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Cytotaxonomy of Meliaceae

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Interrelations within the family differ according to authors. Sequences that have been suggested are:

1) Bentham and Hooker (1862) — *Melieae* — *Trichilieae* — *Swietenieae* — *Cedreleae*.
2) Kribs (1930) — *Swietenioideae* — *Melioideae* — *Lovoinoideae*.
3) Scholz (1964) — *Cedreloideae* (*Cedeleae* — *Ptaeroxylae*) — *Swietenioideae* — *Melioideae* (*Carapeae* — *Turraeae* — *Vavaceae* — *Melieae* — *Trichilieae*).
4) Hutchinson (1969) — *Cedreleae* — *Swietenieae* — *Trichilieae* — *Melieae*.

So the attempt was to collect as much informations as possible, of the chromosome number and morphology and to try those informations in solving some controversies.

Materials and methods

Root tips from cuttings were squashed by usual aceto-orcein technique after pretreatment with saturated solution of aesculine. Figures were drawn with camera-lucida at a projected magnification of 2200, which were drawn by enlarging thrice by projecting.

The species are: *Melia azedarach* L. (Indian Botanic Garden, Calcutta, P. Samanta, 34); *Azadirachta indica* A. Juss. (Indian Botanic Garden, Calcutta, P. Samanta, 35); *Walsura piscida* Roxb. (Indian Botanic Garden, Calcutta, P. Samanta, 38); *Aglaia odorata* Lour. (Indian Botanic Garden, Calcutta, P. Samanta, 37); *Swientenia macrophylla* King ;Indian Botanic Garden, Calcutta, P. Samanta, 32); *S. mahagoni* Jacq. (Indian Botanic Garden, Calcutta, P. Samanta, 33); *Toona ciliata* Roem. (Indian Botanic Garden, Calcutta, P. Samanta, 34).

Results and conclusion

Karyotype and chromosome number

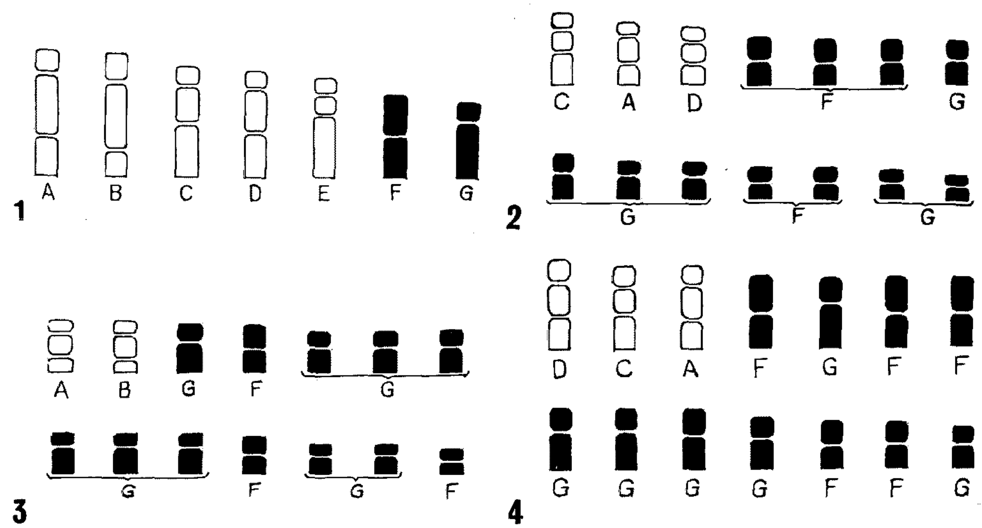
Chromosome study of this woody family is very difficult, particularly for troubles in staining. The seven species examined here show the following chromosome types (Fig. 1):

A: Of the three segments formed by two constrictions, the middle longest, two terminals shorter and unequal.

B: Of the three segments formed by two constrictions, the middle longest, two terminals shorter and equal.

C: Of the three segments formed by two constrictions, the shortest and the longest at two ends.

