepancies from the orthodox, which the more astute among pupils would question. Hence I came upon the centrifugal stamens, the dicyclic vasculature of peduncle and pedicel, and the cymose-racemose construction of the inflorescence. It appears, generally, as a simple raceme of 4–10 flowers, 8–11 cm wide, with yellow petals. The raceme projects obliquely upwards and the distichous flowers, turned successively to the same side, face downwards. Some plants, however, have inflorescences up to 40 cm long, with 1–3 branches, and up to 18 flowers in all. Such an inflorescence is shown diagrammatically in fig. 3e, along with the manner of elaboration from the simple raceme. The flowers are labelled in the figure as in figs 1 and 2, and the effect is a construction similar to that of the simpler inflorescences of *D. albiflos*, especially that of fig. 2a. However, flowers B and C of *D. suffruticosa* never have bracts; they seem, as with flower A, to be truly terminal. The other flowers have each a small caducous

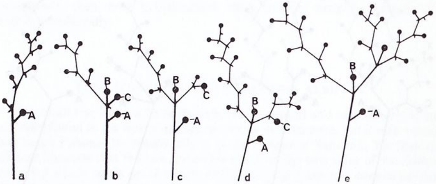

FIG. 3. *Dillenia suffruticosa*, diagrams of the variations in the inflorescence: a, the common form of the inflorescence; b, with a flower C from the axil of the bract of flower B; c, d, with a second racemose branch developing; *e*, with three racemose branches; in c-e flower B without a bract.

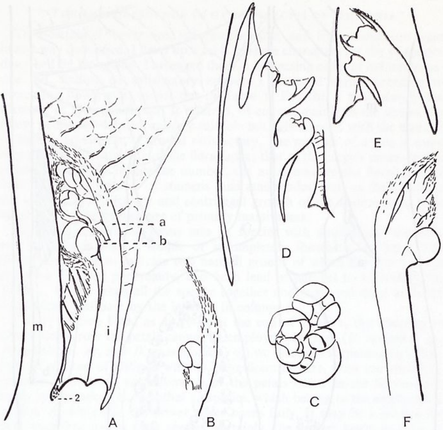

FIG. 4. *Dillenia suffruticosa*, developing inflorescences. A, a terminal bud in l.s. with young inflorescence (i), the first leaf of the new sympodial shoot, the midrib (m) of the subtending adult leaf with the lower axillary bud (2), and the two bracts (a, b) of the second flower, × 2. B, the second flower-bud with its two bracts, × 2. C, the apex of the young raceme with four flower-buds and their bracts (that of the upper flower removed) × 30. D, E, young inflorescence-primordia in l.s., showing the apex of the new, sympodial, vegetative shoot, × 15. F, the inflorescence-primordium showing the first flower without a bract, × 2.

bract but the second flower of the simple raceme and the first flowers on the branches of the branched raceme usually have a second, smaller, and postero-lateral bracteole which never develops an axillary flower or branch (fig. 4 A, B). Details of the early development of the simple raceme are shown in fig. 4; unfortunately I did not have similar material for the branched raceme, trees of which I had observed by the Sedili River in Johore.

There are some points to note about the vegetative shoots which may bear on the inflorescence. There are two buds in each leaf-axil, inserted one above the other on the stem at the base of the internode (fig. 5). The upper becomes the new side-shoot to carry on the growth of the twig when the inflorescence terminates the growth of the main shoot; the lower remains dormant or it may become a second side-shoot, especially if the first is damaged. These side-shoots have at the base 2–3 prophylls, as reduced leaves with little or no lamina. How far this construction may be reflected in the inflorescence I do

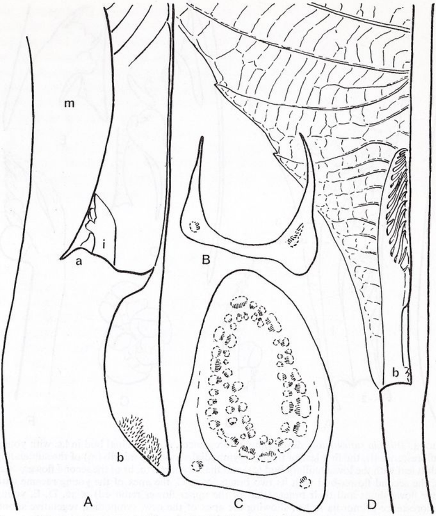

FIG. 5. *Dillenia suffruticosa.* A, the terminal bud in l.s., showing the terminal inflorescence-primordium (i), the new vegetative apex (a) from a lateral bud, and the two lateral buds (b) at the base of the ultimate internode of the last leaf with midrib (m), × 7. B, a bract in t.s. with 2 vascular bundles, × 15. C, the peduncle in t.s., showing the double ring of vascular bundles and the insertion of a bract, × 15. D, a terminal bud in l.s., showing the two lateral buds (b) in the axil of the open leaf, × 1.

