CYTOLOGICAL STUDIES IN THE DIPTEROCARPACEAE, I.

CHROMOSOME NUMBERS OF CERTAIN MALAYSIAN GENERA

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The Dipterocarpaceae are one of the larger families of exclusively woody angiosperms. As at present understood, the family comprises 17 genera and about 490 species, unequally divided between two subfamilies: (i) Dipterocarpoideae (15 genera, approx. 450 spp.) and (ii) Monotoideae (2 genera, 34 spp.). Members of the Dipterocarpoideae are predominantly tall primary forest trees, distributed over a vast area of tropical Asia, with the richest representation in both species and genera in Borneo and the Malay Peninsula (Symington, 1943; Foxworthy, 1946). The presence on Mount Elgon in East Africa of pre-Pleistocene (probably late Tertiary) fossil dipterocarp woods, which show a remarkably close resemblance to certain extant members of the genus *Dipterocarpus*, indicates a former much wider distribution of the subfamily (Bancroft, 1933 & 1935a). The true dipterocarps, as the Dipterocarpoideae are often called, constitute one of the most important components of lowland evergreen rain forests, and include most of Malaysia's economically valuable timber species. In North Borneo (Sabah), for example, 90% of the timber extracted comes from members of this subfamily (Meijer & Wood, 1964). In addition, many species produce a resin or damar in commercial quantities. The Monotoideae, on the other hand, are a small group of dubious dipterocarp affinity, widely spread in savanna areas of tropical Africa (Bancroft, 1935b).

The taxonomy of the Asian subfamily is currently being reappraised in the light of more extensive collections in the Malaysian region, especially in Brunei, Sabah and Sarawak, and several precursory papers and foresters' manuals have recently appeared (Ashton, 1962, 1963 & 1964; Meijer, 1963; Meijer & Wood, 1964). These together with earlier works (Brandis, 1895; Foxworthy, 1932; Symington, 1943, and others) have contributed greatly to our knowledge of the family. To date, however, little is known about its cytology.

As in many tropical families, flowering in the Dipterocarpaceae is rather spasmodic, but in 1963 following a long dry period from January to April, there was an abundance of flowering material in the Malay Peninsula. From flower buds and seeds collected at this time, and in a few cases at smaller subsequent flowerings, it has been possible to determine the chromosome numbers of 19 species in 7 genera, using mainly the squash technique and its modifications. Voucher specimens are being kept at the Botany Department Herbarium, University of Malaya, Kuala Lumpur. The results are presented in Table 1.

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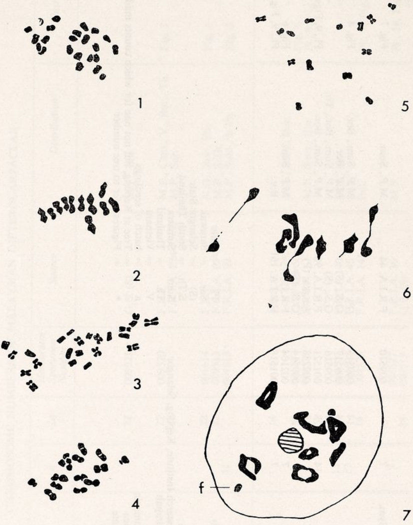
TABLE I

