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Meiotic chromosomes of monoecious Kentucky hemp *(Cannabis sativa)*

Margaret Y. Menzel

Crops Research Division, Agricultural Research Service, United States Department of Agriculture, Department of Biological Sciences, Florida State University, Tallahassee, Florida.

MENZEL, MARGARET Y. (Agricultural Research Service, **U.S.D.A.**) . ***Meiotic chromosomes of monoecious*** *Kentucky* ***hemp*** (Cannabis sativa.) Bull, Torrey Bot. Club, 91: 193–205. 1964. Staminate plants of dioecious 'Kentucky' hemp (Ky-d) and of three other dioecious strains had a heteromorphic pair of chromosomes at diakinesis and at metaphase I and were assumed to have the sex chromosome constitution XY. All analyzed plants of female-habit (Ky- ♀ m) and male-habit (Ky- ♂ m) 'Kentucky' monoecious hemp and of a German monoecious strain lacked the heteromorphic pair as did a pistillate plant of Ky-d, and hence were presumbly XX. Ky- ♂ m plants differed from other strains in having a large extra piece of heterochromatin attached to the short arm of both nucleolar chromosomes distal to the nucleolus organizer. The pachytene bivalents of hemp are characterized by proximal blocks of heterochromatin flanked by faintly-staining distal segments which terminate in deeply-staining telochromomeres. The short arms of the nucleolar chromosomes and of one other pair terminate with heterochromatic

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segments. Comparison of pachytene idiograms of Ky-d males (XY) and G-m (XX) failed to reveal differences which would identify the sex chromosomes at this stage.

Cannabis sativa L. is normally a dioecious species in which staminate and pistillate plants differ in habit and date of maturity. Pistillate plants of the 'Kentucky' variety can be induced to produce some staminate flowers under certain photoperiods (Borthwick and Scully, 1954). From the selfed progeny of such plants, selection over several generations gave rise to a uniformly late-ripening strain with female growth habit which, although it produced predominantly pistillate flowers, had sufficient pollen-shedding staminate flowers to maintain the line (Feaster, no date ; 1956 ; and unpublished). Female plants were rogued and the monoecious plants permitted to intercross.

In 1955, in a field plot of female-habit monoecious hemp, four monoecious plants were found which had the early-ripening, high-fiber male habit. When selfed or intercrossed, these plants bred true for male habit but segregated widely for the proportion of pistillate to staminate flowers. In 1956 a cytological study was initiated to see whether chromosome morphology could clarify the basis of monoecism and afford a rational basis for further breeding.

Strasburger (1910) and McPhee (1924) failed to find heteromorphic sex chromosomes in hemp, but most other workers (Hirata, 1924, 1929 ; Sinôto, 1929; Mackay, 1939; Yamada, 1943; Hoffman, 1947, 1952) agree that dioecious hemp has heterogametic males with a heteromorphic pair of X and Y chromosomes. The genetic and cytological basis of derived monoecism, however, remains in dispute; the evidence has been summarized and criticized by Westergaard (1958). The principal hypotheses are (a) that monoecious plants are all XX, variation in sex expression being due to heterozygosity of genes on X chromosomes and autosomes (Sengbusch, 1952), and (b) that monoecious plants may be XX, XY, and YY, the main function of sex determination having been pre-empted by autosomal genes (Hoffman, 1947, 1952).

Westergaard, noting that most of the available data stem from large-scale breeding programs in which pollination was insufficiently controlled for precise cytogenetic analysis, has clearly outlined the experimental procedures necessary to clarify the genetic basis of monoecism. The studies reported here were far from meeting the rigorous requirements stipulated by Westergaard. Field and garden facilities which met the security requirements of state and federal narcotics agencies were not available in Tallahassee and the plants did not thrive under local greenhouse conditions. Hence it was not feasible to carry out controlled crosses or selfings or to grow single-plant progenies. The study was confined to plants drawn from breeding experiments of Dr. Carl V. Feaster at the Plant Industry Station,

Beltsville, Maryland and to first-generation progeny of such plants. The breeding program was terminated in 1955 before definitive answers could be obtained to several cytogenetic questions. But since the--material examined included male-habit monoecious plants regarded by Sengbusch as non-existent and by Hoffman as extremely rare, it seems worthwhile to record the observations for the benefit of later students of the problem.