D: Of the three segments formed by two constrictions, the shortest at one end, the other two longer and equal.



Figs. 1–4. 1, chromosome types observed in the study. 2, idiogram for *Melia azedarach*. 3, idiogram for *Azadirachta indica*. 4, idiogram of *Walsura piscida*.

E: Of the three segments formed by two constrictions, the longest at one end, the other two shorter and equal.

F: One median constriction forming equal arms.

G: One submedian constriction forming unequal arms.

On this basis, the karyotype of the seven species can be represented in Table 1 (Figs. 2–8). Meiosis was studied in *Azadirachta indica*, which revealed clear 14 bivalents in metaphase I and 14 chromosomes in metaphase II. Division was normal.

Table 2 represents the reports of chromosome numbers of Meliaceae.

Basic numbers for the family

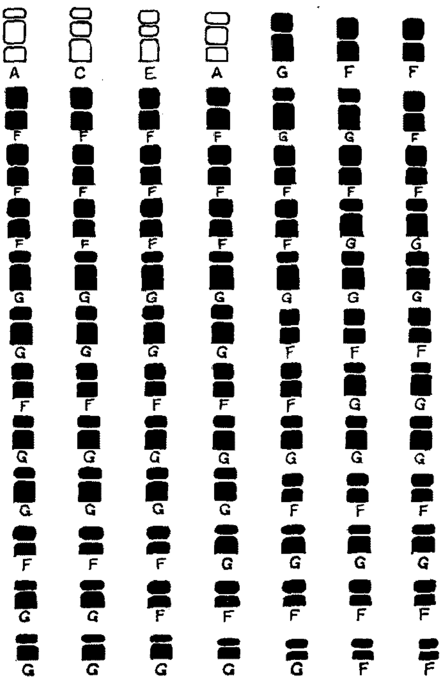
Although the family has been variously related to other taxa by different taxonomists, recent anatomical (Heimsch 1942, Metcalfe and Chalk 1950) and chemotaxonomical (Charkavorty and Datta 1969) studies showed that Rutaceae, Simaroubaceae, Sapindaceae, Burseraceae, Anacardiaceae and Meliaceae form a more or less natural group. The basic numbers of chromosome are: 9 and 10 for Rutaceae, 9 for Simaroubaceae; 10–11 for Sapindaceae, 13 for Burseraceaev 10–14 for Anacardiaceae (vide Darlington and Wylie 1955).

In Meliaceae, the reported numbers are mostly multiples of 9, 10, 11, 12, 13 and 14.

In tribe I *Melieae*, x=14 (in *Melia*, *Azadirachta* and *Pterorhachis*), or 12 (if 2n=50 is derived as $12\times4+2$, that is two chromosomes are added to a tetraploid as in

Turraea and *Cipadessa*. Similarly 2n=58 in *Calodecaryia, Naregamia, Nymania, Munronia* may be derived as 14×4+2, that is two chromosomes were added to a tetraploid with basic 14.

In tribe II *Trichilieae* of B. and H., *Dysoxylum, Amoora, Aglaia, Turracanthus* have (9–10)×4, 8 or 10, *Sandoricum* x=11; *Chisocheton* (11×4+2), *Lansium, Guarea,*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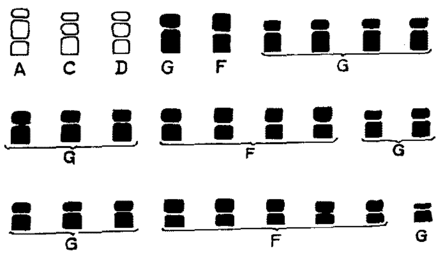
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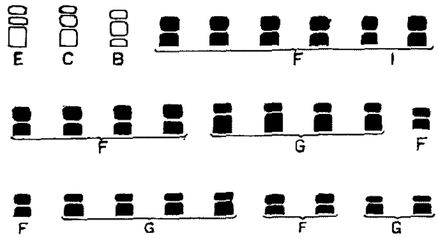
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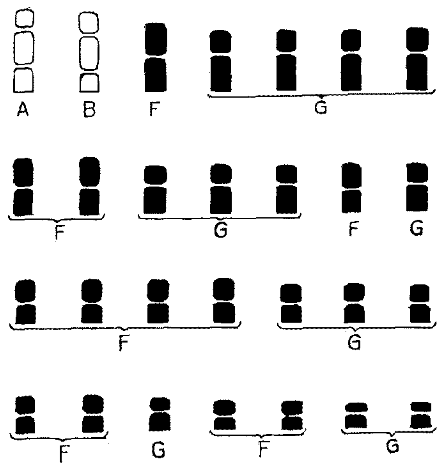
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Figs. 5–8. 5, idiogram of *Aglaia odorata*. 6, idiogram of *Swietenia macrophylla*. 7, idiogram of *S. mahagoni*. 8, idiogram of *Toona ciliata*.