CHROMOSOME NUMBERS OF MALAYSIAN DIPTEROCARPACEAE

Name	*n*	*2n*	*Herbarium Specimen Number*	*Source*	*Distribution*	*Illustration*
Subfamily: Dipterocarpoideae						
Group I, x = 11						
ANISOPTERA Korth.						
A. ? laevis Ridl.		22	009521	G.S. (S)	M.P., Bor.	—
DIPTEROCARPUS Gaertn. f.						
D. baudii Korth.		22	009520	F.R.I.	M.P., Cam., V., Bur., Th.	Fig. 3
D. sarawakensis V. Sl.		c22	—	F.R.I.A. Lot 35/60^a	M.P., Sar.	—
VATICA Linn.						
V. papuana Dyer		22	001614	F.R.I.	N.G., Bor., Ph.	Fig. 1
V. stapfiana (King) V. Sl.		22	009513	F.R.I.A. 92*	M.P., S.Th.	—
V. wallichii Dyer	11		001613+	F.R.I.A. 99	M.P., Sum., S.Th.	Fig. 2
Group II, x = 7						
DRYOBALANOPS Gaertn. f.						
D. aromatica Gaertn. f.		14	—	F.R.I.A. Lot 120/62^a	M.P., Sum., Bor.	—
D. aromatica Gaertn. f.		14	001287	Lake Gardens, (S)		Fig. 5
D. oblongifolia Dyer		14	001519+	F.R.I.A.	M.P., Sum., Bor.	Pl., 9, Fig 10
HOPEA Roxb.						
H. nutans Ridl.	14		009507	F.R.I.A. 40	M.P., Bor.	—
H. pubescens Ridl.	c7		001528	F.R.I.A. 45	M.P.	—
H. wightiana Wall.		14	004529	F.R.I.A. 141	Ind.	Pl., 9, Fig. 9
BALANOCARPUS Bedd.						
B. heimii King	7		001527	F.R.I.A. 36	M.P.	Pl., 10, Fig. 15
B. heimii King		14	009519	G.S. (S)		—

SHOREA Roxb. ex Gaerth. f.						
(i) *Balau Group*						
S. sumatrana (V. Sl. ex Foxw.) Sym.	7		009510	F.R.I.A. 44	M.P., Sum.	Fig. 7
(ii) *Red Meranti Group*						
S. pauciflora King		14	009515	(P)	M.P., Sum., Bor.	Fig. 4
S. curtisii Dyer ex King		14	009517	G.S., (S)	M.P., Bor.,	—
S. leprosula Miq.		14	009516	G.S., (S)	M.P., Sum., Bor., Th.	—
S. ovalis (Korth.) Bl.	14	28	001521	F.R.I.A. 98	M.P., Sum., Bor.	Pl., 9, Figs. 11 and 12
S. ovalis (Korth.) Bl.		28	002238	Jengka, (P)		
S. ovalis (Korth.) Bl.		28	009514	G.S., (S)		
S. singkawang (Miq.) Burck	7		002104^{+}	F.R.I.	M.P., Sum.	Fig. 6
S. smithiana Sym.	7		001518	F.R.I.A. 161	Bor.	Pl., 9, Fig. 8

Key to TABLE I.
A. = Arboretum
Bor. = Borneo
Bur. = Burma
Cam. = Cambodia
F.R.I. = Forest Research Institute, Kepong, Selangor
G.S. = Genting Simpah
Ind. = India
M.P. = Malay Peninsula
N.G. = New Guinea
(P) = Pahang State
Ph. = Philippines
Pl. = Plate
Sar. = Sarawak
(S) = Selangor State
S.Th. = South Thailand
Sum. = Sumatra
Th. = Thailand
V. = Vietnam
a = batch of seedlings
\+ = Tree at Kepong, but not one for which counts made
* = Figures refer to tree number



FIGS. 1–7. Chromosomes of the Dipterocarpaceae. Camera lucida drawings. Approx. 2,000x. 1. *Vatica papuana* Dyer, somatic root tip metaphase $2n=22$, pretreated with α-bromonaphthalene for $1\frac{1}{2}$ hrs. 2. *Vatica wallichii* Dyer, pollen mother cell Metaphase I, $n=11_{\text{II}}$. 3. *Dipterocarpus baudii* Korth., somatic root tip metaphase $2n=22$, pretreated with p-dichlorobenzene (PDB) for $1\frac{1}{2}$ hrs. 4. *Shorea pauciflora* King, somatic root tip metaphase $2n=14$, pretreated with PDB for 3 hrs. 5. *Dryobalanops aromatica* Gaertn. f., somatic root tip metaphase $2n=14$, pretreated with α-bromonaphthalene for 3 hrs. 6. *Shorea singkawang* Sym., pollen mother cell Metaphase I, $n=7_{\text{II}}$. 7. *Shorea sumatrana* (V. Sl. ex Foxw.) Sym., diakinesis showing $n=7_{\text{II}}$ + fragment (f).

