

Karyology of Some Indian Annonaceae

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Accepted September 1, 1989

Members of Annonaceae are distinct for their morphological homogeneity. Yet their inter- and intrafamilial relationships are relatively obscure. The most recent phylogenetic classification, based on floral morphology and palynology is that of Walker (1971, 1972a). This comprehensive novel taxonomic framework has been shown to be consistent with the available data of chromosome numbers (Walker 1972b). Study of chromosome morphology of as many species as possible and reporting of chromosome numbers of more species will certainly help in better understanding of the intrafamilial relations. The paper devotes, therefore, for consideration of chromosome morphology and a few additions of reports of chromosome number.

Materials and methods

The following materials arranged according to Walker (1971) were collected (Table 1).

Table 1.

Name	Voucher	Material
<i>Desmos chinensis</i> Lour.	A, An. 3.	Seed
<i>Uvaria cordata</i> (Dunal) Alston	B, An. 12.	Sapling
<i>U. narum</i> (Dunal) Bl.	B, An. 13.	Sapling
<i>Polyalthia coffeoides</i> (B. et H.) Hook. f. et Thoms.	A, An. 4.	Seed
<i>P. longifolia</i> (Sonnerat) Thwaites (Type A)	C, An. 11.	Seed
<i>P. longifolia</i> (<i>angustifolia</i>)	B, An. 14.	Sapling
<i>P. longifolia</i> (<i>pendata</i>)	B, An. 16.	Sapling
<i>P. suberosa</i> (B. et H.) Hook. f. et Thoms.	A, An. 5.	Seed
<i>Artabotrys uncinatus</i> (Lamk.) Merr.	D, An. 1	Seed
<i>Miliusa roxburghiana</i> Hook. f. et Thoms.	A, An. 6.	Seed
<i>Canaga latifolia</i> (Hk. f. et Th.) Finet et Gagnep	B, An. 15.	Sapling
<i>Monodora myristica</i> Dun.	A, An. 9.	Sapling
<i>Annona muricata</i> Linn.	A, An. 7.	Seed
<i>A. purpurea</i> Moc et Sesse	A, An. 8.	Seed
<i>A. reticulata</i> Linn.	D, An. 2.	Sapling
<i>A. squamosa</i> Linn.	C, An. 10.	Seed

A: Indian Botanic Garden, Howrah, India; B: Imperial Nursery, Calcutta, India; C: Chandernagore, India; D: Calcutta University Garden, Calcutta, India.

Herbarium sheets prepared from these plants have been deposited to the Herbarium of the University of Calcutta.

Root tips were squashed by usual aceto-orcein technique after pretreatment with aesculin (Sharma and Sarkar 1955) at 12°C for two hours. For observation, oil immersion lens and 15× eyepiece was used. Figures were drawn at a magnification of 2000.

Results and discussion

Analysis of karyotype

Total chromosome length per chromosome are stated in Table 2.

In general the following types of chromosomes are found in the species studied (Figs. 1, 2)

A-A type with two constrictions forming three equal segments.

B-A type with two constrictions forming three unequal segments, longest and shortest at the two ends.

Table 2.

	Chromosome No. (diploid)	Mean (n=5) haploid length (μm)		Average chromosome length	
		Per species	Per genus	Per species	Per genus
<i>Desmos chinensis</i>	20	29.0	29.0	1.4	1.4
<i>Uvaria cordata</i>	22	36.0	34.0	1.6	1.5
<i>U. narum</i>	22	32.0		1.4	
<i>Polyalthia coffeoides</i>	18	27.2		1.5	
<i>P. longifolia</i>	18	30.5		1.7	
<i>P. longifolia (angustifolia)</i>	18	30.2	29.2	1.6	1.6
<i>P. longifolia (pendata)</i>	18	35.0		1.9	
<i>P. suberosa</i>	18	24.0		1.3	
<i>Artabotrys uncinatus</i>	18	34.0	34.0	1.5	1.5
<i>Milium roxburghiana</i>	18	24.0	24.0	1.3	1.3
<i>Cananga latifolia</i>	16	21.4	21.4	1.3	1.3
<i>Monodora myristica</i>	16	29.5	29.5	1.8	1.8
<i>Annona muricata</i>	14	28.5		2.0	
<i>A. purpurea</i>	14	27.5	31.5	1.9	2.2
<i>A. reticulata</i>	14	34.5		2.4	
<i>A. squamosa</i>	14	35.5		2.5	

C-A type with two constrictions forming three segments, the two longer adjacent segments equal in size and one satellite.

