CYTOTAXONOMIC NOTES ON THE GENERA INDIGOFERA L. AND CYAMOPSIS DC.

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Continuing cytotaxonomic research in the genera *Cyamopsis* and *Indigofera*, this time with attention payed for the greater part to East Tropical African species yielded the following results:

1. Except for four rather small subsections of *Indigofera* proper and the related genus *Rhynchotropis* HARMS, information was obtained about all taxa. Of the 283 species described in GILLETT's monograph, some 80 species, among them a few with subspecies and varieties, now have been cytologically examined.

2. All through both genera *Cyamopsis* and *Indigofera* there exists a diversity in dimensions and types of chromosomes which usually does not appear to be consistent with the accepted taxonomical classification.

3. Nevertheless, *Cyamopsis* thus far is characterized by 2n = 14 chromosomes, whereas 2n = 16 chromosomes is the most common number in *Indigojera*. On the other hand the section *Indigastrum* of the latter genus uniformly has 2n = 14 chromosomes, strengthening the supposition that this section may be closely related to *Cyamopsis*.

4. The species *I. macrocalyx* GUILL. & PERR. classified in the *Paniculatae* has 2n = 12 chromosomes. The species *I. emarginella* STEUD. ex A. RICH. classified in the *Tinctoriae* has 2n = 24, favouring the suggestion that the 48-chromosome Himalayan and East-Asiatic shrubby *Indigofera*'s may not be hexaploids with base number x = 8, but octoploids in an x = 6 range.

5. Polyploidy in the x = 8 range, such as 2n = 32 seems to be fairly common all through the genus *Indigojera* and occurs, perhaps, more in the widely-spread African-Asiatic – (American) sections and subsections than in the African endemic taxa. In some cases the habitat of these polyploids appeared to be in higher altitudes and/or under less favourable climatic conditions.

6. The occurrence of giant chromosomes in the number 2n = 8 in *I*. *richardsiae* GILLETT points to a new base number of x = 4 in the Leguminosae and suggests that the Galegeae may be considered as a very old group. The 2n = 16 plants, consequently, must be taken as tetraploids.

7. Implications as to evolutionary relationship in the *Indigotera* and adjacent genera for the present appear to be impossible on the basis of

cytotaxonomy. At most may be suggested that an intricate polyphylesis lies at the roots of the *Galegeae* and its genera.

Introduction

The evidence published in two earlier papers on the cytotaxonomy of the genus *Indigofera* L. and *Cyamopsis* DC. (FRAHM-LELIVELD, 1960, 1962) showed the desirability of further research in order to attempt to reach a genetic basis for the relations between subgenera and species.

In 1962 there was an opportunity of collecting a number of seed samples of East African species during a three months' tour in Tanganyika, Kenya and Ethiopia, the herbarium material of which was identified by Mr. J. B. GILLETT at Kew Herbarium. In 1964 a search for seed samples was made in the *Indigofera* sheets of Kew Herbarium, resulting in more than 60 batches, out of which 42 germinated and rendered root tips in which metaphase plates could be studied. This material now makes possible a survey of the chromosomal situation in African *Indigofera*, although deviations in hitherto rather uniform systematic groups may still be expected. This is suggested by similar deviations found in our material.

The main basis for African Indigofera taxonomy is GILLETT'S (1958) monograph of Tropical African Indigofera's and the related genera Cyamopsis and Rhynchotropis HARMS. The large genus Indigofera has been divided into five subgenera, two of which again have more sections and subsections. Out of the 283 species enumerated there, approximately 80 species, some with subspecies and varieties have been cytologically investigated. No material became available from the genus Rhynchotropis and from four rather small subsections of Indigofera: a certain amount of information is present now on 19 sections or subsections.

Table 1 contains the classification of GILLETT extended by the number of species hitherto cytologically investigated. From these data it is evident that surprises may be still expected in several groups. The difficulty is, however, that the majority of modern collectors bring home the plants in their flowering stages, thereby, if possible taking care that immature fruits are present. In our search for seeds in the Kew herbarium we observed that in former periods the botanists

TABLE 1

SYNOPSIS OF CLASSIFICATION ADAPTED FROM GILLETT (1958)

Genus, Subgenus, Section & Subsection		No. of species		
	de-	cytol.		
	scribed	invest.		
Genus Cyamopsis DC.	3	3	(1)	
Genus Indigofera L.				
Subgenus A. Acanthonotus (Benth.) Benth. & Hook	r.f. 3	2	(2)	
Subgenus B. Amecarpus Benth. ex Harvey				
Section 1 Amecarpus	21	4	(3)	
,, 2 Demissae Gillett	3	1		
Subgenus C. Indigofera L.				
Section 1 Latestipulatae (Bak.f.) Gillett	11	4	(4)	
,, 2 Paniculatae (Bak.) Gillett				
Subsection a Paniculatae	18	6	(5)	
,, b Trichopoda (Bak.) Gillett	3	1	(6)	
Section 3 Indigofera				
Subsection a Juncifoliae Harvey	1	1		
,, b Brevi-erectae Gillett	15	5	(7)	
,, c Anomalae Gillett	1	—		
,, d Dissitiflorae (Bak.) Gillett	26	9	(8)	
,, e Spinosae (Bak.) Gillett	4	1		
,, f Brevipatentes Gillett	7	—		
,, g Pilosae Gillett	8	3	(9)	
,, h Viscosae Rydberg	18	2	(10)	
,, i Centrae Gillett	12	2	(11)	
,, j Atratae Gillett	15	7	(12)	
" k Psiloceratiae Gillett	11	3	(13)	
,, 1 Geanthae Gillett	2			
,, m Tinctoriae (Bak.) Gillett	32	14	(14)	
,, n Hirsutae Rydberg	4	3	(15)	
,, o Microcarpae Rydberg	1	1	(16)	
,, p Alternifoliolae (Harvey) Gillett	28	8	(17)	
,, q Simplices-reflexae Gillett	4	_		
Subgenus D. Indigastrum (Jaub. & Spach) Gillett	7	3	(18)	
Subgenus E. Microcharis (Benth.) Gillett	23	4	(19)	
Genus Rhynchotropis Harms	2			

(*) Classification code number for use with Table 2.

obviously were collecting more leisurely and were bringing back far more complete material, including ripe fruits and seeds. Although our seed sampling goes back as far as to material from the early twenties,

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TABLE 2

species and varieties investigated, with their origin and accession, diploid chromosome numbers (2n) and classification (*) in table 1, and with reference to figures in the text