etc. x=12 (12×6); *Heynea, Trichilia, Walsura,* x=14 (14×2); *Pseudobersama, Trichilia, Ekebergia, Lepidotrichilia* x=12 (12×4+2 or −2=50 or 46); *Carapa* and *Xylocarpus* x=14 (14×4 or 14×4+2); *Aphanamixis* has probably 9×4.

In tribe III *Swietenieae, Swietenia, Soymida* and *Pseudocedrela* have x=13 (13×4, or 13×4+2), *Khaya, Neobeguea, Lovoa* have probably 12×4 or 12×4+2, *Chukrasia* 13×2, *Entrandrophragma* 12×3 or 12×6 (secondarily balanced).

In tribe IV *Cedreleae, Cedrela* and *Toona* have x=12, 13 or 14 (12×2, 12×4, 12×4+2, 13×4, 13×6, 14×4).

It seems that from lower basic numbers like 9 or 10, the higher basic numbers like 11, 12, 13 or 14 have evolved in the interlinked plexus of Rutaceae, Meliaceae, Simaroubaceae, Burseraceae, Anacardiaceae and Sapindaceae. But the links are almost impossible to trace. Since all the basic lines are represented by the family Meliaceae, a polyphyletic origin of the genera of the family seems to be the most

Table 1. Chromosome characters of a few species examined here

Species	2n	Size range	Complements; chromosome types with or without constrictions			Position of primary constrictions*
Melia azedarach	28	0.7–1.3–2.2	with	2A	6	sm
				2C		m
				2D		sm
			without	10F	22	m
				12G		sm
Azadirachta indica	28	0.7–1.2–1.6	with	2A	4	sm
				2B		sm
			without	6F	24	m
				18G		sm
Walsura piscida	28	1.18–1.88–2.65	with	2A		sm
				2C	6	m
				2D		sm
			without	10F	22	m
				12G		sm
Aglaia odorata	168	0.6–1.0–1.5	with	4A		sm
				2C	8	m
				2E		m
			without	80F		m
				80G	160	sm
Swietenia macrohylla	54	0.6–1.0–1.6	with	2A		sm
				2C	6	m
				2D		sm
			without	20F	48	m
				28G		sm
S. mahagoni	54	0.51–0.9–1.5	with	2B		sm
				2C	6	m
				2E		m
			without	28F	48	m
				20G		sm
Toona ciliata	56	0.7–1.4–2.6	with	2A	4	sm
				2B		sm
			without	24F	52	m
				28G		sm

* m=median; sm=submedian.