The results indicate that at least two basic chromosome numbers occur in this family, namely, $x = 11$ in *Anisoptera*, *Dipterocarpus* and *Vatica* (Figs. 1-3) and $x = 7$ in *Dryobalanops*, *Hopea*, *Balanocarpus heimii* and *Shorea* (see reference to figures in Table 1). The earliest records of chromosome counts in the Dipterocarpaceae are those of Tixier (1953, 1960), for several Indo-Chinese taxa. He reports diploid numbers $2n = 12$ for *Pentacme* (1)* and *Shorea* (2), and $2n = 20$ for *Anisoptera* (2), *Dipterocarpus* (6), *Hopea* (1) and *Shorea* (1), but Rao (1954) reported $2n = 14$, (a count confirmed by Roy & Jha, 1956; Nanda, 1962) for *Shorea robusta* Gaertn. f., the sãl of India, a xerophytic species that is well adapted to a monsoon climate. Tixier also remarks (1953) that there seems to be an association of a higher chromosome number $2n = 20$ with taxa possessing 2-winged fruits, and of a lower one $2n = 12$ with those that are 3-winged. The present study shows, however, that such a correlation is of doubtful validity. For example, all three of the species of *Hopea* included in the present investigation possess 2-winged fruits (the wings being enlarged sepals), but all have a lower basic number $x = 7$. Similarly, *Dryobalanops* fruits are 5-winged, but the two species we have examined have the same basic number as *Hopea* and *Shorea*, the latter typically with 3-winged fruits. Furthermore, in the genus *Vatica*, two distinct forms occur, the calyx lobes are either equal or two are larger than the other three. The three species listed in Table 1 have a higher chromosome number $2n = 22$ ($x = 11$), and all have short equal sepals.

We have as yet little indication of how the two apparently widely different basic numbers $x = 11$ and $x = 7$ are related, but Tixier's counts of $2n = 20$ and $2n = 12$ (hence $x = 10$ and $x = 6$ respectively) might suggest the presence of a dysploid series in this exclusively woody family. So far, we have not been able to confirm Tixier's results which are entirely different from ours, even though they have been derived, with the èxception of *Pentacme*, from some of the genera we have examined†. It is clearly necessary to conduct a more extensive survey before the full range of basic numbers occuring in the Dipterocarpaceae is determined.

Two of the taxa we have examined are tetraploids; they are *Shorea ovalis* and *Hopea nutans*, both with $n = 14$.

Shorea ovalis (Korth.) Bl. ($2n = 4x = 28$).

S. ovalis is a polymorphic species, consisting of three fairly distinctive vegatative forms, each of which has been accorded subspecific rank by Ashton (1963). Two of these are represented in the Malay Peninsula (Symington, 1943); the other is restricted to Sabah, Sarawak and Brunei (Meijer & Wood, 1964). The chromosome numbers listed in Table 1 for this species are for the common form from the Malay Peninsula, which has

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*Figures in parentheses refer to number of taxa.

†Since this paper went to press, a publication reporting further cytological observations in five species of Indian dipterocarps has appeared (Roy and Jha, 1965: J. Indian Bot. Soc. 44 : 387–397).

Chromosome numbers recorded are:- *Dipterocarpus alatus* Roxb., *Vatica grandiflora* Dyer ($2n = 22$); *Hopea odorata* Roxb., *Shorea robusta* Gaertn. f., *Shorea talura* Roxb., ($2n = 14$).

All these counts conform to the two basic numbers $x = 11$ and $x = 7$ found by us in the same genera, but their counts for *D.alatus* and *H. odorata* disagree with those published by Tixier (1953).

larger, distinctly boat-shaped leaves. An analysis of meiosis reveals the presence at Metaphase I of varying proportions of quadrivalents, trivalents, bivalents and univalents in all the pollen mother cells examined (Plate 9 Figs. 13 & 14), but this irregularity in chromosome pairing did not seem to appreciably lower pollen fertility, which is 88% (Jong & Lethbridge, 1964) A fuller analysis of meiosis is continuing, and details will be published later.