Species	(*)	Fig.	2n	Coll. no.	(Herbarium) 1) and origin
Cyamopsis					
serrata Schinz	(1)	1.	14**	64060	(K) Wild 5127 Bechuanaland 1960
id.		2.	14	64066	(K) Leistner 1809 Leonardville (Gobabis) Windhoek Distr. S.W. Africa 1960
Indigofera					
drepanocarpa Taub. ssp.					
drepanocarpa	(2)	З.	16	64034	(K) Tanner 4210 Tanganyika 1959
id., ssp. littoralis Gillett		4.	16	64001	(K) Rawlins 193 Kenya Coast 1956
senegalensis Lam.	(3)	5.	16	64015	(K) Moiser 252 Fodoma N. Nigeria 1921
gairdnerae Hutch. ex Bak. f.	(4)	6.	16	64002	(K) Verboom 835 Luangwa Valley Malawi f
burtii Bak. f.	(4)	7.	16	62117	(T) Burtt 2581 Manyoni Distr. Kazikazi T ganyika 1932
paniculata Vahl ex Pers. ssp.					
paniculata	(5)	8.	16**	64033	(K) Latilo 23538THI S. Nigeria 1948
macrocalyx Guill. et Perr.	(5)	9.	12	64014	(K) Roberty 17114 Kenieba Fr. Sudan 195
dasycephala Bak. f.	(5)	10.	14	64006	(K) Hepper 1303 Adamawa, Vogel Peak Di Camerouns 1957
nigritana Hook. f.	(6)	11.	16	64012	(K) Adams 4448 Burufa Tana 1950
cordifolia Heyne ex Roth.	(7)	12.	16**	64032	(K) Bally 6890 Halibai N. Eritrea Sudan border 1949
sessiliflora DC.	(7)	13.	32**	64040	(K) Bally 6893 Wadi Asserai N. Eritrea 1
mildbraediana Gillett	(7)	14.	16	64039	(K) Morton 344 Bauchi Rd., Jos Nigeria 1
microcalyx Bak.	(7)	15.	32**	62307	(N) Mahinda 7 Kibweza Kigoma Kenya 1
elliottii (Bak. f.) Gillett	(8)	16.	16	64041	(K) Thomas 6938 Kumoroboi Sa. Leone 1
brevicalyx Bak. f.	(8)	17.	16	62167	(W) Frahm-Leliveld Ruiru Kenya 1962
id.		18.	16	62336	(W) Frahm-Leliveld Wonji Ethiopia 1962
tanganyikensis Bak. f. var.					
tanganyikensis	(8)	19.	16	62122	(T) Burtt 4656 Manyoni near Kazikazi T ganyika 1933
id.		20.	16	62217	(Kitale) Bogdan K. 51257 South Nyanza Kenya 1961
id.		21.	32	id.	id.
ambelacensis Schweinf.	(8)	22.	16	62302	(N) Pedro & Pedrogão 3127 Moçambique 1
congolensis De Wild. & Th. Dur.		23.	16	64013	(K) Liben 2731 Dibaya Kassai Congo 195
hedyantha Eckl. & Zeyh.	(8)	24.	16	64045	(K) Verboom 636 Nyika Plateau Malawi 1
erythrogramma Welw. ex Bak.	(9)	25.	16	64035	(K) Balsinhas & Marrime 443 Moçambi 1961

Species	(*)	Fig.	2n	Coll. no.	(Herbarium) ¹) and origin
glandulosa Gillett	(9)	26.	16	64018	(K) Richards 9213 Lake Tanganyika 1957
losa Poir. var. pilosa	(9)	27.	32	64038	(K) Wavel 734 Nigeria 1950
lutea (Burm. f.) Merrill var.					
colutea	(10)	28.	16*	*62129	(W) Frahm-Leliveld Rift Wall Estate W. Lake Manyara Tanganyika 1962
id.		28.a	16	62132	id.
id.		29.	16	63015	(W) Mlingano L 61 Tanganyika 1963
icrocephala Bak. f.	(11)	30.	16	64064	(K) Welch 166 Ol Shinyanga Tanganyika 1952
cioides Jaub. & Spach var.					
vicioides	(11)	31.	16	62265	(W) Bogdan K52264 Kapenguria Kenya 1961
scosetosa Bak.	(12)	32.	16	64063	(K) Richards 9873 Rungwe Distr. Tang. 1957
riceps Hook. f. ssp. atriceps	(12)	33.	32	62008	(W) Breteler Mt. Cameroun 2850 m. 1962
id. ssp. rhodesiaca Gillett		34.	32	62116	(T) Burtt Zambia 1936
id. ssp. kaessneri (Bak. f.)					
Gillett		35.	32	64021	(K) Purseglove 3467 Zambia 1954
hliebenii Harms	(12)	36.	16	64052	(K) Milne Redhead & Taylor 10992 Njombe Distr. Tanganyika 1956
asyantha Bak. f. var. brevior					
Gillett	(12)	37.	16	64025	(K) Milne Redhead & Taylor 10605 Tundura Distr. Tanganyika 1956
tiflora Bak.	(12)	38.	16	64030	(K) Richards 12300 Ufipa Distr. Tang. 1959
xeracemosa Bak. f.	(13)	39.	16	64029	(K) Faulkner 2592 Zanzibar 1960
therlandioides Welw. ex Bak.	(13)	40.	32	64061	(K) Richards s.n. Abercorn Distr. Zambia 1952
omblei Bak. f. & Martin ssp.					
longiflora Gillett	(13)	41.	16	64003	(K) Christiaensen 535 Ruanda 1954
odocarpa Bak. f. & Martin	(14)	42.	16	64031	(K) Newbould & Harvey 4313 Kasoje Tan ganyika 1959
narginella Staud. ex A. Rich.					
var. emarginella	(14)	43.	24	64020	(K) Mahimba HSM163 Kigoma Distr. Tan ganyika 1958
vaziensis Bolus. var. swaziensis	(14)	44.	16	64062	(K) Kerfoot 1910 MC. Nyiru Kenya 1960
id. var. perplexa (N.E.	. /				
Brown) Gillett		45.	16	64026	(K) Williams 677 Mbulu Distr. Tang. 1955
patana Bak. f.	(14)	46.	16	62306	(N) Bally 7903 Mlali Korogwa 1950
ita L. f. var. scabra (Roth.)	.)				
Meikle	(14)	47.	16	63014	(W) Mlingano L 110 1963
id.	. /	48.	16	63016	(W) id. L 36A 1963
id.		49.	32	63017	(W) id. L 89 1963
ticulata Gouan	(14)	50.	16	62304	(N) Hemming 2061 Burao N. Somalia 1960
id.	. ,	51.	16	62320	(W) Frahm-Leliveld Awara Melka Plain Ethiopia 1962