Table 2. Reports on chromosome number (arrangement mainly based on Bentham and Hooker 1862)

Species	Chromosome number n	Chromosome number 2n	Authors
Tribe I. MELIEAE			
Turraea floribunda Hochst.	—	58	Minfray 1963b
T. heterophylla Sm.	—	50	Mangenot and Mangenot 1957
T. nilotica Kot. and Peyr.	—	50	–do–
T. obtusifolia Hochst.	—	50	–do–
T. robusta Grüke	—	50	–do–
T. sp. Nov.	—	50	–do–
T. yogelioides Bagsh	—	50	–do–
**Calodecaryia crassifolia* J. F. Leroy	—	58	Minfray 1963b
	—	36	Styles and Vosa 1971
Naregamia allata Wight and Arn.	—	58	Minfray 1963b
	—	46	Styles and Vosa 1971
**Nymania capensis* (Thunb.) Lindo	—	58	Minfray 1963b
	—	40	Styles and Vosa 1971
Munronia pinnata (Wall.) Harms	—	58	Minfray 1963b
	—	50	Styles and Vosa 1971
Melia azedarach L.	—	28	Minfray 1963
	—	28	Pathak *et al.* 1949
	—	28	Bowden 1945
	—	28	Gadella *et al.* 1966
	—	28	Present report
	14	—	Zerpa 1953
M. azedarach var. "*gigante*"	14	—	Mehra and Khosla 1969
M. composita Willd.	14	—	–do–
Melia floribunda Curr.	—	28	Minfray 1963b
M. toosandan Sieb. and Zucc.	—	28	Minfray 1963b
Azadirachta indica A. Juss.	—	30	Mangenot and Mangenot 1958
	—	28	Bowden 1945
	—	28	Pathak *et al.* 1949
	14	—	Mukherjee 1952
	14	28	Present report
Cipadessa baccifera (Roth.) Miq.	—	50	Mangenot and Mangenot 1957
C. cinerascens (Pell.) Hand.-Zazz.	—	50	–do–
Tribe II. TRICHILIEAE			
Dysoxylum binectariferum Hk. f.	40	—	Mehra and Khosla 1969
D. hamiltonii Hiern	40	—	–do–
D. pachyphyllum Hems.	40	—	–do–
D. pallens Hiern	10	—	–do–
D. procerum Hiern	40	—	–do–
D. ramiflorum Miq.	36, 38	—	Paetow 1931
D. spectabile (Frost. f.) Hk. f.	42	—	Beuzenberg and Hair 1963
**Turraeanthus africana* (W.) Pell.	—	150	Mangenot *et al.* 1957
	—	100	Mangenot and Mangenot 1962

Table 2 (Contd.)

Species	Chromosome number		Authors
	n	2n	
Chisocheton paniculatus Hiern	23	—	Mehra and Khosla 1969
Sandoricum indicum Cav.	—	16, 32	Tixier 1958
S. koetjape (Burm. f.) Merr.	11, 22	—	Ramirez 1961
Aglaia edulis A. Gray	40	—	Mehra and Khosla 1969
Ag. odorata Lour.	—	168	Present report
Ag. perviridis Hiern	20	—	Mehra and Khosla 1969
Lansium domesticum Corr.	72	—	Bernardo and Ramirez 1959
Aphanamixis polystachaya Park.	18	—	Mehra and Khosla 1969
A. rohituka (Roxb.) Pierre	—	76	Minfray 1963b
Amoora spectabilis Miq.	20	—	Mehra and Khosla 1969
Guarea cedrata (A. Chev.) Pell.	—	150	Mangenot *et al.* 1957
G. thompsonii sp. and Hut.	—	c. 72	Mangenot and Mangenot 1962
	—	72	Mangenot and Mangenot 1957
Leplaea mayobenis (Pell.) Staner.	—	72	Styles and Vosa 1971
Ekebergia benguelensis (Well) C. DC.	—	50	Mangenot and Mangenot 1957
E. capensis Sparrm	—	50	Mangenot and Mangenot 1957
**Capuronianthus mahafalensis* Leroy	—	58	Minfray 1963a, b
Carapa grandiflora Spr.	—	56	Minfray 1963a
C. guianensis Aubl.	—	58	Minfray 1963a
Carapa procera DC.	—	58	Minfray 1963a
Xylocarpus granatum Koen.	—	58	-do-
X. moluccensis (Lam.) M. J. Roem.	—	58	-do-
Walsura piscida Roxb.	14	28	Ghosh 1961, 1968
	—	28	Present report
Heynea trijuga Roxb.	—	24	Nanda 1962
	14	—	Mehra and Sareen 1969
Lepidotrichilia volkensee Leroy	—	50	Mangenot and Mangenot 1957
	—	38	Styles and Vosa 1971
Pseudobersama mosambicensis (Sim) Verdc.	—	50	Mangenot and Mangenot 1957
	—	46	Styles and Vosa 1971
**Pterorachis zenkeri* Harms	14	28	Nanda 1962 Mehra and Sareen 1969 Styles and Vosa 1971
Trichilia amentica	—	50	Mangenot and Mangenot 1957
Tr. cannaroides (W. and A.)	14	—	Rao 1967
	14	—	Mehra and Sareen 1969
Tr. dregeana Sond	14	—	-do-
Tr. emetica Vahl	—	50	Mangenot and Mangenot 1957
Tr. hendelottii Plan.	—	50	-do-