Materials and methods. In addition to Kentucky dioecious (Ky-d), female-habit monoecious (Ky-♀m) and male-habit monoecious (Ky-♂m), three other strains of dioecious hemp (P.I.185021, P.I.170264, and Wisconsin 37242) and a monoecious strain said to have come originally from Germany but otherwise of unknown origin (G-m) were examined cytologically. At first, plants were grown at Beltsville and shipped to Tallahassee when almost ready to bloom. In a few instances, buds were collected from Beltsville-grown greenhouse plants and shipped fixed to Tallahassee. Later, plants of all seven strains were grown in greenhouse and garden in Tallahassee, Kentucky strains required artificial short-day treatment to induce blooming if they were planted after about March 15 or before October 15.

Plants of the four dioecious strains were readily scored as male or female, although on one occasion (May, 1956) five out of twenty female plants of Ky-d produced a few staminate flowers at the end of the blooming season when the plants were heavily loaded with seeds. The Ky-♀m plants all had female habit. In Tallahassee, the flowers were predominantly pistillate and many plants never produced staminate flowers. Consequently the proportion of plants which could be analyzed was low. Of nine plants analyzed in 1956, one had only staminate flowers, and three had mostly staminate flowers and produced a few pistillate flowers only toward the end of the blooming season. The other five plants had mixed pistillate, staminate, and a few hermaphroditic flowers throughout the season.

The Ky-,$m plants were more variable in habit than Ky-d staminate plants, but none of the plants was classified as having female habit. The proportion of pistillate and staminate flowers varied widely from plant to plant and on individual plants at different times during the season. Since the two principal cytological features being scored appeared unrelated to the ratio of pistillate to staminate flowers, it was not recorded in detail.

The G-m strain did not show a photoperiod response in Tallahassee. The plants were dwarfed and so variable in habit and flower type that classification was impracticable. Analyzed plants ranged phenotypically from strict female to strict male habit, and produced 5–100% staminate flowers, but no variation in chromosome morphology was noted.

Buds for cytological study were fixed in 3 parts 95% ethanol: 1 part glacial acetic acid, stored in a refrigerator at about 3°C, and examined in standard temporary aceto-carmine squashes. A phase contrast micro-

scope was used to enhance contrast at pachytene and diakinesis. Some pachytene slides were prepared by hydrolyzing in 10% HCl at 60° for 10 minutes, staining in leucobasic fuchsin or Gomori's hematoxylin, and squashing in 45% acetic acid or in aceto-carmine.

Observations. DIOECIOUS STRAINS. At MI, all males examined from the four dioecious strains had a slightly unequal and asymmetrical one-chiasma bivalent (Fig. 1, 15; Table 2), one of the largest in the complement and frequently lying at the periphery of the plate a little distant from the other bivalents. In a total of 225 cells in which the heteromorphic pair was identified, it always had a single, terminalized chiasma and usually seemed to be composed of a rod- or J-shaped element and a V-shaped element. The asymmetry was more pronounced than the inequality; frequently the rod and the V appeared to be of about the same volume; if unequal, the V was larger.

TABLE 1. *Frequencies with which a heteromorphic bivalent (het II) was identified at diakinesis and metaphase I in pollen mother cells (PMC's) of male plants of four dioecious strains of hemp.*

Strain	No. Plants	Diakinesis			Metaphase I		
		No. PMC's	No. with het II	% with het II	No. PMC's	No. with het II	% with het II
P.I.170264	2	20	19	95	5	5	100
P.I.185021	6	90	89	99	22	22	100
Wisc. 372–42	12	138	133	96	13	12	92
Ky-d	20	349	324	93	245	186	76
Total	40	597	565		285	225	

The heteromorphic pair was regularly detected in Wisconsin 372–42, P.I.185021 and P.I.17064, but was less reliable in Ky-d for two reasons: (a) the two halves of the bivalent appeared less sharply differentiated in size and shape, and (b) the lower MI chiasma frequency in Ky-d males, resulting in an average of 6–7 one-chiasma bivalents per cell, made it more difficult to distinguish the heteromorphic from the homomorphic pairs.