not know, or whether multiple axillary buds are typical of the genus. The bracts certainly correspond with the prophylls, but are more reduced. They have 2(–3) vascular bundles connected with the inflorescence-axis, but this does not imply that they are double, or treble, structures; each arises from a single primordium. The small number of vascular bundles is a reduction from the 3–9 in the prophylls, as this number is a reduction from 16–20 vascular bundles for the normal leaves. Then, the double ring of vascular bundles in the axis of the inflorescence and in the pedicels of the flowers, with inverted bundles in the inner ring (fig. 5), suggests that the inflorescence has traces of a massive and primitive pachycaul construction.

THE INFLORESCENCE IN OTHER SPECIES OF DILLENIA

To ascertain if flower-size, inflorescence-size, and fruit-mechanism were in any way connected, I drew up a table of these characters for the 59 species described by Hoogland. I arranged them in decreasing order of inflorescence-size but, finding no satisfactory answer, I arranged them according to decreasing flower-size, as set out in Table 1. For this I used simply the diameter of the open flower. It referred, of course, mainly to the size of the flimsy petals and seemed scarcely suitable but, when tested with the number of sepals and carpels, it proved satisfactory. The number of sepals is some measure of the initial size of the floral apex; that of the carpels measures the residual apex. The higher the number, the more massive the floral apex. I have added the number of stamens (and staminodes) but, as they indicate the amount of intercalary and centrifugal growth of the androecium, their number is no direct measure of primary massiveness.

Hoogland divides the genus into 35 species with amplexicaul leaf-base and 24 species with a simple or incompletely sheathing leaf-base. The distinction seems to indicate two natural groups of which the first has the primitive relics of pachycauly, and both lead in parallel to leptocauly. In Table 1, I have taken all the species together and indicated those with the amplexicaul leaf-base by the letter A in column 1.

For 17 species, listed as n. 43–59 at the end of Table 1, the measure of flower-size across the petals cannot be employed. In three (*D. serrata* n. 43, *D. celebica* n. 47, and *D. grandifolia* n. 59) we meet the surprising fact that, in both sections of *Dillenia* with its magnificent flowers, there are apetalous species; whether or not rudiments of the petals occur in the flower-buds needs investigation. In the other 14 species, which belong to the amplexicaul section, it seems that the flower never opens fully. It may be a matter for field-study because in some species, certainly, the flowers begin to close at midday and, unless collected earlier, open flowers will not be obtained; some of these species may, however, be cleistogamous. The most remarkable is *D. pteropoda* (n. 53) of the Moluccas and west New Guinea (Hoogland 1959 figure 1, and 1976). Its solitary terminal flower has c. 18 sepals (indicative of the most massive construction in the genus), seven red petals (10 × 4 cm). and ten carpels. If the corolla opened, the flower might be the most spectacular. It seems, nevertheless, that *Dillenia* is on the way to losing the corolla; a derivative apetalous family is not known (Corner 1976), and the apetalous species may be on the way to extinction.

SIZE OF FLOWER AND NUMBER PER INFLORESCENCE

1. Flowers 10 cm or more wide (Table 1, n. 1–13):—flowers solitary (5 species), 1–2 (2 species), 1–3 (3 species), 2–4 (1 species), 4–7 (1 species), up to 18 (1 species, also with a branched inflorescence, *D. suffruticosa* n. 11).
2. Flowers 6–10 cm wide (n. 14–32)—flowers solitary (2 species), 1–3 (6 species), 2–6 (5 species), 3–10 (1 species), with more numerous flowers up to 12, 15, 20, or 30 (5 species); branched inflorescence in 4 species (*D. excelsa* n. 15, *D. reticulata* n. 22, *D. triquetra* n. 25, *D. borneensis* n. 30).
3. Flowers 2–5 cm wide (n. 33–42):—flowers 1–3 (3 species), 2–7 (4 species), 3–9 (1 species), more numerous up to 18 or 30 (2 species); branched inflorescences in *D. mansoni* n. 36 and *D. albiflos* n. 40.