D-A type with two constrictions forming three segments, the two adjacent segments shorter than the third one.

E-A type with two constrictions forming three segments, middle one shorter than terminal ones.

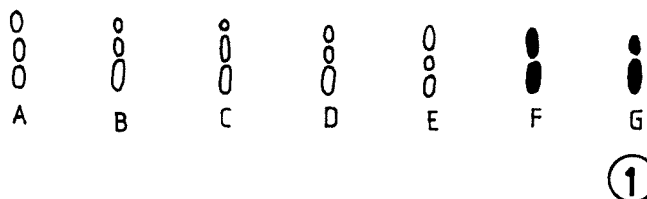
F-A type with a median primary constriction.

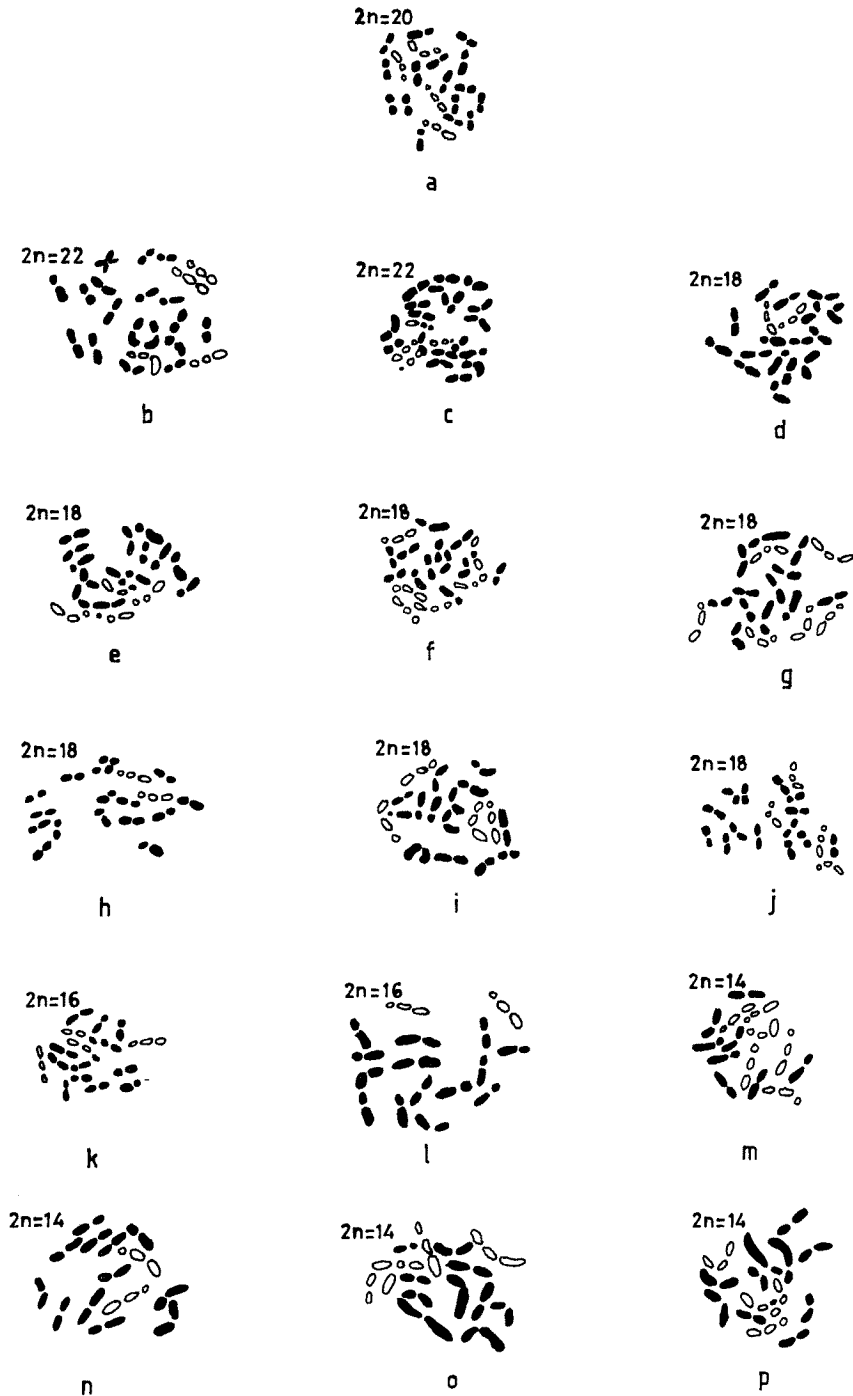
G-A type with a sub-median primary constriction.