At diakinesis, however, a heteromorphic pair of chromosomes, usually the largest in the complement, was readily identified with phase contrast illumination in more than 90% of pollen mother cells from all four strains (Table 1). One member of the pair had the same fuzzy appearance, with somewhat more diffuse distal regions, as the other chromosomes. The other member had one such end, in which at least one chiasma was invariably present in the 565 cells in which it was identified. The other end of this chromosome was sharply outlined and deeply stained and appeared compact and dense under phase contrast illumination; this "heterochromatic" arm did not taper out into faint threads as did other ends of bivalents (Fig. 2–5, 11–14). Since all males of dioecious strains possessed

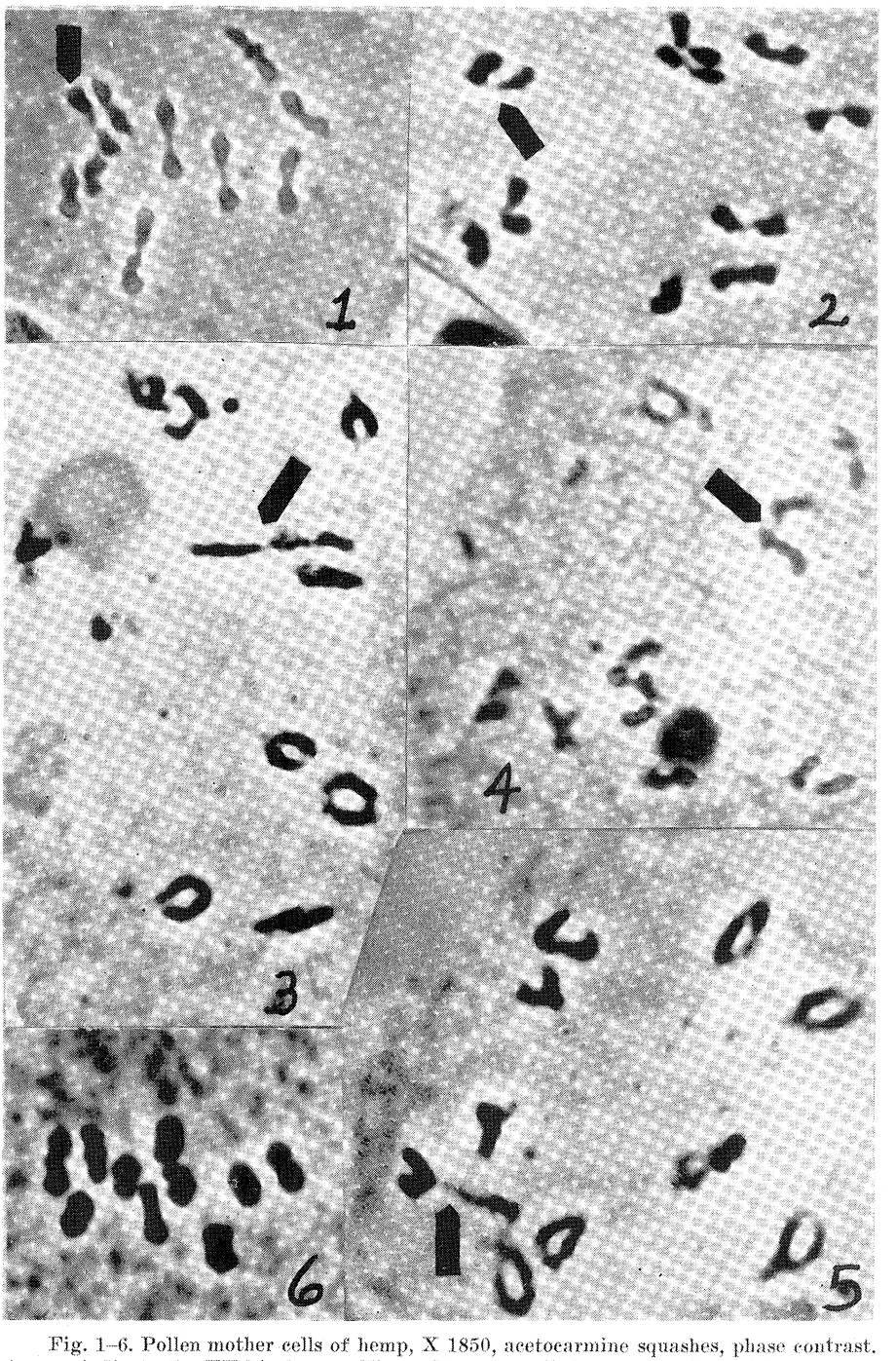

Fig. 1–6. Pollen mother cells of hemp, X 1850, acetocarmine squashes, phase contrast. Arrows indicate the XY bivalents.—Fig. 1. Metaphase I. Ky-d ♂.—Fig. 2. Metaphase I, P.I.185021.—Fig. 3, 5. Diakinesis, Ky-d ♂.—Fig. 4. Diakinesis, P.I.185021.—Fig. 6. Metaphase I, G-m.— Photomicrographs by P. L. Redfearn, Jr.

the heteromorphic pair while other kinds of plants did not, it is interpreted as the XY pair. The partially heterochromatic member of the pair occurred only in males and is assumed to be the Y chromosome.

One other chromosome pair, the smallest, could be identified at diakinesis by its attachment to the nucleolus. It characteristically appeared as a ring (2-chiasma) bivalent with two small heterochromatic "ears," distal to one of the chiasmata, attached to the nucleolus. The ears had the same optical

