MEIOTIC CHROMOSOMES IN AFRICAN COMMELINACEAE

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Following a limited study of Ethiopian Commelinaceae[14*] an opportunity existed to expand the chromosomal survey to other parts of Africa. Such an attempt seemed warranted for a number of reasons. Early evidence indicated that basic numbers of genera had been misinterpreted, that polyploidy and aneuploidy, but rarely both, were characteristic of different genera, and that infraspecific polyploidy and aneuploidy were widespread and also typical of certain genera. I supposed that a study of these features might lead to a clearer understanding of their roles in speciation and significance in phylogeny. Not least among my considerations were the varying definitions of commelinaceous subdivisions, perhaps best illustrated by Brenan's[2] discussion on assigning his newly described *Triceratella* to a tribe. Preliminary counts in Africa in conjunction with existing data disclosed a marked similarity of basic chromosome numbers for associated genera which in some degree corresponded to major subdivisions of the Commelinaceae. All these trends needed exploration and to this end the study was undertaken.

MATERIALS AND METHODS

Immature flower buds and herbarium specimens of *Cyanotis* (Tradescantieae), and *Aneilema*, *Commelina*, and *Murdannia* (Commelineae), were collected in east, central, and south Africa during September-December, 1962. Buds were fixed in 4 parts chloroform, 3 parts absolute ethanol, and 1 part glacial acetic acid; as soon as possible thereafter, usually up to 10 days, the vials were airmailed to England for storage at −40°C. Buds were examined for PMC meiosis in 2% acetic-orcein and satisfactory squash preparations were mounted in euparal for future reference. No difficulty in staining was experienced even after 9 months of fixation and presumably if needed buds could be kept satisfactorally at this temperature for longer periods of time. Whenever possible collections from more than 1 plant were examined and these results are indicated in parenthesis following my collection numbers in tables listing the chromosome numbers. It is regrettable, particularly in view of the marked frequency of infraspecific aneuploid and polyploid races in most genera, that this procedure is not followed elsewhere. The importance of knowing how many plants have a particular number under these circumstances can not be overemphasized.

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* Superscript numerals refer to list of references at end of article.

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Although useful meiotic plates were found for most collections, about 20% of those collected failed to show meiosis even when a wide range of buds had been fixed. By referring to my field notes, I found that by and large such buds had been fixed between 11 a.m. and 3 p.m. on clear days in more or less exposed localities. On the other hand, meiosis was found rapidly in buds fixed from 8-11 a.m. and from 3-5 p.m. on clear days without shade or at any time during the day if cloudy or if the plants were growing in the shade providing the 'correct' size had been preserved. These plants appear to have a decreased meiotic activity during mid-day under hot, exposed, often dry conditions, whereas this decrease was not demonstrable either earlier or later in the day. Similar daily 'meiotic cycles' have been noted in collections of Linaceae, Polygalaceae, and Rubiaceae from Mexico and the southwestern U. S.

A complete set of voucher specimens has been deposited at the Royal Botanic Gardens, Kew (K); duplicates are in the U. S. National Museum (US) and the Missouri Botanical Garden (MO). As the systematic study of the African Commelinaceae proceeds at Kew, the unnamed collections listed here will eventually be associated with binomials.

CYANOTIS

For 5 species listed in Table 1, basic numbers of $x=11$, 12 and 13 are reported with the $x=13$ line new to *Cyanotis*. When these data are combined with other African reports, [5,14] $x=12$ is the most common basic number for species native to that continent.

Generally the meiotic process was regular. An exception was the nondisjunction noted in about 20% of the anaphase plates of 1 plant of *C.* sp. (Fig. 4) giving cells with 11+13 rather than the normal complement of 12 chromosomes. Otherwise the plates were normal in appearance. Unequal distribution of chromosomes during anaphase has recently been reported for *Setcreasea*.[16] From a casual observation of pollen, I found only a small number of hollow and shrivelled grains, no more than for those plants with normal disjunction, suggesting that the loss or gain of 1 chromosome had no deleterious effect on the new haploid cells.

Even the infrequent occurrence of nondisjunction in *Cyanotis* could explain, at least in part, the fairly high incidence of aneuploidy within species populations. For example, among a sample of 6 plants from the Transvaal (Table 1), the homomorphic *C. speciosa* was found with 3 cytotypes: typical plants with 13_{II} (Fig. 5) as well as those with $13_{II}+1_{I}$ and 15_{II} (Fig. 6). The anticipated trivalent and quadrivalent configurations were not observed. Infrequently the extra chromosome in the $2n=27$ plants lagged at anaphase and these might have been excluded from the usual groupings of 13+14 found. It is not inconceivable that these hyperaneuploids had their origins from nondisjunction forming aneuploid races without, as yet, recordable morphological

TABLE 1.

GAMETIC CHROMOSOME NUMBERS IN AFRICAN *CYANOTIS*

Species	n	Voucher & locality
Basic number $x=11$		
C. barbata D. Don	11	KENYA: Rift Valley Prov., Navasha Dist., 2 miles W of west entrance to Aberdare National Park, *Lewis 5927* (1), Figs. 1-2.
Basic number $x=12$		
C. longifolia Benth. (dwarf form)	12	N. RHODESIA: N W Prov., Mwinilunga Dist., Mujileshi River, ca.4 miles E of Angola-N.R. border, *Lewis 6133* (2).
(tall form)	12	N. RHODESIA: N W Prov., Mwinilunga Dist., Zambesi River, 4 miles N of Kalene mission, *Lewis 6206* (2).
C. sp.	12	N. RHODESIA: N W Prov., Mwinilunga Dist., 3-4 miles SE of Angola-N.R. border & 1-4 miles SW of Mujileshi River, *Lewis 6147* (2). Figs. 3-4.
Basic number $x=13$		
C. foecunda Hassk.	13	KENYA: Rift Valley Prov., Trans Nzoia Dist., ENE slope of Mt. Elgon, *Lewis 5964* (1).
C. speciosa (L.f.) Hassk.	13	N. RHODESIA: N W Prov., Mwinilunga Dist., 1-4 miles E of Angola-N.R. border, *Lewis 6134* (1); 3-4 miles SE of Angola-N.R. border & 1-4 miles SW of Mujileshi River, *Lewis 6157* (1). S. AFRICA: Natal, Hlabisa Dist., Charters Creek, *Lewis 6304* (2).
	$13,+1_{I},2_{II}$	S. AFRICA: Transvaal, Pretoria Dist., Pretoria, Wonderboom, *Lewis, 6344* ($3,13_{II}$; $2,13_{II}+1_{I}$; $1,15_{II}$), Figs. 5-6.