TABLE 2 (continued)

				_ (con	
Species	(*)	Fig.	2n	Coll. no.	(Herbarium) ¹) and origin
coerulea Roxb. var. occidentalis	3				
Gillett & Ali	(14)	52.	16	6 2 319	(W) Frahm-Leliveld Awash Station Ethio: 1962
bogdanii Gillett var. bogdanii	(14)	53.	16	62305	(N) Greenway 9156 Moru Lower Water Ho Tanganyika 1956
amorphoides Jaub. & Spach	(14)	54.	16	64051	(K) Newbould 720 Somalia 1957
id.		55.	16	62349	(W) Frahm-Leliveld Atok Khebede Wonj
					Ethiopia 1962
id.		56.	16	62354	(W) Frahm-Leliveld Shoa Wonji Ethiopia 19
deightonii Gillett	(15)	57.	16	64043	(K) Lalilo & Olorunfeni THI24446 Aponol
					Forest Res. Sth. Nigeria 1949
microcarpa Desv.	(16)	58.	16	63018	(W) Mlingano L 76 1963
diphylla Vent.	(17)	59.	16*	*64054	(K) Jackson 2497 Jebel Shuweih Somalia 15
oblongifolia Forsk.	(17)	60.	16	62311	(N) Hemming s.n. Wadi Gargore N. Soma 1959
schimperi Jaub. & Spach	(17)	61.	16	62316	(W) Frahm-Leliveld Metahara Ethiopia 19
semitrijuga Forsk.	(17)	62.	16	64050	(K) Hemming 1137 Abdibabo Eritrea 1957
volkensii Taub.	(17)	63.	32	62216	(W) Bogdan K57116 Mwea Embu 1957
id.	(11)	64.	16	63009	(W) Mlingano L 120 1963
id.		64.a		64007	(K) Corbett 10 Masailand Tanganyika 1951
spicata Forsk. f. parvula	(17)	65.		*62368	(W) Frahm-Leliveld Jimma Ethiopia 1962
alternans DC.	(17)	66.	32	64053	(K) De Winter 2528 Gobabis Windhoek Dis
atternaris De,	(17)	00.	52	04000	S.W. Africa 1955
argyroides E. Mey.	(18)	67.	14	64058	(K) Leistner & Joint 2842 Gordonia Ca
argyroidos 2. moy,	(10)	01.	1 1	04000	Prov. 1961
richardsiae Gillett	(19)	68.	8	64047	(K) Robinson 5145 Kasima Zambia 1962
welwitschii Bak. var. welwitschii	` '	71.	16	64055	(K) Robinson 3630 Mwinchinga 1960
butayei De Wild.	(19)	72.	16	64024	(K) Hepper 1432 Vogel Peak Camerouns 19
Subayor Do Willi.	(17)	12.	10	07024	(in) riopper 1402 voger i ear Camerouns (

TABLE 2 (continued)

1) (K): Kew, (N): Nairobi, (T): Tengeru, (W): Wageningen.

** Chromosome number tallies with earlier reports.

and has met occasionally even with success in those older samples, it is clear that herbarium sheets from the 19th century, complete as they are, do not yield suitable material for chromosome investigations. Modern disinfecting methods also have shown themselves to be advantageous to seed viability. The same seems to be true for the climatological conditions under which the herbarium is stored. The chance of seed survival is, on the whole, much larger in herbaria situated in temperate regions than in those stored in the tropics.

Table 2 contains an enumeration of the material investigated, its origin and collector, location of herbarium specimens and diploid chromosome number. The numbers tally with those of the metaphase figures numbered 1 to 72. A double asterisk after the diploid chromosome number indicates that the number tallies with that earlier reported in the literature.

For the sake of clearness each division discriminated as such by GILLETT will be discussed apart, so that, eventually, the cases where cytological evidence points to deviations from the taxonomical classification can be discussed more easily.

Root tips were obtained from seedlings; fixed in Navashin; sectioned at 15μ and stained with crystal violet.

Results

Cyamopsis DC. (Plate I, Fig. 1 and 2).

The three species belonging to the genus *Cyamopsis* have been studied as to their chromosomes: the number 2n = 14 reported by HYMOWITZ & UPADHYA (1963) for *C. serrata* could be confirmed, but two batches of various origin show a considerable difference inter se as to chromosome dimensions. Leistner's material from S.W. Africa allows a comparison with our fig. 5 of 1962 (FRAHM-LELIVELD, 1962) from *C. psoralioides* (LAM.) DC. presently named *C. tetragonoloba* (L.) TAUB., stbk. no. 34; the Bechuanaland material, however, shows much larger dimensions. All the *Cyamopsis* species possess 2n = 14 chromosomes (MIÈGE, 1960: *C. senegalensis* GUILL et PERR. 2n = 14).

Indigofera L.

Subgenus A. Acanthonothus (BENTH.) BENTH. & HOOK.F. (Plate I, Fig. 3 and 4).

The species *I. drepanocarpa* yielded material in both its subspecies *drepanocarpa* and *littoralis*. Both have 2n = 16 small chromosomes, and the two chromosome portraits are very similar. Comparison to the metaphase plate of *I. nummulariijolia* (FRAHM-LELIVELD, 1960, fig. 4) shows that the two species possess the same small chromosome type.

Subgenus B. Amecarpus BENTH. ex HARVEY. (Plate I, Fig. 5).

From this subgenus four species were studied earlier (FRAHM-LELIVELD 1962, figs. 1-4), viz. I. hochstetteri, praticola, charlieriana, and demissa, the latter one

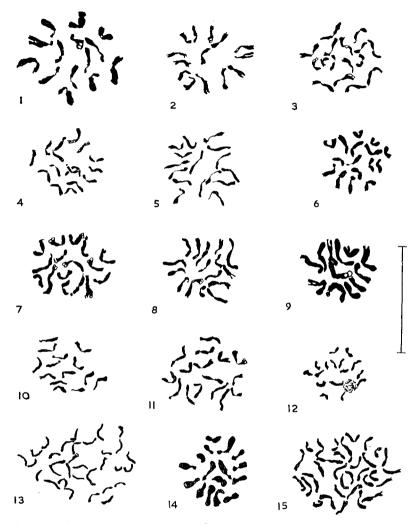


Plate I. (Unit of scale 10 μ) Fig. 1. Cyamopsis serrata Schinz 64060. Fig. 2. Cyamopsis serrata Schinz 64066. Fig. 3. Indigofera drepanocarpa Taub. ssp. drepanocarpa 64034. Fig. 4. Indigofera drepanocarpa Taub. ssp. littoralis Gillett 64001. Fig. 5. Indigofera senegalensis Lam. 64015. Fig. 6. Indigofera gairdnerae Hutch. ex Bak. f. 64002. Fig. 7. Indigofera burtii Bak. f. 62117. Fig. 8. Indigofera paniculata Vahl ex Pers. ssp. paniculata 64033. Fig. 9. Indigofera macrocalyx Guill. & Perr. 64014. Fig. 10. Indigofera dasycephala Bak. f. 64006. Fig. 11. Indigofera nigritana Hook.f. 64012. Fig. 12. Indigofera cordifolia Heyne ex Roth. 64032. Fig. 13. Indigofera sessiliflora DC. 64040. Fig. 14. Indigofera mildbraediana Gillett 64039. Fig. 15. Indigofera microcalyx Bak. 62307.