Table 3 and Fig. 3 represents the chromosome morphology of the species.

Table 4 represents the up-dated reports on chromosome numbers of the family.

A perusal of chromosome numbers from the present and previous reports shows that





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Figs. 1, 2. Annonaceae. 1, types of chromosomes found in the species studied. 2, camera lucida drawings of somatic metaphase plates. (a) *Desmos chinensis*. (b) *Uvaria cordata*. (c) *U. narum*. (d) *Polyalthia coffeoides*. (e) *P. longifolia (sonnerat)*. (f) *P. longifolia (angustifolia)*. (g) *P. longifolia (pendata)*. (h) *P. suberosa*. (i) *Artabotrys uncinatus*. (j) *Miliusa roxburghiana*. (k) *Cananga latifolia*. (l) *Monodora myristica*. (m) *Annona muricata*. (n) *A. purpurea*. (o) *A. reticulata*. (p) *A. squamosa*. $\times 2,000$.

out of a total of 87 counts, 26 are $2n=14$ or 28, 36 are $2n=16$ or 48, 21 are $2n=18$ or 36, 2 are $2n=22$, one is $2n=20$ and one $2n=27$.

Chromosome number and evolution

After a critical analysis of the chromosome numbers, Walker (1972b) concludes that "evidence is strong for considering $x=7$ as the base chromosome number for the family, with parallel ascending aneuploidy". Grant (1963), Raven and Kyhos (1965), Stebbins (1966) and Ehrendorfer *et al.* (1968) also consider that $x=7$ is the probable base chromosome number of Angiosperms.

Walker's (1972b) sketch of phylogeny based on morphology, palynology and cytology, shows that the basic line having $n=7$ has diverged in the Malmea Subfamily at first into one diploid and two tetraploid genera *Unonopsis* ($2n=28$) (Malmea Tribe), *Cleistopholis* ($2n=14$) (*Uvaria* Tribe) and *Guatteria* ($2n=28$) (*Guatteria* tribe), probably three basic genera for the three taxa. Most of the other numbers of the Subfamily have either 16 or 18 (or 36) chromo-

Table 3.