TABLE 2. *Distribution of the heteromorphic bivalent and the nucleolar knob in analyzed strains of hemp.*

Strain	No. Plants	Habit	Flowers	Het II	Knob	Putative Sex Genotype
Dioecious						
Wisc. 372–42	12	♂	♂	yes	no	XY
P.I.185021	6	♂	♂	yes	no	XY
P.I.170264	2	♂	♂	yes	no	XY
Ky-d	23	♂	♂	yes	no	XY
Total	43					
Ky-d No. 75	1	♀	♀ (♂)*	no	no	XX
Monoecious						
G-m	3	♂	♂	no	no	XX
	1	♂	♀ ♂	no	no	XX
	5	♀	♂	no	no	XX
	6	♀	♂ (♀)**	no	no	XX
Total	15					
Ky-♀m	5	♀	♀ ♂	no	no	XX
	3	♀	♂ ♀	no	no	XX
(No. 31)	1	♀?	♂	no	yes	XX
Total	9					
Ky-♂m	4	♂	♂	no	yes	XX
	17	♂	♀ ♂	no	yes	XX
Total	21					

* Flowers were predominantly ♀ until late in blooming period, when a few ♂ flowers were produced.

** Flowers were predominantly ♂ until late in blooming period, when a few ♀ flowers were produced.

and staining properties as the heterochromatic portion of Y. All 43 males studied (Table 2) had the same karyotype and were assumed to be XY.

Twenty-five pollen mother cells at diakinesis were analyzed from a single female plant (No. 75) of Ky-d which produced a few staminate buds late in the blooming season. All the bivalents were of similar chromaticity; the partially heterochromatic chromosome characteristic of males (Fig. 2–5, 11–14) was absent. The nucleolar pair was similar to that in the males. These results would be expected if the female plant were XX.

KENTUCKY FEMALE-HABIT AND GERMAN MONOECIOUS STRAINS. The phenotypic behavior of Ky-♀m and G-m in both Beltsville (Feaster, unpublished)

and Tallahassee clearly indicated that the genetic basis of monoecious habit was different in the two strains; for instance, G-m regularly produced some male-habit, male-flowered plants while Ky-m did not. Since the two