placed by GILLETT in a separate section *Demissae*. The species studied at present *I. senegalensis* also has 2n = 16 chromosomes. Chromosome length on the whole does not deviate much from that in its vicarious species *I. praticola*; thus both of them vary somewhat from the other three species with longer chromosomes. The effect of slenderness may be attributed to the fact, that Moiser's material from which the seeds were obtained dates from 1921. Apparently with 40 years we reach the limit of viability: as far as the chromosomes are concerned this results in reduced stainability, part of the chromosome material no longer being able to take up stain. Notwithstanding this, the similarity to the chromosomes of *I. paniculata* (FRAHM-LELIVELD 1960, figs. 2-5, this article fig. 8) is suggestive; the more so if we take into account GILLETT's remark that the flattened pod character which is present in the subgenus *Amecarpus*, also occurs in the subgenus *Microcharis* and in the section *Paniculatae* of the subgenus *Indigofera*.

Subgenus C. Indigofera L.

Section 1. Latestipulatae (BAK.F.) GILLETT. (Plate I, Fig. 6 and 7).

As to the chromosomes, this group appears to be rather inconsistent. Whereas the two species studied earlier (FRAHM-LELIVELD, 1962 figs. 7, 8 and 9) possess 2n = 14, *I. ischnoclada* having longer chromosomes and *I. strobilifera* var. *lanuginosa* having shorter ones, the two species now studied are *I. gairdnerae* (fig. 6) with 16 short to very short chromosomes and *I. burtii* (fig. 7) with 16 chromosomes of a decidedly longer type, both with 2 satellited ones. The *I. burtii* seeds originated from herbarium material stored in Tengeru, Tanganyika under rather disadvantageous circumstances. These specimens had been collected by Burtt himself in 1932 and it may be noted that the root tips yielded extraordinarily fine material for cytological investigation. The other species placed in the section *Latestipulatae* decidedly require further cytological investigation.

Section 2. *Paniculatae* (BAK.) GILLETT. Subsection a. *Paniculatae*. (Plate I, Fig. 8-10).

From the standpoint of chromosomes this is a rather heterogeneous group. Four species, viz. I. paniculata ssp. paniculata, I. paracapitata, I. congesta and I. pulchra, were reported as having 2n = 16 chromosomes (FRAHM-LELIVELD, 1960). From a Southern Nigerian source well germinating seeds collected in 1948 gave excellent slides, from which fig. 8 was drawn this time; there appears to be a striking accordance as to length and shape of these slender chromosomes (FRAHM-LELIVELD, 1960, figs. 2-5) and also with those of I. paracapitata (ibidem, 1960, fig. 6). The two species studied at present show quite another aspect: I. macrocalyx with 2n = 12 rather compact chromosomes (fig. 9) and I. dasycephala with 2n = 14 small and rather slender ones (fig. 10). In rare cases the latter ones have a tendency to break, thus causing the presence of 2n = 15-16 units.

It is noteworthy that I. mysorensis ROTTB. from India is included in this

section, suggesting that the *Paniculatae* may be taken as taxon with a widely spread distribution.

As to the presence of satellited chromosomes, two of these are present in I. *paniculata*; in I. *congesta* they could not be observed; in I. *dasycephala* there seem to be two to four and I. *pulchra* also has two to four satellited ones.

Subsection b. Trichopodae (BAK.) GILLETT. (Plate I, fig. 11).

From this subsection *I. nigritana* has been verified: there are 2n = 16 chromosomes, matching those of the 16-chromosomic *Paniculatae* in general.

GILLETT (l.c. p. 32) observed a similarity of flowers and fruits in some species of the *Trichopodae* and those of the *Dissitiflorae*. This similarity finds a certain parallel in the chromosome portraits of the *Trichopodae* and a number of species belonging to the *Dissitiflorae*. These are: *I. dendroides* (FRAHM-LELIVELD, 1960, fig. 11), *I. heudelotii* (ibidem, figs. 12 and 13), *I. vohemarensis* (FRAHM-LELIVELD, 1962, fig. 11), and the following ones which will be discussed later on, *I. elliottii*, *I. brevicalyx* and *I. tanganyikensis*.

Section 3. Indigotera.

Subsection b. Brevi-erectae GILLETT. (Plate I, Fig. 12-15).

Tetraploidy in I. sessili/lora and I. microcalyx (2n = 32) which was earlier reported by HAGERUP (1932) and TURNER & FEARING (1959) could be confirmed, as well as 2n = 16 for I. cordifolia (HAGERUP 1932) (figs. 13, 15 and 12 resp.). I. simplicifolia (2n = 16) has been investigated earlier (FRAHM-LELIVELD 1960, fig. 10). New is I. mildbraediana 2n = 16 with extremely compact chromosomes, at least six of them satellited. Out of these five species, three are endemic for Africa, among them one of the two tetraploids, I. microcalyx. I. cordifolia with its extremely small chromosomes has a quite considerable area of dispersion eastwards to the island of Timor. It would be interesting to know chromosome number and -type of the two other species in this subsection (c.f. GILLETT 1.c. p. 35) which also extend over Africa and a good portion of Asia.

Subsection d. Dissitiflorae (BAK.) GILLETT. (Plate II, Fig. 16–24).

Except for an obvious chance polyploidy in one seed of *I. tanganyikensis* originating from Sth. Nyanza, Kenya, all nine species studied in this subsection have 2n = 16 chromosomes. There appears to exist some variation in chromosome dimensions between the species, e.g. *I. congensis* (fig. 23) has short chromosomes; and even within a species, e.g. *I. tanganyikensis* (figs. 19 and 20, both diploid).

Subsection e. Spinosae (BAK.) GILLETT.

Except for *I. basiflora* reported upon by FRAHM-LELIVELD in 1962 (fig. 12) no further material from this subsection has become available.