differences. Other examples of infraspecific aneuploidy have been observed in more heteromorphic species than *C. speciosa*. The present count of $n=11$ for *C. barbata* from Kenya confirms the report from Ethiopian populations,[14] but Sharma and Sharma[24] found $n=12$ for an Indian collection. It would be interesting to know how widespread the $n=12$ race is in Asia and whether or not *C. barbata* is multibasic according to a continental distribution. It is well worth noting that the interpretation of meiosis at diakinesis is often confusing in *Cyanotis* and other Commelianaceae and this factor can not be overlooked in

explaining some of the diversity in recorded chromosome numbers. As an example, I can cite the meiosis of *C. barbata* in which the nucleolus resembles a bivalent having 2 chiasmata during mid-diakinesis. Thus the meiotic number for the PMC illustrated in Fig. 2 might be given as $n=12$ (and was by a cytologist who examined the cell), but later diakinesis on the same slide clearly shows PMCs with only 11 bivalents and a more faint nucleolus (Fig. 1). This discussion does not imply an error in the report of Sharma and Sharma for they also examined later stages of meiosis; it does, however, stress the danger of drawing too hasty a conclusion from diakinesis alone. Kammathy and Rolla[12] found a $n=11$ race for *C. arachnoidea* C.B.Cl., a species typically having $n=12$[12, 25, 26], and 'fragments' were noted by Islam and Baten[10] for *C. cristata* Schult.f.*

When the results for 18 Afro-Asian species with known chromosome numbers are summarized, we find: 1 species with $n=8$; 2 species with $n=10$; 1 species with $n=11$; 2 species with $n=11$ and 12; 9 species or 50% with $n=12$, 24, 36; 2 species with $n=13$; and 1 species with $n=14$. By far the most frequent basic number is therefore $x=12$ predominantly at the diploid level but including the only known polyploids (*C. adescendens*, $4x$[21] and *C. tuberosa*, $2x$, $4x$, $6x$[12, 21, 26]). This trend is not likely to be altered as more species are studied and $x=12$ should remain the central focus of chromosomal differentiation in the genus.

How does this number fit those of other genera usually grouped with *Cyanotis*? If one follows Brückner,[3] who included *Cyanotis* in the Subfamily Tradescantieae, Tribe Hexandrae, then *Tradescantia*, *Leptorrhoeo*, *Setcreasea*, and *Zebrina* are the 4 genera most closely associated. The most frequent basic number for *Tradescantia* is $x=6$, for *Setcreasea* $x=6$, for *Zebrina* $x=12$, and none is known for *Leptorrhoeo*. If one follows Clarke,[4] who placed *Cyanotis* in the Tribe Tradescantieae, the only definite count known for those genera listed near *Cyanotis* is $n=12$ for *Floscopa*.[12] Although the data are incomplete, the evidence reveals basic numbers of $x=6$ and 12 for genera associated with *Cyanotis* by Brückner and Clarke. It also supports the inclusion by Clarke and Woodson[28] of *Floscopa* in the Tradescantieae since these numbers are very rare in the Commelineae where Brückner placed *Floscopa*. This suggests that $x=6$ is an original basic complement for these genera, and perhaps for the Tradescantieae, and that the $x=12$ is a polyploid derived from such a prototype having become widespread as a basic number for several genera in this circle of affinity. A significant example would be *Cyanotis*, the largest genus in the Tradescantieae.

* Two species of '*Cyanotis*' considered by Islam and Baten need clarifying. Reference is made to *Cyanotis zenonii* of Darlington[6] which Darlington[7] long ago corrected to *Campelia zanonia* HBK. Secondly they refer to "*C. spironema fragrans*," presumably from the legend on p. 80 of Darlington,[6] which is simply "C." for the third figure of the plate illustrating not the chromosomes of *Cyanotis* but rather of *Spironema fragrans* (= *Callisia fragrans* (Lindl.) Woodson).

Five minor lines of descent, $x=8$, 10, 11, 13, and 14, are each represented in *Cyanotis* by only 1 or 2 species. These could have formed by a gain or loss of chromosomes from $x=12$ in a similar way to the examples of infraspecific hypo- and hyper-aneuploidy outlined above except that they have reached a morphological differentiation recognizable at the rank of species. Probably *C. somaliensis* C.B.Cl. with $n=14$[5] has not yet attained such a level. According to Brenan (oral communication), this species may represent but a part of the *C. foecunda* complex ($n=13$) and as such *C. somaliensis* may eventually be recognized merely as an infraspecific aneuploid race.

Based on chromosome numbers and frequencies, a hypothetical evolution of *Cyanotis* has been constructed (Fig. 7). Some alterations in the figure are anticipated as the cytotaxonomic analysis of the genus proceeds (e.g., changing the $x=14$ basic line represented by *C. somaliensis* to $x=13+1$), but these are not expected to alter the principal features illustrated.

I have ignored chromosome size largely because meiotic chromosomes are inexact for comparative purposes and most research has been confined to meiosis. Exceptions are 2 photomicrographs of pretreated somatic cells illustrated by Shetty and Subramanyan.[26] From these I estimate the chromosomes of *C. axillaris* (L.) R. & S. to be 3.2-5.5 microns in length and for *C. arachnoidea* C.B.Cl. only 1.8-2.8 microns. In the same paper Shetty and Subramanyan described bivalents of *C. papilionacea* as "larger" than and those of *C. arachnoidea* as "smaller" than the other species studied which included *C. axillaris*, *C. cristata* (L.) D. Don, *C. fasciculata* R. & S., *C. tuberosa* R. & S., and *C. villosa* R. & S. Their bivalents would be considered as more or less intermediate in size. On comparing these results with the meiotic plates of *C. barbata*, *C. speciosa*, and an undescribed species (Fig. 1-6), I find the bivalents and chromosomes approximately intermediate in size and quite comparable with the majority illustrated by Shetty and Subramanyan. These sketchy data suggest that mitotic chromosomes and bivalents of *Cyanotis* species are predominantly of an intermediate size (e.g., 3.2-5.5 microns in *C. axillaris)* with a few species having smaller (e.g., *C. arachnoidea)* or larger (e.g., *C. papilionacea)* chromosomes.

When the anaphase I chromosomes of *C.* sp. (Fig. 3-4), *Commelina benghalensis* (Fig. 10-11), and *C. diffusa* (Fig. 14) are measured, the meiotic chromosomes of *Cyanotis* average 3.0 microns while those of the *Commelina* species are smaller at 2.6 and 2.1 microns, respectively. Apparently *Cyanotis* chromosomes on the average are somewhat larger than are those of *Commelina* and also *Murdannia* (see further discussion below).