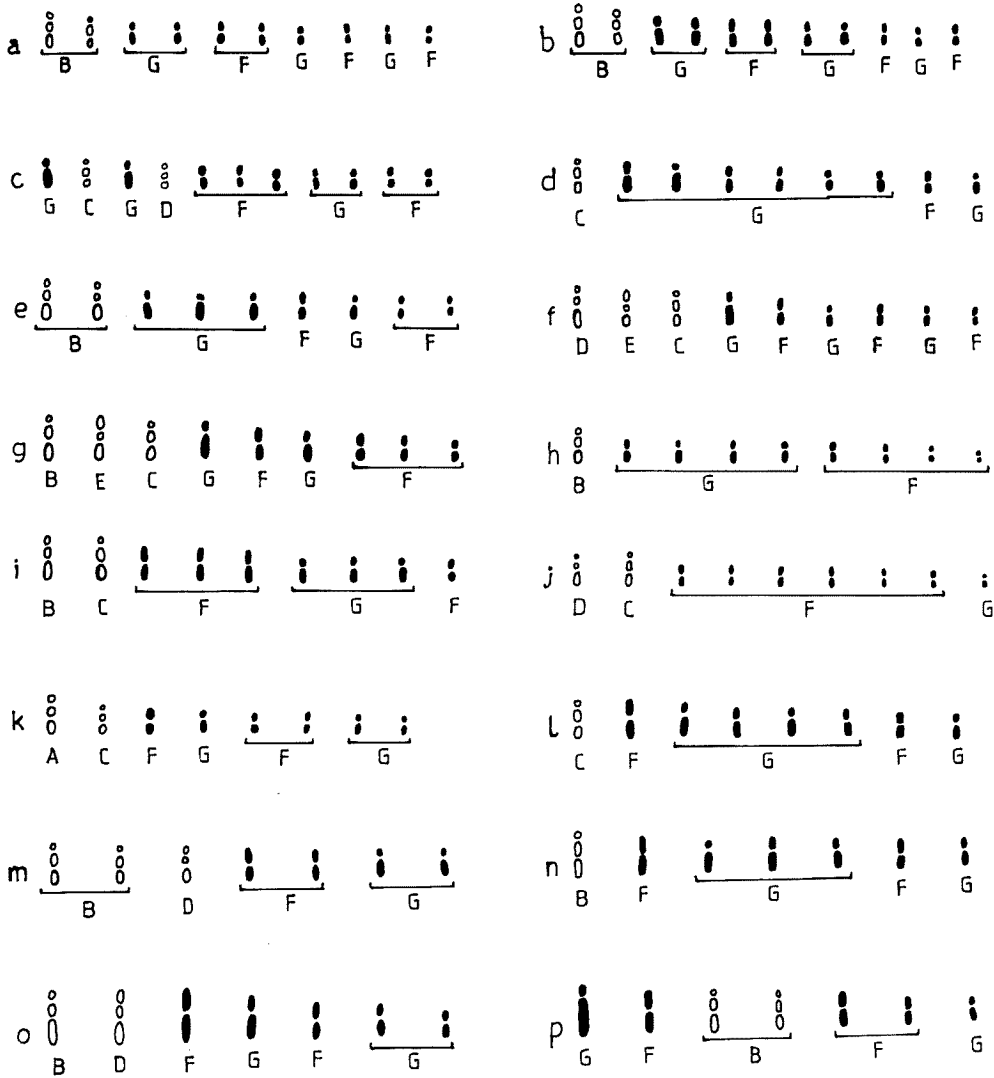
Species	Chromosome types ($2n$)	Most frequent position of primary constrictions	Secondary constrictions ($2n$)
<i>Desmos chinensis</i>	4B, 8F, 8G	median	4
<i>Uvaria cordata</i>	4B, 8F, 10G	sub-median	4
<i>U. narum</i>	2C, 2D, 10F, 8G	median	4
<i>Polyalthia coffeoides</i>	2C, 2F, 14G	sub-median	2
<i>P. longifolia</i>	4B, 6F, 8G	sub-median	4
<i>P. longifolia (angustifolia)</i>	2C, 2D, 2E, 6F, 6G	sub-median	4
<i>P. longifolia (pendata)</i>	2B, 2C, 2E, 8F, 4G	median	4
<i>P. suberosa</i>	2B, 8F, 8G	sub-median	2
<i>Artabotrys uncinatus</i>	2B, 2C, 8F, 6G	median	4
<i>Milusa roxburghiana</i>	2C, 2D, 12F, 2G	median	4
<i>Cananga latifolia</i>	2A, 2C, 6F, 6G	sub-median	4
<i>Monodora myristica</i>	2C, 4F, 10G	sub-median	2
<i>Annona muricata</i>	4B, 2D, 4F, 4G	median	6
<i>A. purpurea</i>	2B, 4F, 8G	sub-median	2
<i>A. reticulata</i>	2B, 2D, 4F, 6G	sub-median	4
<i>A. squamosa</i>	4B, 6F, 4G	median	4

somes in the somatic cells, which, according to Walker (1972b) have arisen in an ascending aneuploid sequence of $7 \rightarrow 8 \rightarrow 9$. In that case, the position of *Desmopsis* ($2n=16$) is not so primitive as shown by palynology (Walker 1971). Of course, a single report does not justify revision of a classification, because a different chromosome number with gradation of evolution may occur within the same genus, *e.g.* *Annona* (Table 4). On the other hand, chromosome morphology of *Cleistopholis* (with numerically primitive chromosomes but palynologically more evolved than *Desmopsis*) remains to be studied. Evolution involves not only numerical change of chromosomes but also structural change (of a numerically unaltered set).

Desmos chinensis ($2n=20$), a first report, may evolve through triploidy ($21 \rightarrow 20$), becoming secondarily balanced by a loss of one chromosome. This genus also may reveal in future $2n=14$ chromosomes in some species.