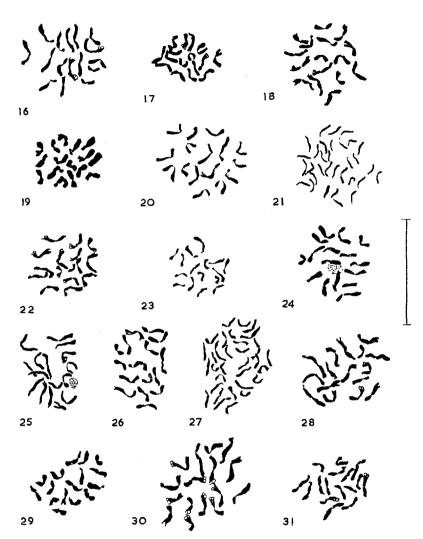


Plate II. (Unit of scale 10μ). Fig. 16. Indigofera elliottii (Bak.f.) Gillett 64041. Fig. 17. Indigofera brevicalyx Bak.f. 62167. Fig. 18. Indigofera brevicalyx Bak.f. 62336. Fig. 19. Indigofera tanganyikensis Bak.f. var. tanganyikensis 62122. Fig. 20. Indigofera tanganyikensis Bak.f. var. tanganyikensis 62217. Fig. 21. Indigofera tanganyikensis Bak.f. var. tanganyikensis 62217. Fig. 22. Indigofera ambelacensis Schweinf. 62302. Fig. 23. Indigofera congolensis De Wild. & Th. Dur. 64013. Fig. 24. Indigofera hedyantha Eckl. & Zeyh. 64045. Fig. 25. Indigofera erythrogramma Welw. ex Bak. 64035. Fig. 26. Indigofera biglandulosa Gillett 64018. Fig. 27. Indigofera pilosa Poir. var. pilosa 64038. Fig. 28. Indigofera colutea (Burm.f.) Merrill var. colutea 62129. Fig. 29. Indigofera colutea (Burm.f.) Merrill. var. colutea 63015. Fig. 30. Indigofera microcephala Bak. f.

64064. Fig. 31. Indigofera vicioides Jaub. & Spach var. vicioides 62265.

Subsection g. Pilosae GILLETT. (Plate II, Fig. 25-27).

The type species of this subsection *I. pilosa* (fig. 27) appears to be tetraploid in its var. *pilosa*. The Kew material identified by Mr. Gillett has been collected in Nigeria. MiÈGE (1961), however, gives 2n = 16. This discrepancy cannot be resolved without examination of more material from the Sudano-Guinese region, where a.o. *I. fulvopilosa* BRENAN is present, formerly described as *I. pilosa* POIR, var. *multiflora* BAK. F. (c.f. GILLETT 1958 p. 58). The latter species did not yield viable seeds for cytological inspection. Two more species, *I. erythrogramma* and *I. biglandulosa* have 2n = 16 chromosomes. It is evident that a more thorough cytological investigation would be worthwhile.

Subsection h. Viscosae Rydberg. (Plate II, Fig. 28 and 29).

Of this large group, according to Gillett "a difficult group containing several ill-defined polymorphic species" (GILLETT 1958, p. 59) only three species have been examined as yet viz. *I. secundi/lora* (FRAHM-LELIVELD 1960 fig. 14, MIÈGE 1962) and *I. colutea* (figs. 28 and 29), both with 2n = 16 chromosomes. For *I. colutea* this result is in accordance with that of HAGERUP (1932). RAMANATHAN (1955) reports 2n = 16 for *I. argentea* BURM. F. collected in India. Also in this subsection a more elaborate cytological investigation would be necessary.

Subsection i. Centrae GILLETT. (Plate II, Fig. 30 and 31).

Out of the twelve species defined by GILLETT in this subsection only two became available for investigation, viz. *I. microcephala* and *I. vicioides* var. *vicioides*, both with 2n = 16 chromosomes (figs. 30 and 31).

Subsection j. Atratae GILLETT. (Plate III, Fig. 32-38).

Type species of this subsection is *I. atriceps* HOOK. In 1962 *I. atriceps* ssp. setosissima was investigated (FRAHM-LELIVELD 1962 fig. 13): 2n = 16 chromosomes. This time a number of other subspecies defined by GILLETT came under examination. *I. atriceps* ssp. atriceps in 1962 collected by BREELER on Mt. Cameroun at an altitude of 2850 m has 2n = 32 (fig. 33). Ssp. rhodesiaca and ssp. haessneri also are tetraploid with 2n = 32 (figs. 34 and 35). The other four species investigated, viz. *I. juscosetosa, I. schliebenii, I. dasyantha* var. brevior and *I. seti/lora* all have 2n = 16 chromosomes, the latter species with very small ones. On account of the fact that several species in this subsection are found in habitats at rather great altitudes it may be possible that there are more species with chromosome numbers varying in ploidy.

Subsection k. Psiloceratiae GILLETT. (Plate III, Fig. 39-41).

In this subsection again there is the remarkable fact that the species chosen as type species appears to be tetraploid: *I. sutherlandioides* with 2n = 32 (fig. 40). But the variability in this species signalled by GILLETT (l.c. 1958, p. 86) requires further investigation within the taxon as well as in neighbouring species.

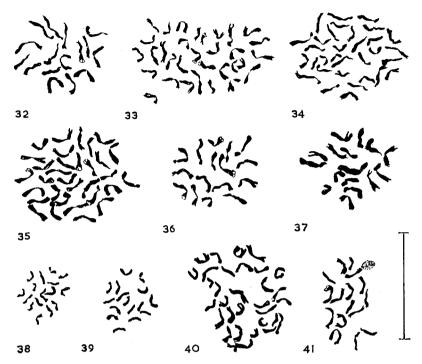


Plate III. (Unit of scale 10 μ). Fig. 32. Indigofera fuscosetosa Bak. 64063. Fig. 33. Indigofera atriceps Hook.f. ssp. atriceps 62008. Fig. 34. Indigofera atriceps Hook.f. ssp. rhodesiaca Gillett 62116. Fig. 35. Indigofera atriceps Hook.f. ssp. kaessneri (Bak.f.) Gillett 64021. Fig. 36. Indigofera schliebenii Harms 64052. Fig. 37. Indigofera dasyantha Bak.f. var. brevior Gillett. Fig. 38. Indigofera setiflora Bak. 64030. Fig. 39. Indigofera laxeracemosa Bak.f. 64029. Fig. 40. Indigofera sutherlandioides Welw. ex Bak. 64061. Fig. 41. Indigofera homblei Bak.f. & Martin ssp. Iongiflora Gillett 64003.