Table 2 (Contd.)

Species	Chromosome number		Authors
	n	2n	
Tr. lanata A. Chev.	—	50	–do–
Tr. odorata Andr.	—	92	Minfray 1963b
Tr. prieuriana A. Juss.	—	50	Mangenot and Mangenot 1957
Tr. rubescens Oliv.	—	50	Mangenot and Mangenot 1957
Tribe III. SWIETENIEAE			
Swietenia humilis Zucc.	—	50, 52	Minfray 1963a
Sw. macrophylla King	—	54	–do–
	—	54	Present report
Sw. mahagoni (L.) Jacq.	—	46–48	Krishnaswamy and Raman 1949
	—	54	Present report
Khaya anthotheca (Welw.) C. DC.	—	50	Mangenot and Mangenot 1957
K. grandifoliola C. DC.	—	50	–do–
K. ivorensis A. Chev.	—	50	–do–
	—	46–48	Miege 1954
K. madagascariensis Jumel. and Perr.	—	50	Mangenot and Mangenot 1957
K. nyasica (Des.) Juss.	—	50	Miege 1960
	—	46	Minfray 1963a, b
	—	50	Mangenot and Mangenot 1958
K. senegalensis (Desv.) Juss.	—	50	Miege 1960; Mangenot and Mangenot 1958
K. senegalensis	—	46	Minfray 1963b
Soymida febrifuga Juss.	—	52	Minfray 1963a
Soymida febrifuga	—	56	Styles and Vosa 1971
Chukrasia tabularis Juss.	13	—	Rao 1967
**Entandrophragma angolense* (Welw.) C. DC.	—	36, 72	Nanda 1962; Mangenot and Mangenot 1957
	—	66	Miege 1954
E. cordatum (Spr.) Spr.	—	36	Mangenot and Mangenot 1957
E. cylindricum Sp.	—	36, 72	–do–
E. delevoyi DC. Wild.	—	36	–do–
E. exelsum (Dawe) Spr.	—	36	Mangenot and Mangenot 1957
E. utile (Dawe and Spr.) Spr.	—	72	–do–
Lovoa swynnertonii Bak. f.	—	52	Styles and Vosa 1971
L. trichilioides Harms	—	50	Mangenot and Mangenot 1957
Neobeguea mahafalensis Leroy	—	50–52	Minfray 1963b.
	—	50	Styles and Vosa 1971
Pseudocedrela kothchoyi (Schweinf.) Harms	—	50, 52	Minfray 1963
Tribe IV. CEDRELEAE			
Cedrela angustifolia Sesse and Moc. ex C. DC.	—	46, 48	Krishnaswamy and Raman 1949
C. fissilis Vell.	—	46, 48	–do–
C. mexicana M. Roem.	—	56	Minfray 1963b
C. microcarpa DC.	12	—	Mehra and Khosla 1969

Table 2 (Contd.)