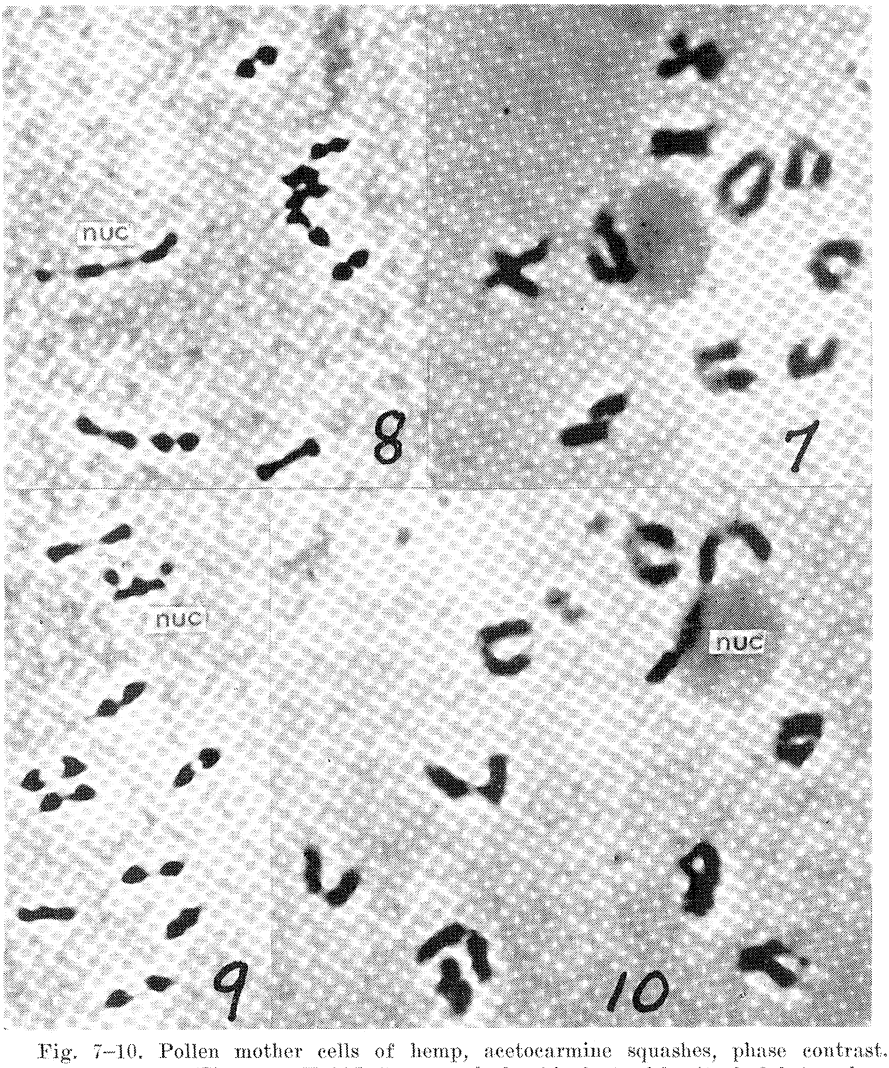

Fig. 7–10. Pollen mother cells of hemp, acetocarmine squashes, phase contrast. Fig. 7, 10, X 1850. Fig. 8, 9, X 925. "nuc"-nucleolar bivalent with attached heterochromatic knob.—Fig. 7. Diakinesis in G-m.—Fig. 8, 9. Metaphase I, Ky-♂m.—Fig. 10. Diakinesis, Ky-♂m (See also Fig. 22).—Photomicrographs by P. L. Redfearn, Jr.

strains proved to be cytologically indistinguishable, however, they are considered together here. Both appeared to differ in chromosome constitution from the German material described by Hoffman (1947, 1952).