ANEILEMA

The 5 species of *Aneilema* examined (Table 2, Fig. 8-9) are grouped

TABLE 2.
GAMETIC CHROMOSOME NUMBERS IN AFRICAN *ANEILEMA*

Species	n	Voucher & locality
Basic number $x=9$		
A. sp. aff. *pedunculosum* C.B.Cl.	9	KENYA: Rift Valley Prov., Trans Nzoia Dist., ENE slope of Mt. Elgon, *Lewis 5973* (2), Fig. 8.
Basic number $x=13$		
A. tacazzeanum Hochst.	13	UGANDA: E Prov., Teso Dist., 1.8 miles W of Wera, *Lewis 5999* (2), Fig. 9.
A. welwitschii C.B.Cl.	26(+1?)	CONGO: Katanga Prov., Lualaba Dist., 15 miles NNW of Kalene mission, *Lewis 6229* (1); N. RHODESIA: N W Prov., Mwinilunga Dist., Mujileshi River, 4.5 miles E of Angola-N.R. border, *Lewis 6143* (1).
Basic number $x=15$ or 10		
A. aequinoctiale (P.Beauv.) Kunth	30	KENYA: Central Prov., Meru Dist., 8 miles NE of Runyenje's, *Lewis 5911* (1); S. AFRICA: Natal, Durban Dist., Durban, *Lewis 6279* (1).
Basic number $x=16$ or 8		
A. johnstonii K. Sch.	16	N. RHODESIA: N Prov., Abercorn Dist., Chilunoma River, nr. Abercorn, *Lewis 6113* (3).

under 4 newly reported basic numbers, $x=9$, 13, 15 (or 10), and 16 (or 8). To these can be added the counts of $n=14$ for *A. montanum* Wight[12, 25, 26] giving 5 basic complements for a sample of only 6 species. (Many species with established chromosome numbers have been published under *Aneilema*, but all are referrable to *Murdannia.)* The genus is a rather large one and until more data are accumulated, little can be noted regarding chromosomal trends other than that aneuploidy and polyploidy have apparently played significant roles in the evolution of *Aneilema* giving rise to a multibasic group of species at several levels of ploidy.

COMMELINA

From a sample of 37 populations involving at least 26 taxa, basic numbers of $x=11$, 13, 14, and 15 are reported for *Commelina* (Table 3, Fig. 10-16). Those species with $x=15$ are in the majority, about 70% of the total; species with $x=14$ and 13 are infrequent, and the $x=11$ series is represented solely by *C. benghalensis.* Infraspecific polyploidy is reported for *C. africana* with $2x$, $4x$, and $8x$ races and for *C. beng-*

halensis with $2x$ (Fig. 10) and $4x$ (Fig. 11) races. The results also add a diploid race (Fig. 12) to the report of $n=30$ ($4x$) for *C. imberbis*.[14] No infraspecific aneuploid is recorded and regular meiosis was characteristic throughout (ignoring clumping and various adhesions attributed to fixation).

In a strict sense, $x=13$ is a newly reported basic number. The related *Commelinantia* is known with $n=13$[1] and its transfer to *Commelina* by Woodson[28] is now supported by the existence of similar complements in typical commelinas. However, Rowley[22] reported *Commelinantia* as having pollen with 3 colpi rather than the single colpus found for all other Commelinaceae studied; hence it might be argued that this unique micromorphological feature, together with certain gross characters, is worthy of generic recognition.

Seven species listed in Table 3 have been examined previously, all but one by Morton[18] from west African material. His results for these species are summarized in Table 4 together with those for the present study and for others. Morton's counts are based on $x=14$ in contrast to mine and most others which are characteristically $x=15$. The exception is $x=11$ for *C. benghalensis* having diploids widely distributed in India and both diploids and tetraploids frequent in Africa. The $n=$ca.24 count by Anderson and Sax[1] and $2n=$ca.68 by Darlington[5] suggest $4x$ and $6x$ races; unfortunately original localities were not given. But Morton's data are not similar. Possibly infraspecific aneuploidy exists for all these species, yet I think it peculiar that this mechanism should be largely confined to west African populations. It is clearly infrequent elsewhere. Regrettably my collections based on $x=14$ must for the present remain unnamed; among these a verification of some of Morton's numbers may be possible.

At least three suggestions regarding the original basic number of *Commelina* have been proposed. Certainly the oddest is found in an abstract by Deodikar[8] in which no evidence is given to corroborate the statement that "there are two polyploid series in primary and secondary chromosomal balance with 8 and 16 as their respective monoploid number." Not only does this quotation lack meaning to me, but $n=8$ has yet to be found in the genus. Unquestionably this abstract is to be ignored until some results are published to support the conclusions. On the basis of associations of groups of bivalents, Sharma[23] has suggested $x=4$ as the basic number of *Commelina*. I find the evidence inconclusive based as it is on the very questionable premise of bivalent association and then for only 2 species. Perhaps it is noteworthy that in a later paper Sharma and Sharma[24] fail to make further use of such associations in deriving basic numbers and evolutionary groups in the family. Morton[18] has proposed $x=7$, but I have shown that his results are not characteristic of *Commelina* as known today. In short, I find little evidence to support $x=4$, 7, or 8 as basic numbers.

TABLE 3.

CAMETIC CHROMOSOME NUMBERS IN AFRICAN *COMMELINA*.