Species	Chromosome number		Authors
	n	2n	
C. odorata Linn.	—	50–52	Simmonds 1954
C. sinensis A. Juss.	—	56	Minfray 1963b
Toona ciliata M. Roem	26	—	Mehra and Sareen 1969
	28	—	Mehra and Khosla 1969
	—	56	Singh 1951
	—	56	Present report
T. ciliata var. *pillistaminea* C. DC.	39	—	Mehra and Khosla 1969
T. ciliata var. *toona*	28	—	-do-
T. microcarpa (C. DC.) Harms	12	—	-do-
T. serrata (Royle) Roem.	—	52	Mehra and Sareen 1969
T. sinensis (A. Juss.) Roem.	—	56	Minfray 1963a

* Not mentioned by Benthan Hooker. This position is based on Harms (1940) modified by Leory (1958) and Styles and Vosa (1971).

reasonable conclusion. The various high chromosome numbers represented by the family can only be explained by assuming their evolution through alloploidy, autoploidy and aneuploidy from the mentioned basic numbers.

Possible trends of evolution of chromosome number in Meliaceae:

It is very difficult to discover a clear principle of evolution of the chromosome numbers of the family, where occurrence of so many secondary basic numbers and high levels of heteroploidy are apparent. Lower basic numbers and diploids should be regarded as lower in gradation. Homoploids (4n, 6n, 8n) should be regarded less advanced than aneuploids (4n+2, 6n+2, 8n+2, etc.). On the basis of this assumption we have made arbitrary divisions or steps of advancement: 1) (x=9, 2n); 2) 9×2+2 (i. e. 2n+2)=10×2 (n=10); 3) 9×4; or 10×2+2=11×2; 4) 9×6 or 8; or 9×4+2, 11×3—1; 5) 10×4; or 11×2+2=12×2; 6) 10×6 or 8; 10×4+2; 7) 10×10; 11×4; or 12×2+2=13×2; 8) 11×6 or 8; 11×4+2; 9) 12×4; or 13×2+2=14×2; 10) 12×6 or 8; or 12×4+2 or 12×4—2; 11) 13×4; or 14×2+2=15×2; 12) 13×6 or 8; or 13×4+2; 13) 14×4; or (15×2+2=16×2); 14) 14×6 or 8; or 14×4+2. Bracketed conditions are rare in reports.

Thus in *Melieae* (and *Turraeeae*), two basic lines of numerical change of chromosomes are noticed (Fig. 9). One from 12×2 to 12×4 to 12×4+2 in *Turraea* and *Cipadessa*. The other of 14×2 in *Pterorhachis, Melia* and *Azadirachta,* then to 14×4+2 in *Calodecaryia, Naregamia, Nymania* and *Munronia. Calodecaryia* probably evolved earlier with 9×4 chromosomes. *Cipadessa* (2n=50) has been placed in *Trichilieae* by Styles and Vosa (1971). But both chromosome number and external morphology suggest a relation in *Turraea.*

In *Trichileae* of older classifications, one line is from (9×2) to 9×4 in *Aphanamixis* and *Dysoxylum,* another is from 10×2 to 10×4 (*Amoora, Aglaia*) to 10×8 (*Aglaia, Dysoxylum*), to 10×10 (*Turraeanthus*), the third is from 11×2 to 11×4+2 (*Chisocheton*), the fourth is 12×2 to 12×6 (*Lansium, Guarea* and *Leplaea*). These