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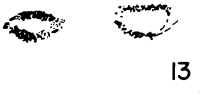
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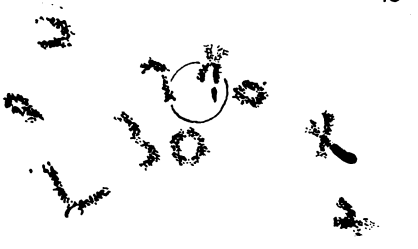
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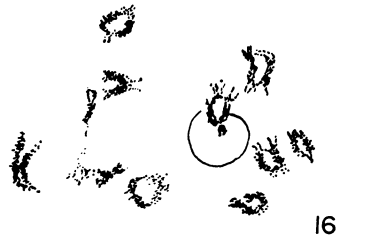
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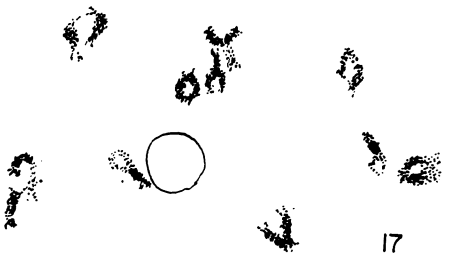
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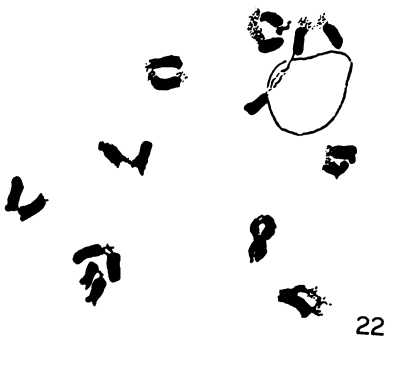
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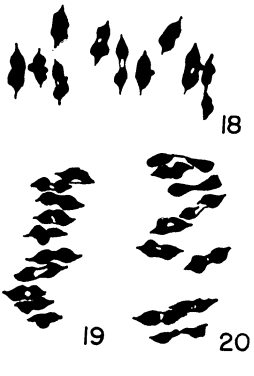
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Meiotic stages were studied in 9 Ky-♀m and 15 G-m plants (including 3 of the latter which had male habit and only male flowers). All 24 plants, regardless of habit or type of flowers, had only equal, symmetrical bivalents at MI and non-heterochromatic, non-heteromorphic pairs at diakinesis, similar to those in Ky-d female No. 75 (Fig. 6, 7, 16–21). Since Ky-♀m and G-m karyotypes were indistinguishable from each other and from that of plant No. 75 and differed from that of the dioecious males, and since Ky-♀m arose by selection from the progeny of dioecious females which had been induced to produce a few male flowers, all observations appeared consistent with the conclusion that both Ky-♀m and G-m plants were XX. All female monoecious plants had the characteristic nucleolar pair described above except one plant (No. 31) of Ky-♀m. The nucleolar pair of No. 31 had the peculiarities at both diakinesis and MI described below from Ky-♂m plants.

KENTUCKY MALE-HABIT MONOECIOUS PLANTS. Since no differences in karyotype were found between the four lines, or between sibbed and selfed progenies, they will be considered together. Twenty-one Ky-♂m plants, of which 4 had only male flowers and 17 had various ratios of female to male flowers, were analyzed. In all, the nine non-nucleolar bivalents were equal and symmetrical at MI and diakinesis, and "euchromatic" at diakinesis. They are therefore presumed to be of the sex genotype XX.

The nucleolar bivalent at diakinesis in all 21 plants differed from that in all other plants studied (except Ky-♀m No. 31) in that the ears were replaced by a very large heterochromatic structure ("knob") attached to the nucleolus (Fig. 10, 22). The knob together with the bivalent resembled a trivalent of 3 equal members. The knob persisted until metaphase I as a single or a pair of satellite-like structures attached by a thread or constriction to one of the smaller bivalents (Fig. 8, 9). Rarely, it was detached and appeared as a small univalent or free fragment. It sometimes appeared as a fragment or satellite at AI, but in most AI cells only ten bodies were present.

In a few cells, the knob could be interpreted as an extra small chromosome or centric fragment, but its history from pachytene (where it appeared as a large, deeply staining loop or pair of loops on the nucleolus, continuous with the rest of the nucleolar pair) to MII (when it was never

Fig. 11–22. Camera lucida drawings of pollen mother cells of hemp, X 1140.—Fig. 11–14. Diakinesis in Ky-d ♂ showing the heteromorphic XY pair and normal nucleolar chromosomes.—Fig. 15. The XY bivalents from 8 pollen mother cells of Ky-d ♂.—Fig. 16, 17. Diakinesis in Ky-♀m (Fig. 16) and G-m (Fig. 17), showing absence of heteromorphic bivalent and presence of normal nucleolar chromosomes.—Fig. 18–21. Metaphase I in G-m.—Fig. 22. Diakinesis in Ky-♂m, the same cell as Fig. 10, showing absence of heteromorphic pair and presence of a large heterochromatic knob on the nucleolar bivalent.

visible) indicated that it was not a centric element but a large block of heterochromatin associated with the nucleolus-organizing region. Some details of its behavior (e.g. its appearance as the end member of a chain of three bodies at diakinesis *versus* its frequent appearance at MI as two separate bodies attached to opposite ends of a small rod bivalent (Fig. 8–10, 22) are not understood.