Species	*n*	Voucher & locality
Basic number $x=11$		
C. benghalensis L.	11	KENYA: Rift Valley Prov., Trans Nzoia Dist., ENE slope of Mt. Elgon, *Lewis 5961* (1), Fig. 10.
	22	UGANDA: N Prov., Karamoja Dist., base of Mt. Moroto, nr. Moroto, *Lewis 5996* (1), Fig. 11.
Basic number $x=13$		
C. *eckloniana* Kunth	13	N. RHODESIA: N Prov., Abercorn Dist., Chilunoma River, nr. Abercorn, *Lewis 6112* (3).
C. cf. *eckloniana* Kunth	13	N. RHODESIA: N W Prov., Mwinilunga Dist., Mujileshi River, 4.5 miles E of Angola-N.R. border, *Lewis 6142* (2).
	13(+1?)	CONGO: Katanga Prov., Lualaba Dist., 19 miles SSW of Mutschatsha, *Lewis 6142* (2).
Basic number $x=14$		
C. sp. 1	14	N. RHODESIA: N W Prov., Mwinilunga Dist., 1 mile E of Ikelengi, *Lewis 6189* (4).
C. sp. 2	14	N. RHODESIA: N W Prov., Mwinilunga Dist., Mujileshi River, 5-6 miles SE of Angola-N.R. border, *Lewis 6170* (4).
C. sp. 3	14	N. RHODESIA: N W Prov., Mwinilunga Dist., Zambesi River, 4 miles N of Kalene mission, *Lewis 6196* (3), Fig. 13.
C. sp. 4	28	N. RHODESIA: N W Prov., Mwinilunga Dist., 3-4 miles SE of Angola-N.R. border & 1-4 miles SW of Mujileshi River, *Lewis 6146* (2).
Basic number $x=15$		
C. *africana* L. var. *africana*	15	S. AFRICA: Natal, Hlabisa Dist., Charters Creek, *Lewis 6305* (1). UGANDA: W Prov., Toro Dist., Queen Elizabeth National Park, *Lewis 6011* (2).
var. 1	30	S. AFRICA: Natal, Hlabisa Dist., 4.3 miles W of Charters Creek, *Lewis 6309* (1).

TABLE 3 (cont.)

Commelina africana var. 2	30	S. AFRICA: Natal, Estcourt Dist., Drakensberg Mts., base of Mt. Champagne, *Lewis 6266* (1).
var. 3	60	S. AFRICA: Transvaal, Pretoria Dist., Pretoria, Wonderboom, *Lewis 6345* (2).
C. diffusa Burm.f.	15	S. RHODESIA: Wankie Dist., Victoria Falls, *Lewis 6247* (1), Fig. 14. UGANDA: W Prov., Bunyoro Dist., 12 miles S of Victoria Nile on road to Masindi, *Lewis 6004* (2).
C. imberbis Ehrenb. ex Hassk.	15	TANGANYIKA: Tanga Region, Tanga Area, 6.3 miles W of Tanga, *Lewis 6062* (2), Fig. 12.
C. purpurea C.B.Cl.	15	KENYA: Rift Valley Prov., Trans Nzoia Dist., ENE slope of Mt. Elgon, *Lewis 5960* (1).
C. scaposa C.B.Cl.	15	N. RHODESIA: N W Prov., Mwinilunga Dist., 2 miles W of Ikelengi, *Lewis 6193* (1), Fig. 15.
C. sp. 5	15	N. RHODESIA: N W Prov., Mwinilunga Dist., 3-4 miles SE of Angola-N.R. border & 1-4 miles SW of Mujileshi River, *Lewis 6148* (3).
C. sp. 6	15	N. RHODESIA: N W Prov., Mwinilunga Dist., Zambesi River, 4 miles N of Kalene mission, *Lewis 6197* (3).
C. sp. 7	15	S. AFRICA: Transvaal, Pretoria Dist., Pretoria, Wonderboom, *Lewis 6347* (1).
C. elgonensis Bullock	30	KENYA: Rift Valley Prov., Trans Nzoia Dist., ENE slope of Mt. Elgon, *Lewis 5974* (1).
C. gerrardii C.B.Cl.	30	S. AFRICA: Natal, Durban Dist., Durban, *Lewis 6281* (1); Isipingo Beach, *Lewis 6283* (1) & *6285* (1); Hlabisa Dist., Charters Creek, *Lewis 6300* (1).
C. livingstonii C.B.Cl.	30	S. AFRICA: Natal, Hlabisa Dist., Charters Creek, *Lewis 6296* (2); Transvaal, Pretoria Dist., Pretoria, Wonderboom, *Lewis 6346 (1)*. S. RHODESIA: Salisbury Dist., Salisbury, *Lewis 6259* (1).
C. welwitschii C.B.Cl.	30	S. RHODESIA: Salisbury Dist., Salisbury, Cranborne, *Lewis 6252* (1).

C. sp. 8	ca.30	KENYA: Rift Valley Prov., Trans Nzoia Dist., Kitale, *Lewis 5981* (1).
C. sp. 9	30	N. RHODESIA: N W Prov., Mwinilunga Dist., nr. Mujileshi River, 4 miles E of Angola-N.R. border, *Lewis 6185* (1); 7 miles NW of Kalene mission, *Lewis 6226* (3), Fig. 16.
C. sp. 10	30	TANGANYIKA: S Highlands Region, Mbeya Area, Mbeya Range (ca.8 miles NE of Mbeya), *Lewis 6085* (2).
C. sp. 11	ca.45	N. RHODESIA: N W Prov., Mwinilunga Dist., 3-4 miles SE of Angola-N.R. border & 1-4 miles SW of Mujileshi River, *Lewis 6145* (1).

In an attempt to offer an alternate suggestion, I have summarized the gametic numbers known for *Commelina* in Table 5 together with frequencies of cytotypes. Each cytotype corresponds to a species excepting the infraspecific polyploids and rarely aneuploids. These are represented once for each race. The most obvious fact is the predominance of the $x=15$ line totaling 75% of all cytotypes. For this group almost twice as many polyploids as diploids are known and these are to a level of $10x$. Minor lines of descent account for the remaining cytotypes with basic numbers of $x=$ 11, 12, 13, 14, and 16, chiefly of diploids, infrequently of tetraploids, and of only one questionable hexaploid race. The table does not reveal the infraspecific polyploidy now known for 8 species or 20% of those species studied. Nearly one-half of these, such as *C. africana*, *C. benghalensis*, and *C. obliqua* Ham., each have 3 races at different levels of ploidy. When one considers that many species have only 1 recorded number from a single plant, the incidence of infraspecific polyploidy becomes even more remarkable and obviously this percentage can be expected to increase as more counts are accumulated. As I have noted above the definite examples of infraspecific aneuploidy are much less notable. Collections originally published under *C. nudiflora* L. were found with primarily $n=15$ and $2n=30$[23] with $2n=28$ and 56,[24] all from India, and with $2n=56$ by Darlington[5] without indication of source (not by Anderson and Sax[1] from North American material as Morton[18] reported). These give *C. nudiflora* 2 primary numbers of $n=15$ and 14 with the latter having a tetraploid race. If *C. diffusa* is considered a part of this complex, then, as I recorded in Table 4, the $n=15$ complement is by far the most common and probably the $n=14$ line arose by hypoaneuploidy from plants with $n=15$. This is the only verified example of aneuploidy within a species of *Commelina;* I expect that when the reports of Morton can be more fully explored and when my collections based on $x=14$ are named more cases with a pattern similar to *C.*

TABLE 4.