Hopea nutans Ridl. ($2n = 4x = 28$).

This is a scaly-barked *Hopea* which belongs to the same section as *H. wightiana*, an Indian species which has a diploid number of $2n = 14$ (Plate 9 Fig. 9). Clearly *H. nutans* is a tetraploid based on $x = 7$; Tixier (1953), however, reports $2n = 20$ for another species of the same section, *H. odorata* Roxb.

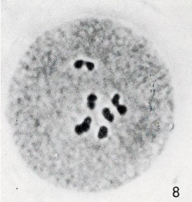
POSITION OF BALANOCARPUS

Balanocarpus heimii King ($2n = 14$).

The systematic position of *B. heimii*, the only species of its genus, has remained uncertain up to the present (Symington, 1943; Ashton, 1963), although available evidence suggests that it is more closely related to the genus *Hopea* (especially section *Hopea*) than to any other groups (Desch, 1941; Bate-Smith & Whitmore, 1959; Whitmore, 1962). It has a haploid number of $n = 7$ (Plate 10, Figs 15 and 17), therefore cytologically conforming with the base number found in other related genera of its tribe *Shoreae*. But, it exhibits certain irregularities during meiosois; varying numbers of univalents (range two to eight per cell) and bivalents being present at Metaphase I (Plate, 10 Fig. 16). Of the pollen mother cells analysed, 80% contained at least 2 univalents. Multivalents, however, have not been observed. Anaphase I and II were correspondingly irregular (Plate 10, Figs. 18–20). Approximately 30% of pollen mother cells showed irregular disjunction of chromosomes at the first anaphase. A small percentage contained laggards and micronuclei (Plate 10 Figs. 19 & 21), and deviant chromosome numbers. Such aberrations in the meiotic process normally lead to the production of chromosomally unbalanced gametes, resulting in lowering of pollen and seed fertility. We hope to confirm this in subsequent work.

It is difficult at this stage to give a satisfactory explanation of the meiotic behaviour in *B. heimii*. Due consideration must be given firstly to the fact that flower buds from only a single tree were available for analysis, so any generalisations concerning this species must await a more detailed study. Secondly, the material was collected during the prolonged dry period of 1963. The possibility that environmental factors were responsible for its abnormal meiotic behaviour cannot therefore be excluded. This has been demonstrated for other plants which had been subjected to unusual environmental conditions, such as high temperatures, by Dowrick, (1957), Dyer (1964) and others.

Also, Foxworthy (1932, p.30) observes that ripening of dipterocarp seeds seems to be affected by moisture conditions prevailing at the time, a greater percentage of sound and larger seeds being produced when ripening occurred during wet weather than very dry weather. He adds that trees of *B. heimii* (and *Shorea curtisii*) which are unfavourably situated may produce a crop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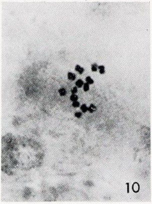
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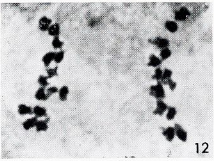
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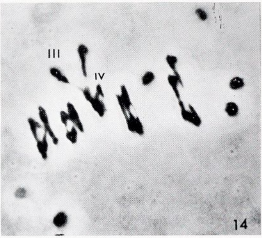

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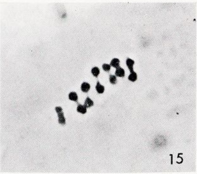
PLATE 9.