ORIGIN OF THE MALE-HABIT PLANTS FROM FEMALE-HABIT MONOECIOUS PLANTS. It seems certain that the male-habit monoecious plants were not attributable to outcrossing and re-introduction of a normal Y chromosome, since they appear to be XX in karyotype. They must have arisen within Ky-♀m by mutation or segregation. The uniform presence of male habit and of a large nucleolar knob which is heterochromatic at diakinesis like the differential portion of the Y suggests that the knob-bearing nucleolar chromosome ("K") arose (a) by translocation of a portion of the Y controlling male habit to the nucleolar chromosome, or (b) by the acquisition by the nucleolar chromosome of a duplication or other extra block of heterochromatin (non-homologous with Y) which *per se* shifts growth habit toward maleness, at least when homozygous. The history of the strain makes (a) seem unlikely, but (b) is attractive if one supposes that the extra material was translocated from an autosome carrying male-determining modifiers which becomes heterochromatic at diakinesis (but not necessarily at the stage at which sexual differentiation is determined) because of a "spreading effect" from the adjacent nucleolar heterochromatin in a manner similar to that suggested by Russell (1961, 1963) for X-autosome translocations in mice. In either case, the Ky-♂m plants would be XX/KK, a constitution which might explain constant male habit as opposed to variability of flower type.

The record of one Ky-♀m plant (No. 31) with a knob casts some doubt on the above hypothesis and suggests that the association of knob and male habit may be coincidence. However, Plant No. 31 may have been incorrectly scored; it was recorded at the time the single bud collection was made as having only male flowers, unlike any other Ky-♀m plant observed by the author. By the time its peculiar chromosome constitution was discovered two weeks later, it had died, well in advance of all the other female-habit plants in the progeny. The suspicion arose that it was actually a male-habit plant like the original four "mutants." At any rate, its presence at least demonstrated that the knob mutation was present in the Ky-♀m line and that the Ky-♂m knob-bearing plants could have originated through segregation rather than through contamination.

All of the Ky-♂m plants were rather infertile and the line was lost before further analyses could be carried out. The history of the line suggests that it might be recovered again among selfed progeny of Ky-♀m.

PACHYTENE KARYOTYPES IN DIOECIOUS AND MONOECIOUS PLANTS. Preliminary observation showed that pachytene chromosomes of hemp are composed of relatively deeply staining condensed segments flanking the centromeres (which appear as gaps, constrictions, or oval grayish regions) passing rather abruptly into long, faintly stained distal regions which terminate in small, deeply stained telochromomeres, much like the chromosomes of *Lycopersicon esculentum* L. (e.g. Barton, 1950). It seemed likely that pachytene might prove to be the most informative stage of meiosis as to the nature and extent of the differentiation between X and Y at the cytological level. Hence a study of pachytene was undertaken with the object of describing the pachytene karyotype and preparing an idiogram of it and of identifying and comparing XX and XY bivalents at this stage. Ky-d males and G-m staminate plants were chosen since they were thought to

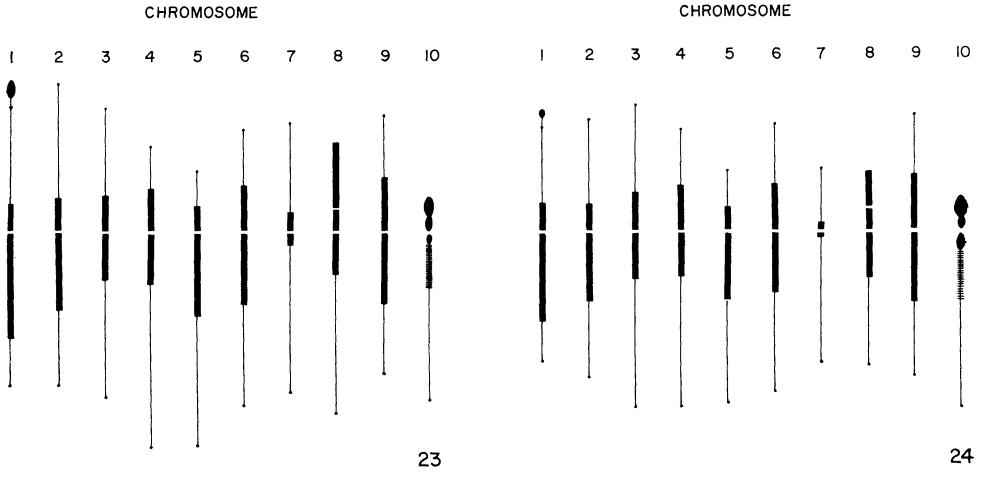

Fig. 23, 24. Idiograms of the pachytene bivalents of G-m (Fig. 23) and Ky-d (Fig. 24) hemp. X1160. Description in the text. (Drawing by G. W. Reinert).

represent XY and XX karyotypes respectively and afforded a large supply of staminate buds.