PRESENT CHROMOSOME NUMBERS IN *COMMELINA* AND PREVIOUS COUNTS

Species	Lewis	Morton[18]	Others
C. *africana*	$n=15,30,60$	$2n=28$	$n=15$[14]
C. *diffusa*	$n=15$	$2n=28$	$n=15$[14,21]; $2n=30$[12,13,27]
C. *forskalaei*	$n=15$	$2n=28$	$n=14$[15]; $n=15$[12,14,21]; $n=15$ & $2n=30$[25,26]
C. *imberbis*	$n=15$		$n=30$[14]
C. *gerrardii*	$n=30$	$2n=56$	
C. *livingstonii*	$n=30$	$2n=56$	
C. *benghalensis*	$(2x)n=11$	$2n=28$	$n=11$[12,14]; $n=11+0-2B$[15]; $n=11$ & $2n=22$[9,23,25,26]
(polyploid)	$n=22$	$2n=56$	$n=22$[14]; $n=$ca.24[1]; $2n=$ca.68[5]

nudiflora may come to light. Undoubtedly, however, the contribution of aneuploidy to speciation in *Commelina* is secondary to the role of polyploidy.

Do these facts and trends suggest an original chromosome number for *Commelina*? The $x=15$ line is certainly of secondary origin and as such gives no direct answer to this question. But consider *Commelina* in relationship with *Murdannia* (Table 6), a genus having a characteristic basic number of $x=10$. Except for *Aneilema*, these are the only large genera in the Commelineae and they are probably indicative of the tribe as a whole. The dominance of $x=10$ and 15 in the tribe suggests an ancient basic number of 5 giving rise by polyploidy to the widespread occurrence of multiples of this number today.

In referring briefly to chromosome size in *Commelina*, a topic already introduced under *Cyanotis*, I should mention again that a discussion based solely on meiotic figures is not satisfactory. However, Anderson and Sax[1] noted small chromosomes for *C. benghalensis* and mitotic chromosomes illustrated for *C. diffusa*[13] measure 1.9-3.7 microns in length. In meiosis there is not much difference between the anaphase I chromosomes of *C. benghalensis* (Fig. 10-11) and *C. diffusa* (Fig. 14). These chromosomes as well as the bivalents of *C. imberbis* (Fig. 12), *C. scaposa* (Fig. 15), and *C.* sp. (Fig. 16) would all be described as more or less small. Yet the bivalents of an unnamed *Commelina* with $n=14$ (Fig. 13) are of intermediate size and not unlike the majority figured for *Cyanotis*.

TABLE 5.

CYTOTYPES REPORTED IN *COMMELINA* WITH FREQUENCY OF PLOIDY*

$n=$	Ploidy					Total
	$2x$	$4x$	$6x$	$8x$	$10x$	
11	1	1	1(?)			3
12		1				1
13	3					3
14	4	2				6
15	12	18	9	2	1	42
16		1				1

* Excluding results of Morton,[18] several circa counts, and the meiotically irregular $5x$ *C. salicifolia*.[23]

MURDANNIA

All plants from 5 populations of *M. simplex* (Vahl) Brenan were found with $n=20$ and regular meiosis. These include collections from: N. RHODESIA—N.W. Prov., Mwinilunga Dist., 3-4 miles SE of Angola-N.R. border & 1-4 miles S.W. of Mujileshi River, *Lewis 6156* (1), 5-6 miles SE of Angola-N.R. border, *Lewis 6172* (2), 4-5 miles SE of Angola-N.R. border, *Lewis 6179* (1) (Fig. 17); TANGANYIKA—E Region, Kilosa Area, 6 miles SW. of Mikumi, *Lewis 6065* (1); and SWAZILAND—Komati River by Forbes Reef-Piggs Peak Rd., *Lewis 6329* (1). This number verifies the reports from India by Shetty and Subramanyam,[25, 26] the first under *M. sinicum* (Lindl.) Brückn. The $4x$ race is more widespread than are the hexaploid[12, 21] and octoploid[20] races which are known only from Asia.

A total of 24 cytotypes have been published for 15 species of *Murdannia* (see excellent review by Shetty and Subramanyam). Six species are known to have 2 or 3 levels of ploidy although several of these may be attributed to misidentification, but at most a fraction. When the n numbers are summarized according to frequency and level of ploidy (Table 6), the most obvious feature is the high frequency (71%) of the basic complement of $x=10$. This frequency is comparable to the 75% for $x=15$ in *Commelina*. In addition more than one-half of all cytotypes are polyploids, multiplied to the $8x$ level in 1 or possibly 2 lines, and this too is parallel to the situation in *Commelina*. Although the range of aneuploid cytotypes is extensive, each aneuploid line has few species and 3 'lines' are known only as infraspecific numbers as indicated by the footnote in Table 6. The most frequent number in these species is usually questionable as for *M. semiteres* (Dalz.) Santapau with $n=7$,[21] 10,[21] 12,[12] and 20,[21] but possibly multiples of 10 will be found most frequently for this species. For the present discussion, it is clear that

TABLE 6.
CYTOTYPES REPORTED IN *MURDANNIA* WITH FREQUENCY OF PLOIDY

$n=$	Ploidy				Total
	$2x$	$4x$	$6x$	$8x$	
7[3]*	1				1
8(?)*				1(?)	1
9	1				1
10	6	6	4	1	17
11	1	1			2
12[1]	1				1
15	1				1

* Known only as infraspecific aneuploids.

$n=7$ and 12 can not represent lines of descent or basic numbers. This leaves $x=9$, 11, and 15, each having 1 species. The origin of $x=9$ by the loss of a chromosome pair and of $x=11$ by a similar increase from $x=10$ are reasonable speculations, but the origin of $x=15$ offers several possibilities. Assuming that the number of $2n=30$ for *M. keisak* (Hassk.) Hand. Mazz.[17] is not that of a naturally occurring triploid, the species could have formed by a succession of chromosomal gains from $n=10$, 11, etc., but this is a long route beset with many gaps. Alternately *M. keisak* could have arisen from stocks of 10 and 5 or 5, 5, and 5. This hypothesis also has major drawbacks (not least among them is the absence of a species with $n=5$); even so the known chromosome numbers in the genus, the high frequency of polyploidy, and the low frequency of aneuploidy all strongly suggest this origin. I might note that the relationship of *Murdannia* and other Commelineae to the Tribe Pollieae needs further study and it should not be overlooked that *Pollia* is known with $n=5$.[7]

In summary, I propose that $x=5$ is an ancient, probably extinct, basic number for *Murdannia* represented today by a dominant $x=10$ line composed of species with $n=10$, 15, 20, 30, and 40.