The other species investigated are *I. laxeracemosa* (2n = 16) and *I. homblei* (2n = 16) (figs. 39 and 41). Whereas *I. sutherlandioides* chromosomes and those of *I. homblei* show a resemblance to such a degree that the tetraploid might have originated by a simple duplication of the diploid chromosomes, the *I. laxeracemosa* chromosomes are smaller and certainly do not support a supposed relationship to *I. vicioides* in the *Centrae* group (cf. fig. 31). A number of East Asian species are thought also to belong to this section, a.o. *I. kirilowii* 2n = 16, and *I. decora* 2n = 48 (GILLETT 1958, p. 84). The cytological status of 48 chromosomic species will be discussed later on.

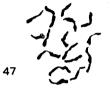


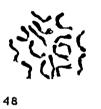




























Subsection m. Tinctoriae (BAK.) GILLETT. (Plate IV, Fig. 42-56).

This rather large subsection allowed a fairly extensive study of African material as well as of some species which owing to their economic importance have found their way in most tropical areas. This is also the reason why various reports are present from authors all over the world on chromosome numbers in the *Tinctoriae*, some of which are controversial, apparently due to erroneous identification of the material in question. The majority of the species thus far investigated (FRAHM-LELIVELD 1960, figs. 15–24, this article, figs. 42–56) possess a consistent type of metaphase plate in the roots with 2n = 16 chromosomes. The only exceptions are one batch of *I. trita* var. scabra which was tetraploid (2n = 32) (fig. 49) and a remarkable tetraploid, *I. emarginella* (2n = 24) (fig. 43). The latter one may be considered as a tetraploid in an x = 6 range as base number when it is taken into account that *I. macrocalyx* in the subsection *Paniculatae* has been reported as having 2n = 12 chromosomes.

Subsection n. Hirsutae Rydberg. (Plate V, Fig. 57).

One more species in this subsection was studied: *I. deightonii* (fig. 57), also with 2n = 16 smallish chromosomes (c.f. FRAHM-LELIVELD, 1960, figs. 27-31).

Subsection o. Microcarpae Rydberg. (Plate V, Fig. 58).

GILLETT (1958, p. 110) mentions only one species for the tropical African flora: *I. microcarpa* (fig. 58) having 2n = 16 chromosomes.

Subsection p. Alternifoliolae (HARVEY) GILLETT. (Plate V, Fig. 59-66).

Again this is one of the larger subsections in tropical Africa. Formerly two species have been studied, viz. *I. schimperi 2n = 16*, and *I. spicata* from several sources, all having 2n = 32 chromosomes (FRAHM-LELIVELD 1953, 1960, figs. 34 and 35-39). For *I. spicata* (syn. *I. endecaphylla* JACQ.) the following reports are

Plate IV. (Unit of scale 10 μ). Fig. 42. Indigofera podocarpa Bak.f. & Martin 64031. Fig. 43. Indigofera emarginella Steud. ex A. Rich. 64020. Fig. 44. Indigofera swaziensis Bolus var. perplexa (N.E. Brown) Gillett 64026. Fig. 46. Indigofera lupatana Bak.f. 62306. Fig. 47. Indigofera trita L.f. var. scabra (Roth.) Meikle 63014. Fig. 48. Indigofera trita L.f. var. scabra (Roth.) Meikle 63016. Fig. 49. Indigofera trita L.f. var. scabra (Roth.) Meikle 63017. Fig. 50. Indigofera articulata Gouan 62304. Fig. 51. Indigofera articulata Gouan 62302. Fig. 52. Indigofera coerulea Roxb. 62319. Fig. 53. Indigofera bogdanii Gillett 62305. Fig. 54. Indigofera amorphoides Jaub. & Spach 62354. Fig. 56. Indigofera amorphoides Jaub. & Spach 64051.





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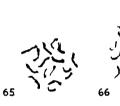


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۱۵ و.و. ۲۷ و.و. ۲۲ آ given in the literature: KISHORE (1951) 2n = 36, SIMMONDS (1954) 2n = 32, TURNER (1956, as "hendocephylla JACQ".) n = 8, and recently PRITCHARD & GOULD (1964) 2n = 16, 32 (Index to plant chromosome numbers for 1964; not seen in original). The Turner material originated from Florida but earlier had been imported there. The investigation of the small-leaved montane form *I*. spicata f. parvula (*I. parvula DEL*. sensu HOCHST. ex A. RICH.) reveals now that 2n = 16 (fig. 65) occurs in this taxon, and this form may, of course, have been introduced in subtropical Florida, owing to the fact that *I. spicata* is used as a cover crop in various tropical regions.

In *I. volkensii* 2n = 16 as well as 2n = 32 was found in samples from different sources. The chromosome dimensions encountered in both types (figs. 63 and 64) suggest a simple reduplication.

I. alternans (2n = 32) appears to have much the same type of metaphase plate (fig. 66) as the tetraploid forms of I. spicata (FRAHM-LELIVELD 1960, figs. 35–39).

I. diphylla (fig. 59) has been reported as having 2n = 16 chromosomes by HAGERUP (1932). I. schimperi (fig. 61) from Ethiopia agrees well with the material investigated earlier (FRAHM-LELIVELD, 1960 (fig. 34)) and originating from Kenya.

Altogether, this subsection with its extensive distribution and many obviously difficult specific delimitations deserves further cytotaxonomic examination.

Subgenus D. Indigastrum (JAUB. & SPACH) GILLETT. (Plate V, Fig. 67).

In 1962 two species I. costata ssp. macra and I. parvi/lora (FRAHM-LELIVELD 1962 figs. 14 and 15) revealed a number of 2n = 14 rather small chromosomes. I. parvi/lora had been examined earlier by HAGERUP (1932) (2n = 14). A third species I. argyroides has been studied now and appears to have the same number of small chromosomes (fig. 67). This fact reinforces GILLETT's supposition as to a close relation between the genus Cyamopsis and the subgenus Indigastrum. More cytological evidence might give a solution to uncertainties as to the delimitation of this subgenus.

Plate V. (Unit of scale 10 μ). Fig. 57. Indigofera deightonii Gillett 64043. Fig. 58. Indigofera microcarpa Desv. 63018. Fig. 59. Indigofera diphylla Vent. 64054. Fig. 60. Indigofera oblongifolia Forsk. 62311. Fig. 61. Indigofera schimperi Jaub. &S pach var. schimperi 62316. Fig. 62. Indigofera semitrijuga Forsk. 64050. Fig. 63. Indigofera volkensii Taub. 62216. Fig. 64. Indigofera volkensii Taub. 63009. Fig. 65. Indigofera spicata Forsk. forma parvula 62368. Fig. 66. Indigofera alternans DC. 64053. Fig. 67. Indigofera argyroides E. Mey. 64058. Fig. 68. Indigofera richardsiae Gillett 64047. Fig. 69. Indigofera richardsiae Gillett 64047. (9 chromosomes). Fig. 70. Indigofera richardsiae Gillett 64047 (9 chromosomes + fragment). Fig. 71. Indigofera welwitschii Bak. var. welwitschii 64055. Fig. 72. Indigofera butayei De Wild. 64024.