It did not prove possible to spread the chromosomes well enough so that all bivalents could be traced from end to end in the same cell except in a single PMC of Ky-d. However, many nuclei in which one to several pairs could be traced were seen. Bivalents were recorded by tracing with a camera lucida at a standard magnification, and the lengths of the various segments, measured with a millimeter ruler to the nearest .5 mm., were recorded. Bivalents so recorded were then matched subjectively into groups. All but about 3% of the bivalents recorded could be assigned without difficulty to one of 10 different types, corresponding to the haploid number of the species. Tentative idiograms based on 85 bivalents from G-m and 179 bivalents from

Ky-d (Fig. 23, 24) showed rather close agreement as to relative lengths of segments for the ten chromosome types, although there was some difference between strains in the relative total lengths of different chromosomes. The shorter arm is designated the left (L) arm and the longer arm right (R). Each chromosome segment can be designated by its class (chromosome 1 to 10), arm (L or R) and position relative to the centromere (proximal, p, or distal, d). For instance, Lp-1 indicates the proximal region of the left arm of chromosome 1. With a little practice, most of the bivalents could be identified without measurement. Chromosomes 3, 6 and 9 in G-m and 4 and 6 in Ky-d were sometimes confused unless absolute lengths were considered. In addition to the relative lengths of Ld, Lp, Rp, and Rd which furnished the main criteria for identification, chromosomes 1, 7, 8, and 10 contain easily recognized landmarks.

CHROMOSOME 1. Ld usually terminates in a large knob rather than a small telochromomere and has a dark, rather heavy chromomere about 1 micron proximal to the knob. CHROMOSOME 7. Both arms are entirely achromatic; the very short proximal regions often consist of only two or three heavy chromomeres flanking the centromere. Rd is often partially or wholly upsynapsed, so that this pair was at first taken for the XY pair in Ky-d males; however, it appears unpaired even more often in G-m plants. CHROMOSOME 8. Ld is chromatic and apparently does not end in a distinct separate telomere, at least in G-m. In a few cases in Ky-d, a suggestion of a separate terminal dot was noted. Ld is usually separated from Lp by a short achromatic or constricted region. CHROMOSOME 10. The nucleolar pair. Ld consists of a large chromatic knob about 2 microns long, to which the nucleolus appears to be attached, followed by two smaller knobs (wider and more rounded than the proximal regions of the other chromosomes) between which the centromere is located. The proximal ⅓ of Rd sometimes appears chromatic, more often not (cross bars in idiogram).

The achromatic distal regions all show a definite chromomere structure, and more extensive study would probably reveal other fine structural detail useful in identification. Short constrictions or gaps are frequently seen within the proximal segments, but it is not certain whether they are constant features.

The most noteworthy feature of the two idiograms is the absence in Ky-d of an unpaired or heteromorphic region which could be interpreted as the differential region of the XY pair. All 40 segments are composed of two identical strands, so far as could be determined with the optical equipment available, and all the types of bivalents found in Ky-d (XY) appear also in G-m (XX). It is known from diakinesis that the nucleolar pair (chromosome 10) is not the sex pair, but there seems no means of distinguishing which of the other 9 pairs may be the sex pair. On general grounds,

it seems likely that chromosome 8 is the sex pair, because its morphology suggests that of the presumed Y of the heteromorphic pair at diakinesis, and because there seems to be a general tendency for sex chromosomes, at least in animals, to become heterochromatinized during evolution. If this is so, however, in hemp both X and Y must be partially heterochromatic at pachytene but only Y retains heterochromaticity until diakinesis.

About 50 pachytene bivalents from Ky-♀m plants were recorded and all 10 chromosome types were identified. Since the types did not differ appreciably from those observed in Ky-d and G-m, this study was not pursued further.

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