In regard to chromosome size, the bivalents of *M. simplex* (Fig. 17) are smaller than those illustrated for *Cyanotis* and *Aneilema* and about equal or smaller in size than those of *Commelina*. Bivalents of *M. elata* (Vahl) Brückn.[12] are similar to *M. simplex*.

CONCLUSIONS

1. Basic numbers of $x=8$, 10, 11, 12, 13, and tentatively 14 are known for *Cyanotis*. This large genus is thought to have arisen from a $x=6$ prototype and to have had its chromosomal differentiation from a $n=12$ stock foremost by aneuploidy and secondarily by polyploidy. Infra-

specific aneuploidy is widespread while infraspecific polyploidy is restricted.

2. The most common basic numbers for *Cyanotis* and the Tradescantieae as a whole are $x=6$ or 12.

3. Basic numbers of $x=9$, 13, 14(7), 15(10), and 16(8) have been found for *Aneilema*. Results from the few species examined suggest a fertile area for additional study.

4. Species with a basic number of $x=15$ form the dominant line of descent in *Commelina*. Based on frequency, all other lines are of minor importance as is infraspecific aneuploidy. In contrast, the majority of known species are polyploids and many have polyploid races.

5. The dominant line of descent for *Murdannia* is $x=10$. All others are of lesser significance and, as for *Commelina*, most species are polyploids with infraspecific polyploidy more common than infraspecific aneuploidy. This parallel chromosomal pattern of speciation in *Murdannia* and *Commelina* is opposed to the major role of aneuploidy and minor contribution of polyploidy in the speciation of *Cyanotis*.

6. Although the common basic numbers of *Commelina* and *Murdannia* differ, i.e., $x=10$ and 15, prototypes of $x=5$ are suggested for both genera.

7. Small chromosomes typify *Commelina* and *Murdannia*, those of *Aneilema* are somewhat larger, while those of *Cyanotis* range from small to large with a majority intermediate in size.

8. The most frequent basic number encountered in the Tradescantieae is $x=6$ or multiples of it, while the most frequent numbers found in the Commelineae are multiples of 5. Probably the prototypes of the tribes differed, the Tradescantieae from a stock based on $x=6$ and the Commelineae on $x=5$. A consideration of typical basic chromosome numbers in the classification of the Commelinaceae will undoubtedly contribute to a more natural grouping of genera than has been heretofore possible.

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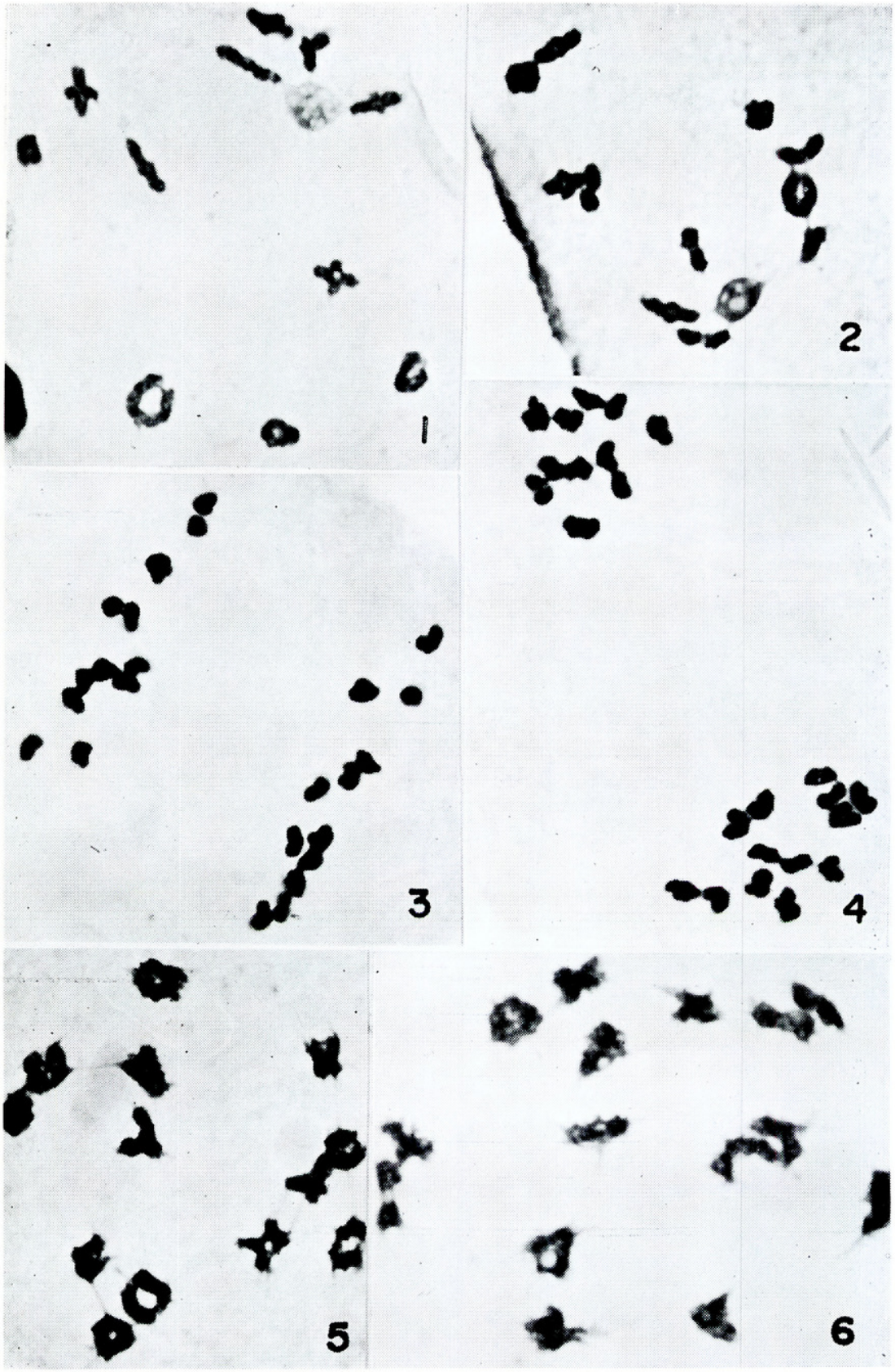
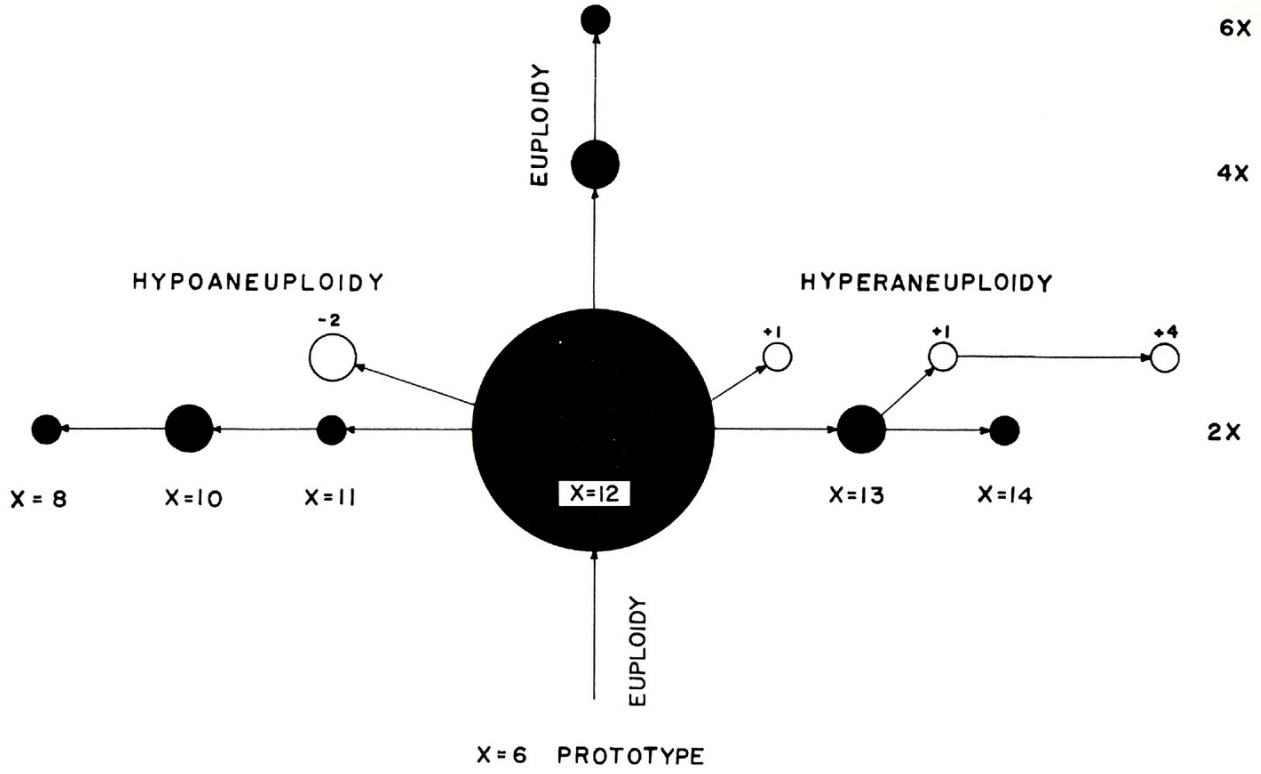