FIGS. 8–14. All approx. 2,000x. 8. *Shorea smithiana* Sym., pollen mother cell Metaphase I, $n=7_{II}$. Two of the bivalents at the bottom left of the photograph are overlapping. 9. *Hopea wightiana* Wall., somatic root tip metaphase $2n=14$, pretreated with PDB for 3 hrs. Note the presence of one pair of satellited chromosomes. 10. *Dryobalanops oblongifolia* Dyer, somatic root tip metaphase $2n=14$, pretreated with α-bromonaphthalene for 3 hrs. 11. *Shorea ovalis* (Korth.) Bl., somatic root tip metaphase $2n=4x=28$, pretreated with 0.02% colchicine for $2\frac{1}{2}$ hrs.

FIGS. 12–14. Meiotic figures in *Shorea ovalis* (Korth.) Bl., 12. Anaphase I, $n=14$. 13. Metaphase I chromosome configutation $6_{II} + 4_{IV}$–chromosomes in 2 of the bivalents have probably separated precociously. 14. Metaphase I, $3_{I} + 1_{II} + 1_{III} + 5_{IV}$.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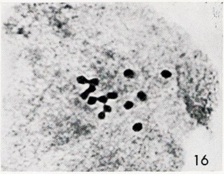
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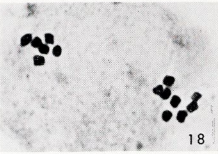
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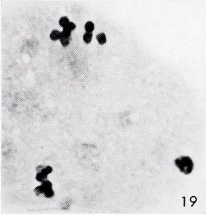
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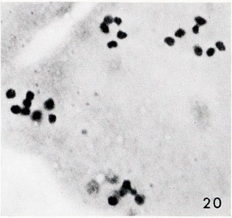
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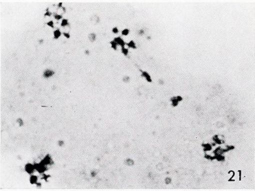
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PLATE 10.

FIGS. 15–21. Meiotic figures in *Balanocarpus heimii* King. 15. Metaphase I, $n=7_{II}$. 16. Metaphase I, $4_{II} + 6_{I}$. 17. Regular Metaphase II, $n=7$. 18. Metaphase II, showing $6 + 8$ distribution as a result of irregular disjunction. 19. Late Anaphase I, with micronucleus; 8 chromosomes can be seen at one pole. 20. Anaphase II showing irregular distribution of chromosomes, $8 + 5 + 7 + ?$ 21. Early Telophase II, showing lagging chromosomes (All figures ×2000).

of small, mostly inviable seeds. Apart from the possible direct adverse effects of very dry weather on seed development, however, defective seeds may also be the product of unbalanced gametes, a point already alluded to earlier.

On the other hand, it is possible that the meiotic pattern observed in this provenance (001527) of *B. heimii* may indeed be typical of the species, suggesting a probable hybrid origin for the taxon. Although Ashton (pers. comm.) expresses the opinion that there is no reliable evidence of interspecific or intersectional hybridization among the dipterocarps, such a possibility as postulated for the origin of *B. heimii* should not be dismissed without further investigation.

GENERAL CYTOTAXONOMIC CONSIDERATIONS

Although the limited cytological information at our disposal does not permit a full discussion of its implications in relation to taxonomy of the Dipterocarpaceae, there are several points which are worth mentioning at this juncture. These will be confined to a consideration of the chromosome number only, as no comparisons of chromosome morphology nor chiasma frequency have yet been undertaken.

Our results as summarised in Table II tentatively show that:–

(i) Malaysian genera which have been examined by us may be divided into two broad groups, each of which is characterised by a single common basic chromosome number.

TABLE II

Basic Chromosome Number	*Groups of Genera*
$x = 11$	I Anisoptera Dipterocarpus Vatica
$x = 7$	II Dryobalanops Hopea Balanocarpus Shorea

(ii) Genera in Group I have a higher basic number $x = 11$. All are considered on systematic grounds (see Ashton, 1963 & 1964) to be clearly defined, homogenous, natural genera which are not closely related to one another.

It should be noted, however, that on the basis of both wood anatomical features (Desch, 1941) and chromosome number, the genus *Vatica* probably has a closer affinity with members of the tribe Dipterocarpeae (*Anisoptera* and *Dipterocarpus*) than suggested by either morphological or chemical criteria.