TABLE 1. The species of *Dillenia* arranged in decreasing order of flower-size

Columns:—I, the amplexicaul section A; II, flower-width; III, flower number per inflorescence; IV, inflorescence length, *br* branches; V, sepal-number; VI, stamen and staminode number; VII, carpel-number; VIII, fruit, *d* dehiscent, *i* indehiscent; IX, seed, *a*, arillate, *e* exarillate.

		I	II Fl.w. cm	III Fl.n.	IV Infl.l. cm	V Sep.n.	VI Stam.n.	VII Carp.n.	VIII Fruit	IX Seed
1	*D. megalantha*	A	20	1		5(–6)	700	14–16	*i*	*a*
2	*D. indica*		15–20	1		5	575	14–20	*i*	*e*
3	*D. reifferscheidia*	A	17·5	1(–3)		11–17	435	15	*i*	*a*
4	*D. ovata*		16	1		5	475	(8–)10–12	*i*	*e*
5	*D. obovata*		14–16	1(–3)		5	240–295	9–11(–14)	*i*	*e*
6	*D. turbinata*		10–13	2–4	–7	5	335–350	8–9	*i*	*e*
7	*D. philippinensis*	A	10–12·5	1–2(–3)	–15	5	270	10–12	*i*	*a*
8	*D. andamanica*		12	1(–2)		5	130	(6–)8	*i*	*e*
9	*D. aurea*		10–12	1(–2)		5	200	10–12	*i*	*e*
10	*D. papyracea*	A	10–12	4–7	–40	5	700	c.10	*d*	*a*
11	*D. suffruticosa*	A	8–12	(4–)6–10(–18)	–30, 0–2*br*	5	275	5–8	*d*	*a*
12	*D. marsupialis*	A	10	1		8–9	335	15	*i*	*a*
13	*D. monantha*		10	1		5	110	4–5	*d*	*a*
14	*D. auriculata*	A	8–10	1–3	–11	5	250	6–10	?	?
15	*D. excelsa*		7–10	(3–)5–8(–12)	–18, 0–1*br*	5	330	(5–)6–8(–10)	*d*	*a*
16	*D. diantha*	A	9	(1–)2	–4	5	175	(5–)7–9	*d*	?
17	*D. bracteata*		9	2–3(–6)	–7	5	230	5	*i*	*a*
18	*D. castaneifolia*	A	6·5–9	1–6	–30	5	275–325	8–10	*d*	*a*
19	*D. parkinsonii*		8	2–3		5	230	5–7	*i*	*e*
20	*D. ochreata*	A	6–8	1		5	165	6–9	*i*	*a*
21	*D. luzoniensis*		6–8	–30	–40	5	170	7–8	*d*	*a*
22	*D. reticulata*		6–8	(3–)5–10(–15)	branched	5	400–440	9–10	*i*	*a*
23	*D. retusa*		6–8	(1–)2–3	–4	5	180	5–6	*i*	*e*
24	*D. alata*	A	7·5	2–4	–12	5	120	6–8	*d*	*a*
25	*D. triquetra*	A	6–7	(3–)5–12(–20)	–25, 0–2*br*	5(–6)	125–140	4–5(–7)	*i*	*a*
26	*D. beccariana*	A	6·5	–20	–60	5	130	5–6	*d*	*a*