Uvaria has $2n=16$ and 22, which suggests a probable diversity in the pattern of evolution. If the numbers originate from a common base $n=8$, as postulated by Walker (1972b), $2n=22$

may arise by aneuploidy from a triploid ($3n=24$) plants. The other possibility is of the aneuploidy occurring both directly in a $2n=14$ set and indirectly in a triploid ($3n=21$) plant. Because the number 22 is nearer to 21, which requires secondary balance for survival, the second alternative seems more possible. Therefore, we suggest modification of the plan of Walker (1972b) accordingly.



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Fig. 3. Annonaceae. Idiograms of different species. (a) *Desmos chinensis*. (b) *Uvaria cordata*. (c) *U. narum*. (d) *Polyalthia coffeoides*. (e) *P. longifolia (sonnerat)*. (f) *P. longifolia (angustifolia)*. (g) *P. longifolia (pendata)*. (h) *P. suberosa*. (i) *Artabotrys uncinatus*. (j) *Miliusa roxburghiana*. (k) *Cananga latifolia*. (l) *Monodora myristica*. (m) *Annona muricata*. (n) *A. purpurea*. (o) *A. reticulata*. (p) *A. squamosa*.

Table 4.

Species	Chromosome No. (2n)	Author
Subfamily Malmea		
Tribe Malmea		
<i>Unonopsis panamensis</i> R. E. F.	28	Ehrendorfer <i>et al.</i> 1968
<i>Enantia</i> sp.	16	Mangenot <i>et al.</i> 1957
<i>E. polycarpa</i> (DC) Eng. et Diels	16	Mangenot and Mangenot 1957
Tribe Uvaria		
<i>Desmopsis</i> sp.	16	Walker 1972b
<i>Cleistopholis</i> sp. (Benth.) Eng. et Diels (1)	14	Mangenot and Mangenot 1958
	14	Mangenot and Mangenot 1962
	14	Mangenot <i>et al.</i> 1957
<i>Desmos chinensis</i>	20	Present report
<i>Uvaria chamal</i> P. Beauv.	16	Mangenot and Mangenot 1962
<i>U. cordata</i>	22	Present report
<i>U. narum</i>	22	Present report
<i>Polyalthia coffeoides</i>	18	Present report
<i>P. flava</i> Merr.	18	Löve 1971
<i>P. grandiflora</i> Elm.	36	Löve 1971
<i>P. longifolia</i> (Sonne) Thwaites	18	Asana and Adatia 1945
<i>P. longifolia</i> var. <i>angustifolia</i>	18	Present report
<i>P. longifolia</i> var. <i>pendata</i>	18	Present report
<i>P. suberosa</i>	18	Present report
<i>Artabotrys uncinatus</i> (Lamk.) Merr.	16	Asana and Adatia 1945
	18	Bowden 1948
	16	Mangenot and Mangenot 1962
	18	Present report
<i>Mitra kentii</i> (Bl.) Miq.	16	Mangenot and Mangenot 1962
<i>Melodorum fruticosum</i> Lour.	16	Mangenot and Mangenot 1962
<i>Miliusa roxburghiana</i>	18	Present report
<i>M. tomentosa</i> (Roxb.) Baill. (= <i>Saccopetalum tomentosum</i>)	18	Mangenot and Mangenot 1962
<i>Sapranthus palanga</i> R. E. Fries	18	Bawa 1973
Tribe Guatteria		
<i>Guatteria olivigotmis</i> Donn.	28	Ehrendorfer <i>et al.</i> 1968
Subfamily Fusaea		
<i>Anaxagorea costaricensis</i> R. E. Fr.	28	Ehrendorfer <i>et al.</i> 1968
<i>Neostenonthera gabbonensis</i> (Eng. et Diels) Exil	16	Mangenot and Mangenot 1957
<i>Xylopia</i> sp.	16	Mangenot <i>et al.</i> 1957
<i>X. rubescens</i> Cliv.	16	Mangenot and Mangenot 1957
<i>X. staudtii</i> Eng. et Diels	16	Mangenot and Mangenot 1957
<i>Cananga latifolia</i>	16	Present report
<i>C. odorata</i> (Lam.) Hk. f.	16	Bowden 1948
	16	Meize 1954
<i>Goniothalamus grandiflorus</i> (Warb.) Boerl.	16	Mangenot and Mangenot 1962
Subfamily Annona		
Tribe Hexalobus		
<i>Uvariopsis guinensis</i> Keay.	16	Mangenot <i>et al.</i> 1957
<i>Monodora myristica</i>	16	Meize 1954
	16	Present report
<i>Isolona campanulata</i> Eng. et Diels	16	Mangenot and Mangenot 1957
<i>I. leonensis</i> Sprague et Hutch	16	Mangenot and Mangenot 1962
Tribe Asimina		

Table 4. Contd.