(iii) Those in group II all have a lower basic number $x = 7$. With the exception of *Dryobalanops*, the other genera are all more or less closely related to one another, belonging to the tribe Shoreae which is quite distinct from the rest of the family (Ashton, 1964). This tribe also includes *Pentacme*, *Doona* (endemic to Ceylon) and *Parashorea*.

Dryobalanops, a small genus of about 7 species, is represented in the Malay

Peninsula by *D. aromatica* and *D. oblongifolia*. It is very distinct and clearly differentiated from all other groups of dipterocarps. Although it has a basic number x = 7, suggesting a closer alliance of the genus with others in Group II, its position must nevertheless remain uncertain, owing to the lack of other corroborating evidence (cf. Bate-Smith & Whitmore, 1959 and Desch, 1941).

Stebbins (1938), has shown that there is a greater stability of the basic number among woody than among herbaceous genera, and Darlington (1956) points out that in view of the immense constancy of the chromosomes of woody plants, it is groups of genera, not of species, that provide the interesting comparisons. So far as our results show, this seems to be true of the Dipterocarpaceae. Not only does the basic number appear to remain constant within a single genus, but between groups of genera. It is characteristic of groups of genera rather than species. Even in large heterogeneous genera like *Hopea* and *Shorea*, each of which is divided into numerous sections and subsections (Symington, 1943, Ashton, 1963), morphological divergence has obviously occurred mainly at the diploid level, with no accompanying alterations in the basic chromosome number. The only numerical variation so far encountered among Malaysian species is in these two genera, one involving polyploidy. It is not known to what extent polyploidy is a source of morphological and adaptive diversity among the dipterocarps, but its contribution is likely to be small. The possibility that dysploidy may also be involved has already been referred to earlier in this paper. Nevertheless, conclusive evidence for this and other problems of dipterocarp cytology can only be provided by a much more extensive and detailed survey of the family and its relatives.

Although the chromosome number of woody plants appears to be generally stable, evidence derived from extensive cytological studies of several Australian hardwood families indicate that "endemic or near endemic groups exhibit marked diversity in chromosome number compared with related extra-Australian groups" (Smith-White, 1959, p. 280). A cytological survey of the Dipterocarpaceae should therefore include not only the endemic genera, as for example those of Ceylon and Africa, but also groups which are at the limits of their distributional range. This may reveal cytological differences and relationships that are not yet apparent at the centre of distribution of the family.

One further point of only theoretical interest at the present stage concerns the presence of two very different basic chromosome numbers x = 11 and x = 7 within the Asian subfamily, and the difference in the amount of genetic recombination that this represents in the two groups of genera. The importance of the number of chromosomes and chiasma frequency as one of the many factors controlling recombination in plants has been emphasised by many authors (Darlington, 1958; Grant, 1958; Stebbins, 1950). Purely on consideration of the chromosome number alone, "a greater number of recombinations will arise if the genes are distributed among many chromosomes than if they are grouped on a few" (Grant, 1958, p. 339). Similarly, assuming the dipterocarps to have normal sexual reproduction, the amount of variability released at each reproductive cycle in those with a relatively higher chromosome number x = 11 is expected to be much greater than in those with a relatively lower one of x = 7. Consequently, this must have a significant effect on the evolutionary potentialities and adaptive diversification between the two groups of dipterocarp genera.

We have, however, as yet little knowledge of the genetic system in the Dipterocarpaceae, and since most of the species are great towering trees, some among the tallest in the tropical rain forest, there are special practical difficulties involved in their study, but as in a large majority of plants of the humid tropics, much remains to be discovered.

ACKNOWLEDGEMENTS

We gratefully acknowledge the valuable assistance and cooperation of the Forest Research Institute, Kepong, Selangor, in providing us with the services of a tree-climber and with material from its Arboretum. In particular we wish to thank Messrs Yong and Ng, of the above Institute, who assisted in collection of material in the field.

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