27	*D. ovalifolia*	A	>6	1		5	900	7–8	*d*	*a*
28	*D. bolsteri*	A	6	2–4	–10	5	185	8–10	*i*	*e*
29	*D. sumatrana*		6	1–2(–3)		5	220	7–10	*i*	*e*
30	*D. borneensis*		6	3–10	branched	5	335	7–8	?	?
31	*D. blanchardii*		6	(1–)2(–3)	–5	5	170	5–7	*i* ?	*a*
32	*D. fischeri*	A	6	2–4(–6)	–5	4–6	120–160	4–6	?	?
33	*D. ferruginea*	A	5	–18	–25	8–11	450–490	(6–)8(–10)	?	?
34	*D. parviflora*		5	(1–)2–4(–7)		5	150–185	5–8	*i*	*e*
35	*D. sibuyanensis*		5	1–3	–3	7–9	90	(5–)7(–8)	*d*	*a*
36	*D. mansoni*		5	3–9	–15, 0–1*br*	5	85	5	?	*a*
37	*D. quercifolia*	A	4–5	2–4	–5	5	60	7–10	?	?
38	*D. hookeri*		4–5	1(–2)		5–6	190	6–7	*i*	*e*
39	*D. scabrella*		4–5	(1–)2–5		5	130	5–7	*i*	*e*
40	*D. albiflos*	A	4–5	–30	–50, 0–4*br*	5	160	5–6	*d*	*a*
41	*D. pulchella*		3·5	1–2(–3)		5	120	4–6	*d*	*a*
42	*D. pentagyna*		2–3	2–7		5	70–100	5(–6)	*i*	*a*
	Flowers not fully opening or apetalous									
43	*D. serrata*	A	7·5	2–6	–15	5	750	18–19	*i*	*e*
44	*D. papuana*	A		4–7	–8	5	185–250	10–15	*d*	*a*
45	*D. talaudensis*	A		2–3	–12	5	330	14	?	?
46	*D. fagifolia*	A		6	–6	5	150	12	?	?
47	*D. celebica*	A		1–5	–5	5	300	c.11	?	?
48	*D. nalagi*	A		2(–3)	–15	5	690	10–11	*d*	*a*
49	*D. cyclopensis*	A		3	–6	5	360	8–11	*d*	?
50	*D. montana*	A		2	–6	5	90	8–11	*d*	*a*
51	*D. schlechteri*	A		2–6	–7	5	100	8–11	*d*	*a*
52	*D. ingens*	A		3–6	–12	5	300	10	*d*	*a*
53	*D. pteropoda*	A		1		c.18	220	10	?	?
54	*D. insignis*	A		2	–5	5	95	8–10	?	?
55	*D. biflora*	A		2(–6)	–10	5	500	5–10	?	?
56	*D. insularum*	A		1		5	320	7–9	*d*	*a*
57	*D. crenata*	A		2(–3)	–6	5	140	6–8	*d*	*a*
58	*D. salomonensis*	A		3–5	–3	5	65	5	?	?
59	*D. grandifolia*			(3–)5–12(–18)	branched	5	150–180	(4–)5(–6]	*i*	*a*

Solitary flowers occur in all three categories but preponderate in the first. Indeed, the largest flowers are either solitary or set 2–3 together (n. 1–5). To these *D. pteropoda* (n. 53) may be added, but *D. serrata* (n. 43) has 2–6 massive flowers on an elongated inflorescence.

Concerning *D. pulchella* (n. 41) with the smallest solitary flower, it is exceptional because these flowers are lateral on the most leptocaul twigs of the genus (Corner 1966, fig. 116). They occur singly or 2–3 above each other and may develop individually from supernumerary axillary buds; thus, they may be terminal on dwarfed lateral shoots. Hoogland (1952) placed *D. pulchella* of the lowland rain-forest of west Malesia with *D. parkinsonii*, *D. pentagyna*, *D. scabrella*, *D. parviflora*, and *D. andamanica* of the monsoon forests (India and south China to Timor), in all of which there appears to be the tendency to small fascicles of flowers on dwarfed axillary shoots. The point needs investigation.

The highest number of flowers (up to 30) occurs in *D. albiflos* (amplexicaul) and *D. luzoniensis* (non-amplexicaul). The first, with branched inflorescence, has smaller flowers than those on the unbranched raceme of the second. Branched inflorescences occur in 7 species (3 amplexicaul, 4 non-amplexicaul) and, except for *D. albiflos*, they bear flowers of medium-size 6–12 cm wide. The three amplexicaul species belong to three specific alliances, the non-amplexicaul to two. Concerning the amplexicaul, there is the close alliance between *D. albiflos* and *D. beccariana*; secondly, there is the widespread alliance of *D. suffruticosa* with *D. biflora* (Fiji, New Hebrides), *D. fagifera* (New Guinea), and *D. ferruginea* (Seychelles); thirdly, *D. triquetra* of Madagascar and Ceylon seems related with the far-eastern *D. fischeri* (Mindanao), *D. quercifolia* (New Guinea), *D. schlechteri* (New Guinea), and *D. crenata* (Solomons). Concerning the non-amplexicaul species, firstly *D. excelsa* of west Malesia is close to *D. luzoniensis* (Palawan, Luzon) and *D. monantha* (Palawan, Calamianes), as noted by Hoogland (1952); in this case there is an alliance from a single terminal flower of medium-size to the many-flowered and branched raceme of *D. excelsa*. Then secondly, there is the alliance of the big stilt-rooted trees of west Malesia, namely *D. borneensis* (n. 30), *D. reticulata* (n. 22), and the apetalous *D. grandifolia* (n. 59). Since it seems improbable that this particular cymose-racemose inflorescence could have arisen independently in so many alliances, it appears to have been a common attribute which, as in *D. albiflos* and *D. suffruticosa*, reverted to the simple raceme.