Species	Chromosome No. (2n)	Author
<i>Asimina incana</i> (Bartr.) Exell.	18	Bowden 1945
<i>A. parviflora</i> (Mich.) Dunal.	18	Bowden 1945
<i>A. pygmaea</i> (Bartr.) Dunal.	18	Bowden 1945
<i>A. reticulata</i> Chapm.	18	Bowden 1945
<i>A. speciosa</i> Nash.	18	Bowden 1945
<i>A. tetramera</i> Small	18	Bowden 1945
<i>A. triloba</i> (L.) Dunal	18	Bowden 1945
	27	Bowden 1948
Tribe Annona		
<i>Annona cherimolia</i> Mill.	14	Kumar and Ranadive 1941
(Florida 1)	16	Bowden 1948
(Florida 2)	16	Bowden 1948
(Florida 3)	16	Bowden 1948
(Toronto)	16	Bowden 1948
(Panama)	16	Bowden 1948
	14	Pawar <i>et al.</i> 1956
<i>A. glabra</i> L.	28	
(Harrisburg)	28	Bowden 1945
(Florida)	28	Bowden 1948
(Cuba)	28	Bowden 1948
	28	Mangenot and Mangenot 1958
<i>A. montana</i> Mac. Fad.	16	Bowden 1945
(Jamaica)		
<i>A. muricata</i>	14	Kumar and Ranadive 1941
	16	Bowden 1945
	14	Present report
<i>A. purpurea</i>	14	Present report
	14	Bawa 1973
<i>A. reticulata</i>	14	Kumar and Ranadive 1941
	14	Asana and Adatia 1945
(Florida 1)	16	Bowden 1945
(Florida 2)	16	Bowden 1948
(Florida 3)	16	Bowden 1948
(Cuba)	16	Bowden 1948
(Costarica)	14	Bawa 1973
	14	Present report
<i>A. squamosa</i>	14	Kumar and Ranadive 1941
	14	Asana and Adatia 1945
(Florida 1)	16	Bowden 1948
(Florida 2)	16	Bowden 1948
(Cuba)	16	Bowden 1948
	14	Pawar <i>et al.</i> 1956
	14	Present report
<i>Rollinia orthopetala</i> DC.	48	Bowden 1948

Mitrella (one report), *Melodorum* (one report) and *Artabotrys* (five reports from different populations) have generally $2n=16$, probably evolved from a common stock, as shown by Walker (1972b). The report of $2n=18$ in *A. uncinatus*, has been interpreted as a result of abnormal plates with accessory chromosomes (Ehrendorger *et al.* 1968, Walker 1972b). Because the reports of $2n=18$ are as many as three and all from different localities and because the present report is based on camera lucida drawings of five distinct plates, the idea of accessory chromosomes seems unnatural. Occurrence of chromosomal biotypes in the same species