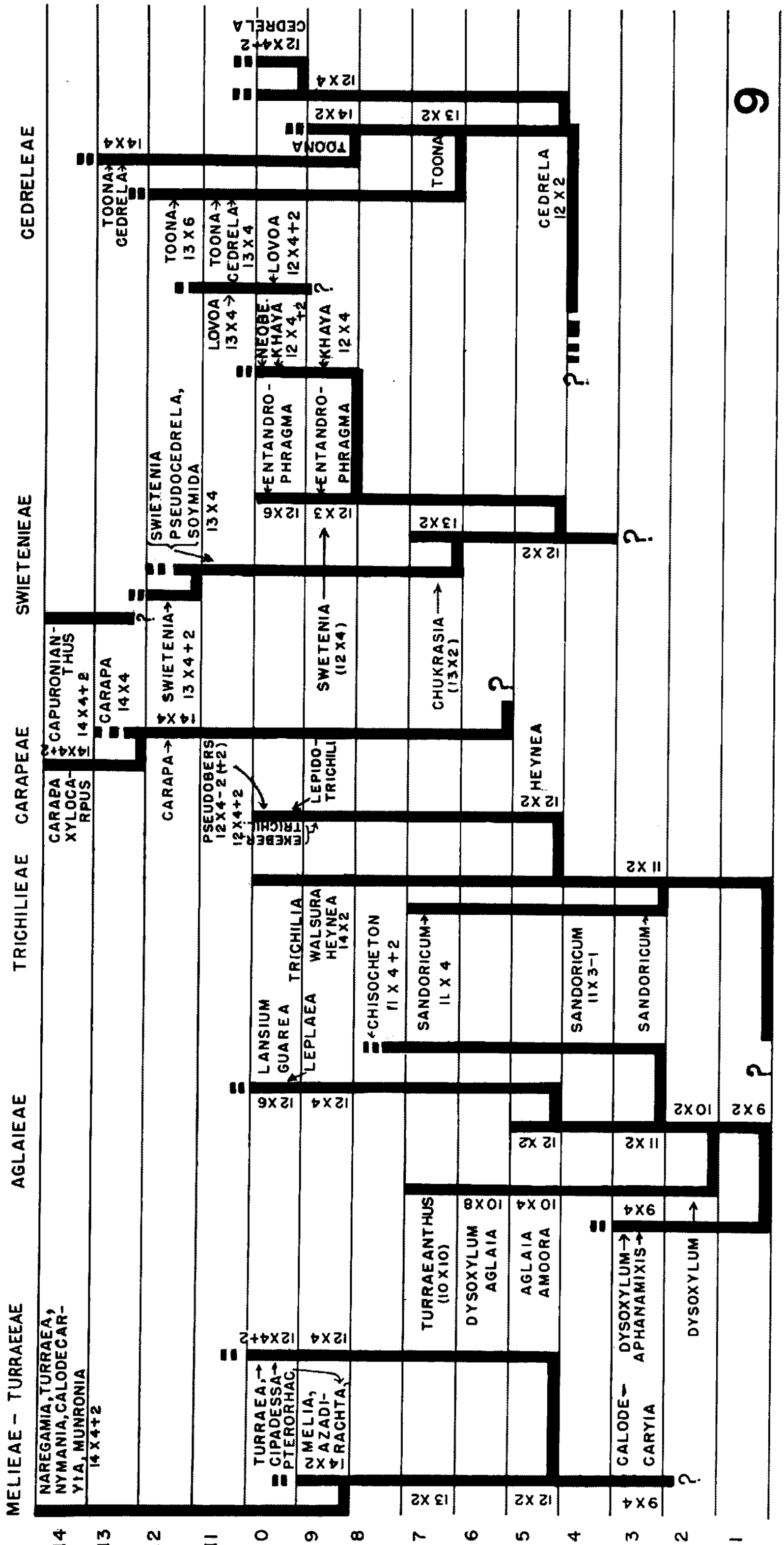

Fig. 9. Tentative plan of evaluation of chromosome number in Meliaceae.