SEPALS. More than the usual five sepals occur in *D. sibuyanensis* (n. 35, 7–9 sepals), *D. marsupialis* (n. 12, 8–9 sepals), *D. ferruginea* (n. 33, 8–11 sepals), *D. reifferscheidia* (n. 3, 11–17 sepals), and *D. pteropoda* (n. 53, c. 18 sepals). The first belongs in the non-amplexicaul section, the others in the amplexicaul as three different specific alliances. Thus, this feature is widely spread through the genus as an indication of the primitively massive flower.

PETALS. Most species have five yellow or white petals, occasionally pink. *D. pteropoda* has seven red petals. Apetaly occurs in the amplexicaul *D. serrata* (n. 43), its ally *D. celebica* (n. 47), and in the non-amplexicaul *D. grandifolia* (n. 59). It is another instance of a parallel trend in the two sections of the genus. Failure of the flower to open fully seems to be peculiar to the amplexicaul species (n. 43–58).

CARPELS. The number varies in different species from 4–20. High numbers (14–20) occur in five amplexicaul species (*D. megalantha*, *D. reifferscheidia*, *D. marsupialis*, *D. serrata*, *D. talaudensis*) and in the non-amplexicaul *D. indica.* All have large, solitary or subsolitary, flowers except *D. serrata* (2–6 flowers) and *D. talaudensis* (2–3 flowers). Of the amplexicaul species the first three occur in the Philippines, *D. serrata* in Celebes, and *D. talaudensis* in the Moluccas, as if this primitive feature had persisted in central Malesia. Low numbers (4–6) occur in four amplexicaul species with small flowers (4–6·5 cm wide) and in seven non-amplexicaul species of which three have small flowers (2–5 cm wide), three have medium-sized flowers (6–10 cm wide), and *D. grandifolia* is apetalous. Indicative of the reduction in carpel-number along with flower-size, there is the fact that the number is low (5–10) in all species with branched inflorescences. The flower has suffered reduction in both sections of the genus.

STAMENS. When stamens and staminodes are reckoned together as in Table 1, their number per flower varies from 60 (*D. quercifolia* n. 37) to 900 (*D. ovalifolia* n. 27). High numbers (300 and more) occur in species with large flowers and low numbers (60–200) in those with small flowers. In the middle range of flower-size the many differences (110–900) show a complexity that needs close specific analysis. Thus, the number ranges in the alliance of the stilt-rooted and non-amplexicaul trees from *D. reticulata* (400–440), through *D. borneensis* (335), to the apetalous *D. grandifolia* (150–150). *D. reifferscheidia* has 435 and its ally, *D. marsupialis*, with smaller flowers has 335. The apetalous *D. serrata has* 750 and its ally *D. celebica* has 300. *D. beccariana* has 130 and its ally *D. albiflos* with smaller flowers has 160. Among those with smaller flowers (5 cm wide) *D. ferruginea* has 450–490. Presumably the number indicates the amount of intercalary growth in the centrifugal androecium; if converted into centripetal growth, it would indicate floral massiveness.

FRUIT-MECHANISM

Between the two extremes of dehiscent and arillate fruit (*da*), from which the seeds are pecked by birds, and the indehiscent and exarillate fruit (*ie*), which becomes a berry enclosed in the persistent and, even, succulent sepals, there is the berry with arillate seeds (*ia*). In some of these, such as *D. grandifolia* and *D. reticulata*, the aril is described as vestigial. No case is known of a dehiscent, but exarillate, fruit.

The first point to note from Table 1 is that all the species with large flowers (n. 1–9) have indehiscent fruits, though three have arillate seeds; the biggest flower of *D. megalantha* develops this vestige in the fruit. The second point is the mixed occurrence of all these kinds of fruit in the ensuing species with flowers of medium-size until one finds that the three species with smallest flowers are consistently arillate, though the smallest (*D. pentagyna*) has an indehiscent fruit. Then, thirdly, among the species with branched inflorescence, the *da* fruit occurs in *D. albiflos*, *D. excelsa*, and *D. suffruticosa*, and the *ia* fruit occurs in *D. triquetra* and the alliance of *D. grandifolia.* Hence it is clear that the passage from *da* fruits to *ie* fruits has occurred independently in both sections of the genus, probably in several specific alliances, and independently of the floral trends, though arillate fruits seem to persist in species with the branched inflorescence. The sectional occurrence of these fruits is shown in Table 2. It appears that the amplexicaul section has *da* fruits, rather than *ie*, in accordance with its more primitive construction, and that the converse occurs in the non-amplexicaul.