Fig. 1-6. Meiosis in *Cyanotis*. 1300X. Fig. 1-2. *C. barbata*, 11_{II} with the nucleolus in Fig. 2 resembling a bivalent, *5927*. Figs. 3-4. *C. sp.*,, 12+12 and 11+13, *6147*. Fig. 5-6. *C. speciosa*, 13_{II} and 15_{II}, *6344*.

Fig. 7. Hypothetical representation based on chromosome number of the evolution of *Cyanotis* from a $x=6$ prototype to a dominant extant group with $x=12$. From this stock it is suggested that cytotypes have evolved by hypoaneuploidy, hyperaneuploidy, and euploidy giving rise to a genus multibasic at the $2x$ level and (as presently known) unibasic at the $4x$ and $6x$ levels. Euploidy is vertically illustrated, aneuploidy horizontally as interspecific (solid circles) or infraspecific (hollow circles). The smallest circle represents one cytotype and is equivalent to one species excepting the infraspecific aneuploids (small circle for each cytotype). Other circles to scale.


6X
4X
2X
EUPLOIDY
HYPOANEUPLOIDY
HYPERANEUPLOIDY
-2
+1
+1
+4
X = 8
X=10
X=11
X=12
X=13
X=14
EUPLOIDY
X=6 PROTOTYPE

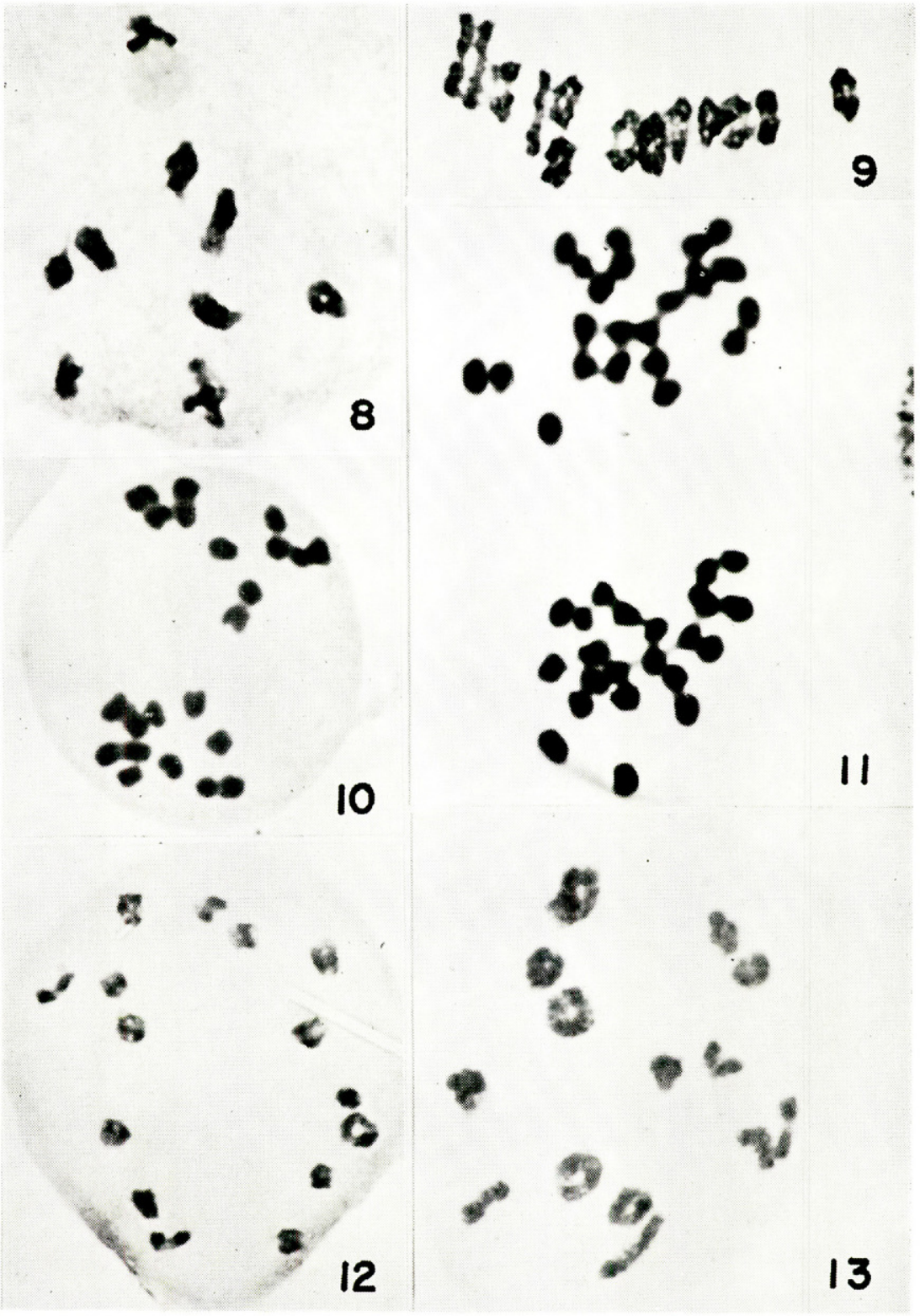


Fig. 8-13. Meiosis in *Aneilema* and *Commelina*. 1300X, 1550X for Fig. 10-11. Fig. 8. *A.* sp. aff. *pedunculosum*, 9_{II}, *5973*. Fig. 9. *A tacazzeanum*, 13_{II}, *5999*. Fig. 10-11. *C. benghalensis*, 11+11, *5961*, and 22+22, *5996*. Fig. 12. *C. imberbis*, 15_{II}, *6062*. Fig. 13. *C.* sp., 14_{II}, *6196*.

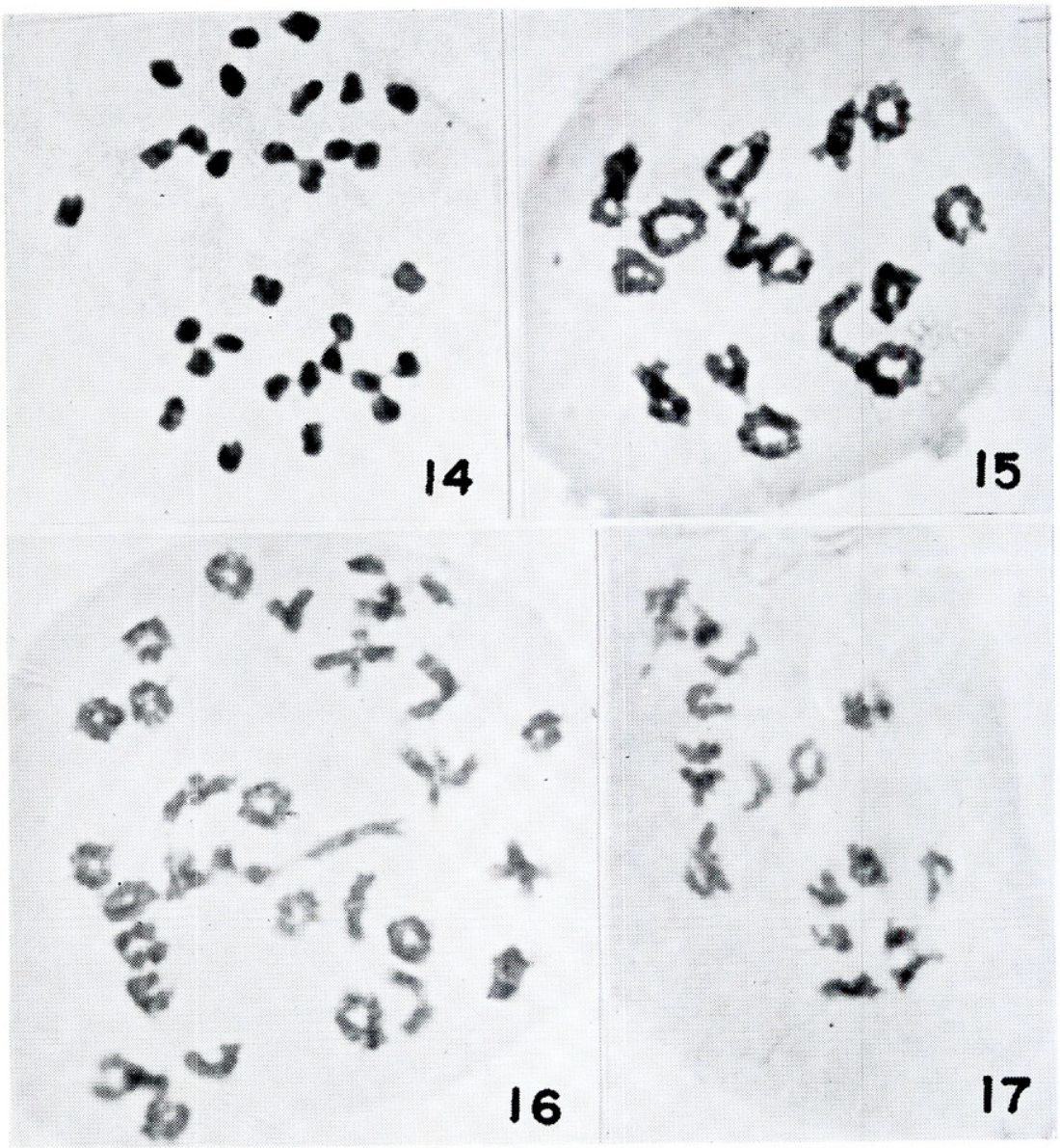


Fig. 14-17. Meiosis in *Commelina* and *Murdannia*. 1550X. Fig. 14. *C. diffusa*, 15_{II}, *6247*. Fig. 15. *C. scaposa*, 15_{II}, *6193*. Fig. 16. *C.* sp., 30_{II}, *6226*. Fig. 17. *M. simplex*, 20_{II}, *6179*.