Subgenus E. Microcharis (BENTH.) GILLETT. (Plate V, Fig. 68-72).

Earlier, two species of this subgenus were studied, viz. I. lobata and I. asparagoides, the latter with two subspecies asparagoides and ephemera (FRAHM-LELIVELD 1962, figs. 16, 19) all three with 2n = 16 rather short chromosomes.

This time I. butayei (fig. 72) with 2n = 16 chromosomes of much the same size and type as those of I. asparagoides and I. welwitschii var. welwitschii were examined (fig. 71), the latter with 2n = 16 extremely small chromosomes. The most remarkable feature in this subgenus is the occurrence of 2n = 8 huge chromosomes in the species I. richardsiae (fig. 68). The seeds were collected at Kew Herbarium and only this sheet yielded viable material. After examining the root tips of ten seedlings all showing excellent metaphase plates, we suspected that the very small seed samples might have been those of contaminating material. Efforts to get seedlings from another source, viz. the East African Herbarium at Nairobi met with no success, as the seeds received by the kind mediation of Mr. GILLETT either were too young or too old to be able to germinate. Dr. VERDCOURT was kind enough to send a second batch of seeds from the same Kew material originally examined. He ascertained once more that both seeds and pods were those from I. richardsiae, the determination being unquestionable. From this second batch another 13 seedlings were examined and the chromosome counts of 23 root tips resulted without exception in the same number. However, it is worth mentioning that a few stray metaphase plates were encountered where fragmentation had taken place so that a number of 9 chromosomal bodies or even 9 and a fragment could be counted (figs. 69 and 70). The diploid complement of chromosomes allows the analysis of two very large. two large and 4 smaller chromosomes.

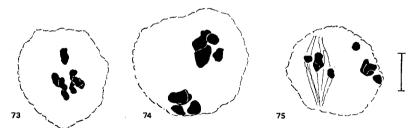


Plate VI. (Unit of scale 10 μ). Fig. 73. Indigofera richardsiae 64047. Metaphase I. Fig. 74. Indigofera richardsiae 64047. Telophase I. Fig. 75. Indigofera richardsiae 64047. Anaphase II.

In consideration of the extraordinary dimensions of the mitotic chromosomes in *I. richardsiae*, an attempt was made to get information on the meiotic behaviour in this species by means of aceto-orcein smears of pollen mother cells from the offspring reared in the hothouse. Figs. 73–75 (Plate VI) render account on the results which point to the ability to undergo a perfectly normal meiotic division. That the abundant flowering under relatively dry hothouse conditions results in a very poor fruit setting may be ascribed to the abnormality of the hothouse ecology. This, apparently, is also the cause of deviations and fragmentations during the reduction division and, consequently, of a large percentage of abortive and dwarf pollen grains. The possibility at least that the original mother plant might have been a haploid may be excluded.

The morpho-taxonomic homogeneity of *Microcharis* definitely finds little support in the metaphase plates hitherto examined.

Discussion

The results of a cytological study of about 28 per cent of the tropical African *Indigofera* species suggest that this rather large and diversified genus may have still more surprises in stock than hitherto encountered, the more so if also the Asiatic and American species of the genus should be involved. At any rate, it is certain that the following base numbers exist: 4, 6, 7 (and 8?). Owing to the variety in dimensions of the chromosome sets any efforts to present a plausible relationship between these base numbers may appear rather prospectless without extensive studies in meiotic division and breeding experiments. Nevertheless, a few points may be suggested. The majority of species hitherto studied possess 2n = 16 chromosomes. The 32-chromosomic species which were considered to be fairly rare in the endemic taxa of Africa are present in several divisions of GILLETT's monograph.

1. The *Brevi-erectae* are a subsection with a centre of distribution reaching from Sudan to Angola, whereas individual species occupy an area extending to Asia. The latter is the case for *I. sessiliflora* (2n = 32) obviously a plant occurring in drier regions. On the other hand, *I. microcalyx* (2n = 32) is an African endemic from much wetter places.

2. The East Tropical African subsection *Dissitiflorae* also has a wide dispersion, viz. in India, South Africa and Madagascar. The East African species *I. tanganyikensis* has 2n = 16 chromosomes, but the occurrence of one seed revealing 2n = 32 in its root tips has been recorded here, although perhaps being a chance duplication.

3. In the South Tropical African subsection *Pilosae*, it is as yet only the African endemic *I. pilosa*, – the type species for this taxon – which appears to have 2n = 32 chromosomes. According to GILLETT the Indian species *I. glabra* apparently belongs to this section.

4. Also in the subsection Atratae with its centre of distribution in South Central Africa, it is the type species *I. atriceps* sensu stricto and another two of its subspecies which possess 2n = 32 chromosomes. A third subspecies setosissima appears to have 2n = 16 chromosomes. This subsection is restricted to Africa. In the enumeration of material of *I. atriceps* ssp. rhodesiaca (2n = 32) the altitude of the habitat is mentioned repeatedly, ranging from 970-1470 m. Moreover, GILLETT emphatically states that the subspecies atriceps and alboglandulosa (ENGL.) GILLETT (the latter one not yet cytologically investigated) both have been reported at altitudes up to at least 3500 m.

5. For the subsection *Psiloceratiae* it is GILLETT himself who suggests that this taxon might be an unnatural group and most of its species closely related to the *Tinctoriae*. As centre of distribution South Tropical Africa is suggested, but the geographical dispersion of its members reaches into China. Its type species *I. sutherlandioides* again appears to be tetraploid (2n = 32), but is variable to such a degree that delimitation against other species such as *I. fulgens* BAK. and *I. baumiana* HARMS (both not yet cytologically studied) meets with difficulties and subdivision of *I. sutherlandioides* into subspecies is barely possible owing to the lack of sufficient material.

6. In the largest subsection, *Tinctoriae*, in which more than 30 species for tropical Africa are registered by GILLETT, 2n = 32 was found in *I. subulata* var. *scabra* in one portion of seeds: all other counts yielded 2n = 16 and this last number of chromosomes also has been reported in this taxon by RAMANATHAN (1955) in India. This case of tetraploidy again suggests chance duplication, this time in a species evidently dispersed by human action in Africa as well as in India and Central America. The other case of tetraploidy does not belong to the same base number and will be discussed later on.