genera form a distinct morphological group (*Aglaieae*) (Datta and Samanta, In press). The fifth is from 12×2 to 12×4 to 12×4+2 or 12×4−2 (*Heynea, Trichilia, Ekeberaia, Lepidotrichilia, Pseudobersama*); which has a side line 14×2 (*Trichilia, Walsura, Heynea*); the sixth line is from 11×2 to 11×3−1 to 11×4 (*Sandoricum*). *Trichilia* shows very much heterogeneity, 2n=50 (12×4+2), 92 (12×8−4?) and 2n=28 (14×2). In this tribe, the new *Trichilieae* are anatomically and chemotaxonomically distinct, from genera of *Aglaieae* (Fig. 9) (Datta and Samanta 1975, Chakraborty and Datta 1969), in which 11×2 (*Sandoricum*) and 11×4 (*Sandoricum*) form one branch, 11×2 to 12×2 to 13×2 to 14×2 (*Walsura, Heynea* etc.) form another branch. *Carapa* and *Xylocarpus* (14×4 to 14×4+2) are cytologically related. Minfray (1963a, b) suggested placing *Carapa* near *Capuronianthus*. Styles and Vosa (1971) have, however, suggested conclusively that *Carapa* and *Xylocarpus* should be placed in their own tribe under *Swietenioideae* not under *Melioideae* (Della De Torre and Harms) nor in the tribe *Trichilieae* (Bentham and Hooker). Wood anatomy (Datta and Samanta 1975) and chemical informations (Chakraborty and Datta 1969) support this conclusion. *Capuronianthus*, though has the same number as that of *Carapa* and *Xylocarpus*, for morphological difference appears as a distinct line of uncertain origin (Capuronianthoideae).

Swietenieae probably started from 12×2 (not reported) and evolved in two lines, one of 13×2 (*Chukrasia*), 13×4 (*Sovmida, Pseudocedrela* and *Swietenia*) and 13×4+2 (*Swietenia*), and the other of 12×3 and 12×6 (*Entandrophragma*) and 12×4 to 12×4+2 (*Khaya, Neobeguea*). Although *Lovoa* has the chromosome number similar to *Khaya, Swietenia*, etc. for morphological and anatomical difference (Kribs 1930) should be regarded as a different line (Lovoinoideae).

Tribe *Cedreleae* needs special mention. Probably 12 was the original basic number (e. g. *Cedrela microcarpa* with 2n=24) from which has evolved the tetraploids (2n=48) in *C. angustifolia, C. fissilis*. Probably from that evolved the aneuploid numbers 50 (12×4+2). Another line from 13×2 to 42 (=13×4) has evolved in *C. odorata*. Thus a secondary basic number 13 arrived in *C. odorata* and *T. T. serrata*. Haploid number 39 in *Toona ciliata* var. *pillistaminea* is a hexaploid of that number (13×6). Probably by similar progressive aneuploidy a tertiary basic number 14 evolved in *T. ciliata, T. sinensis* and *C. mexicana*.

Chromosome morphology appears similar in all the seven species studied here. Length of chromosomes is not different in different species. Number of secondary constriction is proportionately highest in *Melia azedarach*, lowest in *Aglaia odorata*. Submedian primary constrictions (i. e. unequal arms) have the highest proportion in *Melia* and lowest in *Aglaia*. These facts support a low position of *Aglaia*, as suggested in the chromosome number chart (Fig. 9). The difference between the chromosome length within a complement is highest in *Melia* (Melioideae) and *Toona* (Swietenioideae) and lowest in *Walsura*. On the whole, the chromosome morphology suggests that *Azadirachta, Aglaia* and *Walsura* are comparatively primitive, *Melia, Swietenia, Toona* and *Cedrela* comparatively advanced.

Summary

Cytological informations of the family Meliaceae suggest 9, 10, 11, 12, 13 and 14 as basic numbers. Numbers have evolved from lower to higher. In *Melieae* 14 is the basic number. In old *Trichilieae* the numbers are 9–14, which show different ploidy levels, including aneuploids. *Carapa* and *Xylocarpus* are similar in karyology and should be placed as *Carapeae* near *Swietenieae*, not with *Melieae* or *Trichilieae*. *Cedreleae* show a wide range of variation 12×2 to 14×4 and a highly advanced chromosome morphology. *Calodecaryia* (some species), *Azadirachta, Dysoxylum, Aphanamixis, Aglaia, Amoora, Sandoricum* are primitive and *Naregamia, Nymania, Calodecaryia* (some species), *Lansium, Carapa, Xylocarpus, Capuronianthus, Swietenia, Cedrela* and *Toona* are advanced.

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