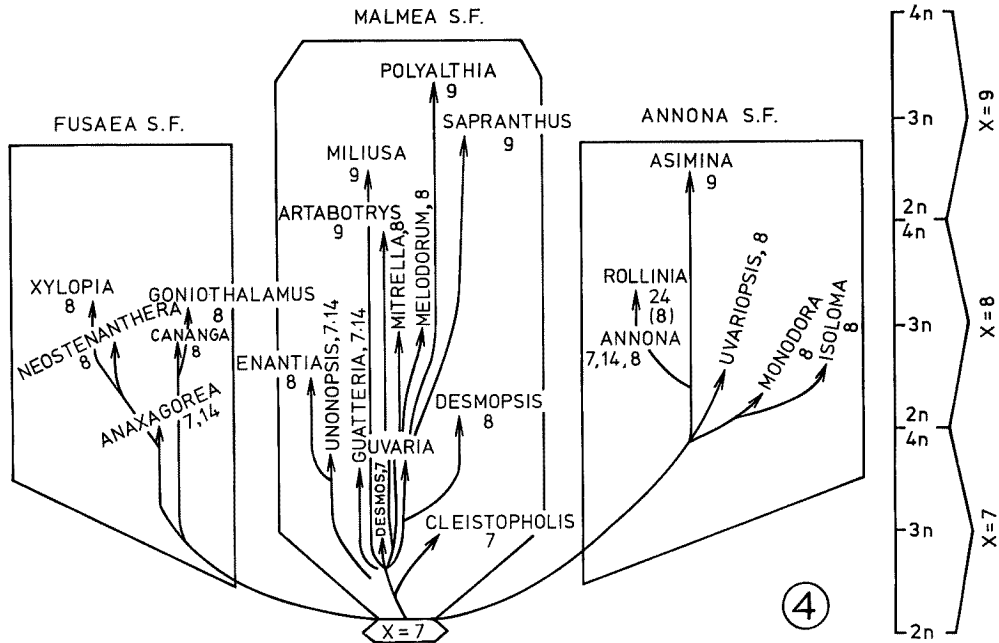


Fig. 4. A plan of evolution in Annonaceae originally suggested by Walker (1972b) and modified by the present authors.

is nowadays an accepted phenomenon, and it appears that two stages of aneuploid ascent (8 and 9) occur in the same species of *Artabotrys*.

All reports on *Polyalthia* and *Miliusa* (*Saccopetalum*) are $2n=18$. Their origin seems to be from a common stock (Walker 1972b), the former showing a tendency to further ascent through polyploidy.

In the Fuseae Subfamily, Walker's plan showing tetraploidy in *Anaxagorea* and aneuploidy in other genera is quite consistent with his classification. In the plan of evolution of the Annona Subfamily, Walker (1972b) has described the genus *Annona* as having diploid and tetraploid numbers of 7. The link between *Rollinia* ($x=8$) and *Annona* ($x=7$) is indistinct. Table 4 shows that *Annona* has $2n=14, 16$ and 28 chromosomes. Similar to *Artabotrys uncinatus*, 14 and 18 chromosomes occur often in the same species e. g. *A. cherimalia*, *A. muricata*, *A. reticulata* and *A. squamosa*. These are also examples of chromosomal biotypes and of two levels of numerical ascent of chromosomes in the same species. Fig. 4 represents a plan of evolution originally suggested by Walker (1972b) and modified by the present authors.

Karyotype and evolution

In the Malmea Subfamily and *Uvaria* Tribe, *Desmos chinensis* has almost uniform length and median primary constriction of all chromosomes. This supports its primitive position in the classification of Walker (1971). The chromosome complements of *Uvaria* resemble closely those of *Desmos* in secondary constrictions, in position of primary constrictions and in general length. *Artabotrys* though differing markedly in chromosome number (having a different base) closely resembles *Desmos* and *Uvaria* in chromosome morphology, all have median constrictions. *Polyalthia*, having variation in total chromosome length, shows many advanced features, such as mostly submedian primary constriction, comparatively high number of secondary constrictions and a longer range of chromosomal length within a single com-

plement. That *Miliusa* represents a different line, considerably evolved, is clear from its shortest chromosomes and the clear difference of chromosome size within a complement. Hence the morphological evolution of chromosomes in this taxon involves changes of 1) uniform length to clear differences, 2) median to submedian primary constrictions, 3) increase in number of secondary constrictions, and 4) reduction of chromosomal length (in *Miliusa*).

Cananga is one of the most evolved genera of the Fusaea Subfamily of Walker. This is evident from chromosome size (which is the smallest of the species studied), large range of chromosome length, the mostly submedian primary constrictions and the high number of secondary constrictions.

In Annona Subfamily, *Annona* appears as the most primitive genus. *Asimina* appears to be most advanced. In the Tribe *Hexalobus*, *Monodora* probably occupied a proper position in Walker's plan. The genome contains a single pair of secondary constrictions, median and submedian constrictions.

Summary

For better understanding of intrafamilial relations of Annonaceae, number and morphology of chromosomes were studied. Additional informations of 16 collections and previous reports were considered. An ascending series of $n=7 \rightarrow 8$ was available in *Annona* spp., Malmea Tribe, *Cleistopholis* sp., Fusaea Tribe, *Uvaria* spp. Number $n=9$ was common in *Polyalthia*, *Miliusa*, *Artabotrys* ($8 \rightarrow 9$) and *Asimina*. In $n=7 \rightarrow 8$ lines, *Uvaria* and *Desmos* had primitive chromosome morphology. In $n=8 \rightarrow 9$ lines *Artabotrys* showed primitive karyotypes, *Miliusa* and *Asimina* the most advanced ones.

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