7. In the Alternifoliolae, also an extensive subsection with centres of distribution in Angola and Sudan and a dispersion reaching to both Madagascar and Mexico, - i.e. when the characteristic of alternate leaflets is taken as a criterium – three cases of tetraploidy were met with; they are *I. volkensii*, *I. spicata* and *I. alternans*. Whereas in the volkensii case one out of three batches appeared diploid, it may be accepted as certain that all three species are polyploid. Both tetraploids of *I. volkensii* were collected wild whereas the diploid represented an obvious selection made by the Sisal Experiment Station at Mlingano.

As to the other polyploid series with base number x = 6, SENN in 1939 reported the count 2n = 12 for "I. anil (sumatrana)." Whereas there may be no doubt as to the exactness of the counting, it is certain that the examination took place in some other species, the identification of which is no longer possible. The number 2n = 12 is present in I. macrocalyx, an endemic species from West Tropical Africa belonging to the subsection *Paniculatae*: another representative of this subsection is I. mysorensis ROTTB. from India. The I. macrocalyx chromosomes are immediately distinguished from those of the other Paniculatae members by their robustness. In the Tinctoriae, I. emarginella with its 2n = 24 chromosomes is an exception; the species is variable in habit and widely spread in Africa. Taking into consideration that GILLETT suggests India as a possible centre of origin for this subsection, it is worthwile remarking that in the related subsection Psiloceratiae are placed a.o. the shrubby Indigofera I. decora, a wellknown ornamental in Europe imported from the Himalayan regions. This species (TSCHECHOW, 1930) as well as *I. dosua* BUCH. – HAM ex D. DON, I. heteranthera WALL. ex BRANDIS, and I. cytisoides L. (FRAHM-LELIVELD 1960, Figs. 25, 26 and 40) have 2n = 48 chromosomes. Until now these species have been supposed to be hexaploids of the base number x = 8 (GILLETT 1958 p. 5), but the fact that x = 6 really exists makes it more plausible to consider them as octoploids. Increase of cytological research into the wild Indigotera species from India may throw more light upon this problem. It is worth noticing that the base number x = 7 has not yielded polyploids so far. Herewith the cases of polyploidy in the classical sense have been analysed. TURNER (1956) mentions two more instances of Texan *Indigoteras* with 2n = 32: the section which they belong to, is not mentioned.

With respect to polyploidy in all the other cases mentioned here, two aspects may be pointed out:

- 1. Until now polyploidy has been observed in the subgenus *Indigotera* exclusively,
- 2. Several cases of this polyploidy have their original habitat in high altitudes or in dry climates (cf. also HAGERUP 1932).

Whether these statements involve further consequences as to our knowledge of the evolution of the genus *Indigofera* and its dispersion must be left open, so long as no eco-statistical information is available.

The base number x = 7 is characteristic for the related genus *Cyamopsis* and for the species of the section *Indigastrum* as yet studied: this may be an indication for a relationship between these two taxa, a relationship still considered disputable by GILLETT, witness the interrogation mark placed in the chart on p. 4 of his monograph. The same base number has also been encountered in stray instances in other taxa e.g. *I. ischnoclada (Latestipulatae)* with large chromosomes, in *I. strobilifera* ssp. *lanuginosa (Latestipulatae)* with rather small chromosomes and in *I. dasycephala (Paniculatae)* with small chromosomes. It is evident that wider knowledge and cytotaxonomic cooperation must decide whether another classification would be advisable.

When using the expression "classical polyploidy" in the discussion on – especially – the 32-chromosome species, this was done with regard to the presence of *I. richardsiae* with 2n = 8 chromosomes. The base number x = 4 is not only new for the *Leguminosae*, it implies also that all 16-chromosome species of *Indigofera* should be considered as tetraploids, a view which shall be discussed presently.

The subgenus *Microcharis* has been subject to uncertainty as regards its taxonomic status. GILLETT (1958 l.c. p. 127) mentions two reasons why he prefers to consider *Microcharis* as a subgenus of the genus *Indigojera* and not as a separate genus: "1° because the subgenus *Indigojera* and not as a connection link between *Microcharis* and *Indigojera* s. str. and 2° because it is in practice more convenient as this involves fewer name changes." From a cytotaxonomic standpoint, the second argument is of no consequence, but the first one becomes highly debatable. As yet, *Indigastrum* stands apart with its base number x = 7, which is present three times in *Indigojera* subsections, and there with chromosomes of rather varying dimensions. *Microcharis*, as far as known now, shows base numbers x = 8 with extremely varying dimensions and x = 4 with giant chromosomes.

The presence of the base number x = 4 overthrows certain speculations on phyletic origins in the *Leguminosae*. SENN (1939) published a scheme in which x = 8 is assumed as a centre, from which all the other base numbers in the family might be derived either by an euploid loss or addition. Since that time our knowledge on cytotaxonomy has been augmented, especially as to the tropical taxa. The basis laid by SENN's scheme, however, has been maintained, and

TURNER & FEARING (1959) only modified this scheme. Later reports by a.o. MANGENOT c.s. and MIÈGE (1960) on chromosome numbers filled up many lacunae.

The base number x = 4, however, calls for further investigations in the *Galegeae* complex, a.o. in the first place in the genus *Rhynchotropis* and the other members of *Microcharis*. This low number suggests that at least part of the *Galegeae* must be of very ancient date and also that the majority of *Indigotera* (2n = 16) should be considered as tetraploids.

It is clear that a more elaborate knowledge of the cytological features in a group does not always simplify the task of the taxonomist, if taxonomy at least endeavours to include an evolutionary picture. Cytological results in most cases point to an intricate pattern of interrelations next to an evident convergence of polyphyletic origins, the roots of which cannot be traced by outward morphological features alone. Cooperation of morphology, genetics, cytology and biochemistry, just to mention a few aspects of modern research, will be necessary.

The present study would not have been possible without the aid of various persons: it is only possible to mention a few here.

In 1962 I made an extended tour through various parts of Eastern Africa, from where I brought back a considerable amount of living material and seed samples pertaining to *Indigojera*. This tour was made possibly by a grant of the Ministry of Agriculture in the Netherlands on advice of the Board of the Agricultural University, Wageningen.

Furthermore I wish to mention the constant help by Mr. J. B. GILLETT and Dr. B. VERDCOURT from Kew Herbarium in identifying material and supplying seed samples.

Finally I would like to render thanks to Mr. TH. E. VEER who, in the short period before his emigration to Argentina, mastered the technique of making cytological slides and with painstaking patience made the hundreds of excellent slides necessary for this study.

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