Table 2. Fruits of *Dillenia*: *d*, dehiscent; *i*, indehiscent; *a*, arillate seed; *e*, exarillate seed.

	da	*ia*	*ie*	unknown
Amplexicaul species	16	6	2	11
Non-amplexicaul species	5	5	12	2
Total	21	11	14	13

CONCLUSION

The large, solitary, and terminal flowers of *Dillenia* retain the vestiges of a primitive polymerous construction. The smaller flowers, typical of the raceme in the genus, have the pentamery that prevails in other genera of the family. If to the flower of the Philippine *D. megalantha* there were added the many sepals of the Moluccan *D. pteropoda* and as many petals, there would be a primitive and cactoid effect. On a primitive and pachycaul stem, such as the great leaves of sapling *D. grandifolia* require, this terminal flower might have reached 30–40 cm in width, as a primitive anthocarp (flower-fruit) In Figure 6 I have sketched what seem to have been the steps in the reduction of this flower and the ramification of its base into the *Dillenia*-inflorescence, consequent on leptocauly and forest-building. The end of the series is *D. albiflos*, and this species shows, as does *D. suffruticosa*, that the branched inflorescence can revert into the simple while retaining the specific size of the flower; it does not revert to a more massive state. Thus it seems that at any stage of the whole sequence increasing leptocauly may have induced this apparent regression to, for example, a few-flowered raceme or even a single terminal flower. The step from stage *b* to stage *c* (fig. 6) introduces the bract from the axil of which the raceme evolves; whether Dillenia was restricted to the single and distichous raceme or other bracts developed racemes to give a clustered inflorescence (? as in *D. grandifolia* and its allies) is uncertain. The bract was, presumably, a basal sepal or a prophyll of the primitive anthocarp. Whether the raceme retained initially the sympodial or cymose construction, suggested by its first flower (as flower B in figs 2a and 3) is also uncertain. The special case of *D. pulchella* with lateral flower seems to have arisen through sterilisation of the terminal flower and its conversion into a vegetative shoot (fig. 6, *c,j,k*).

Concerning the fruit it is clear that it may become indehiscent and exarillate at any stage in the evolution of the inflorescence, as proved by the arillate seed in the indehiscence fruit of *D. megalantha* with the largest flower. Thus I perceive many subsectional lines of evolution in *Dillenia*, parallel in floral and fruit evolution, but identifiable by vegetative and androecial characters as Hoogland brings out in his classification.

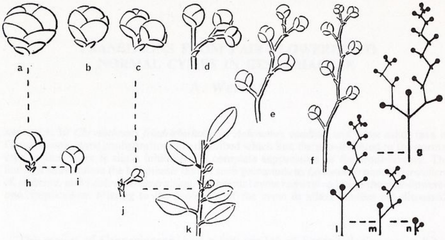

FIG. 6. Sketches of the steps in the supposed evolution of the inflorescence in *Dillenia*, from a single massive terminal flower (a-g) and the reduction of the inflorescence at various stages consequent on leptocauly (h-n). a, the massive, terminal, and multisepalous flower-bud; b, the smaller terminal flower bud with bract-like basal sepals; c, a smaller flower-bud with a lateral flower-bud from the axil of a bract; d, the beginning of the axillary inflorescence on a leptocaul twig, the flowers with 5 sepals; e, a further stage leading through that of 'f' with increasing leptocauly to the inflorescence of *D. albiflos* (g); h, i, the reduction of the single terminal flower; j, k, the evolution of the lateral flower (as in *D. pulchella*) by abortion of the terminal; l, m, n, the simplification of the branched raceme to leptocaul states comparable with the less attenuate stages 'e' and 'c'.

In a study of the American Dilleniaceae, Kubitzki (1971) has also concluded that the cymose inflorescence in the American genera has evolved from the solitary and more massive terminal flower. The flowers of these genera, with flower-buds 2–10 mm wide, are much smaller and more reduced in number of parts than those of *Dillenia* which, in vegetative character and massiveness of flower and fruit, seem to be the genus closest to the ancestral stock of the family.

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