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ACHIASMATE MEIOSIS IN THE *FRITILLARIA JAPONICA* GROUP

I. DIFFERENT MODES OF BIVALENT FORMATION IN THE TWO SEX MOTHER CELLS

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SUMMARY

The *Fritillaria japonica* group consists of six related species with $x = 12$ and its derivative $x = 11$. Irrespective of basic chromosome number, the pollen and embryo sac mother cells in all these species show clearly different modes of bivalent formation.

Although meiosis in EMC's of five species is typically chiasmate, PMC's of all six species show achiasmate meiosis with the following characteristics: (*a*) Synapsis of homologous chromosomes is prolonged up to metaphase I. Separation of non-sister chromatids is suppressed and there is thus no typical diplotene/diakinesis. (*b*) The homologous chromosomes apposed in parallel are usually devoid of chiasmata at metaphase I. Occasionally, concealed chiasmata are observed to be hidden in the synaptic plane. (*c*) Separation of homologues is initiated at the kinetochore regions at early metaphase I and progresses toward the distal ends. (*d*) Meiotic behaviour of the small telocentric B chromosomes seems to be independent of, or incompletely controlled by, the achiasmate meiotic system.

Achiasmate meiosis is assumed to have arisen from the chiasmate one through a transitional step like cryptochiasmate meiosis.

1. INTRODUCTION

REGULAR segregation of the homologous chromosomes at meiosis is essential for production of genetically balanced gametes. The synapsis of homologues and its maintenance are prerequisites of regular assortment of the chromosomes into daughter nuclei. In typical chiasmate meiosis, the synapsed homologues are maintained by lateral association irrespective of the presence of chiasmata until opening-out between non-sister chromatids occurs at late pachytene. The opening-out of chromatids manifests itself immediately with the lapse of the pairing force. Subsequently, the maintenance of bivalents depends upon chiasmata up to anaphase I separation.

It was first ascertained in the achiasmate meiosis of male *Drosophila pseudoobscura* that the bivalents are not always sustained by the chiasmata alone (Darlington, 1934). In achiasmate or non-chiasmate meiosis, the opening-out of chromatids is suppressed and bivalents devoid of chiasmata are continuously held together by the prolongation of lateral association. It can, therefore, be seen that the lateral association consistently plays the leading part in the maintenance of bivalents in this meiotic type Many instances of this specialised form of meiosis have been found in animals such as Protozoa and Metazoa (see table 4 in John and Lewis, 1965). However, it is not confined to the animal kingdom, but also occurs in higher plants, as reported in the *Fritillaria japonica* group (Noda, 1968*b*).

The present paper describes in detail the achiasmate behaviour of

chromosomes in pollen mother cells (PMCs), in contrast to the typical chiasmate meiosis seen in embryo sac mother cells (EMCs) of this species group, and discusses its evolutionary significance.

2. Materials and methods

The *Fritillaria japonica* group belonging to the section *Eufritillaria* (cf. Bentham and Hooker, 1883) is endemic to the central and western parts of Japan (Hara and Kanai, 1958). Recently, the classification of this group was revised so that two species and one variety became six distinct species; *F. koidzumiana* Ohwi, *F. kaiensis* Naruhashi, sp. nov., *F. japonica* Miquel, *F. muraiana* Ohwi, *F. shikokiana* Naruhashi, sp. nov., and *F. amabilis* Koidzumi (Naruhashi and Noda, 1971). The relationship between the revised and previous classifications is presented in table 1.

The bulbs of each species collected from the natural populations at 16 localities were cultivated in our experimental garden (table 1). Meiosis in PMCs of all the six species takes place during a period from mid-November to early December and, after a lapse of about 2 months, meiosis in EMCs progresses during a period from mid-January to early February. Meiotic process in PMCs was examined in iron aceto-carmine smears of living anthers and in anthers fixed and stored in Newcomer's fluid (Newcomer, 1953). Some of the anthers were fixed in La Cour 2BE for 20 minutes, hydrolysed by 1N HCl at 60°C for 6 to 8 minutes, and prepared with Feulgen's squash technique. For meiotic observations in EMCs some of the ovules were fixed in acetic alcohol (1 : 3) for 20 to 30 minutes and rinsed in 1 per cent aceto-orcein for overnight or more (cf. Noda, 1970). The stained materials were hydrolysed by gently heating 0·1N HCl and squashed in 1 per cent aceto-orcein. The other ovules were fixed in La Cour 2BE for 20 minutes, hydrolysed in 1N HCl at 60°C for 8 to 10 minutes, and prepared with Feulgen's squash technique.

Pollen fertility was estimated by counting the good pollen grains well stained in aceto-carmine. Very high fertilities from 94·1 to 99·6 per cent were observed in all plants (43) from six species (table 1).

3. Observations

(i) *Chromosome numbers of the related species*

The basic number of chromosomes, $x = 12$ (2V + 10I), is well-known in most species of the genus *Fritillaria* (cf. Darlington and Wylie, 1955; Cave, 1970). The plants from 10 localities of *F. koidzumiana*, *F. kaiensis*, *F. muraiana*, and *F. shikokiana* were found to have $x = 12$ chromosomes (table 1; Noda, 1964, 1968*a*). A derivative basic number, $x = 11$ (3V + 8I), was observed in the plants from six localities of *F. japonica* and *F. amabilis*. Five types of small B chromosomes were involved, *viz*, acrocentric B_1, two types of telocentric B_2 and B_5, and two types of metacentric B_3 and B_4. Their frequencies varied from population to population in five species.

(ii) *Meiosis in the species with* x = 12

The meiotic sequences and the behaviour of chromosomes in PMCs as well as in EMCs were essentially similar throughout the species with $x = 12$ and 11.

The homologous pairing in PMCs of *F. koidzumiana* from Mt. Iwo-zen is complete at early prophase and the homologues are associated closely along the entire chromosome length at pachytene (plate I, fig. 1). The successive stages following pachytene are characterised by the absence of opening-out between paired segments and between paired kinetochores, and the bivalents become progressively shorter and thicker. Thus typical diplotene and diakinesis are evidently omitted. At the later stages of post-pachytene the 12 bivalents become less and less clearly resolvable, giving them the appearance of being composed of a single element (plate I, figs. 2

TABLE 1

Chromosome number and meiotic type in six species of the F. japonica *group*
(ch: *chiasmate*; ach: *achiasmate*)

Locality	Prefecture	2*n*	Meiotic type: *PMC*	Meiotic type: *EMC*	% of good pollen	Previous classifications (Hara and Kanai, 1958; Ohwi, 1965)
F. koidzumiana						
Ojiya	Niigata	24	ach	ch	94·1	*F. japonica* var. *koidzumiana*
Mt. Iwo-zen	Ishikawa	24+0−1B	ach	ch	95·4	
F. kaiensis						
Hachioji	Tokyo	24	ach	—	—	*F. japonica* var. *japonica*
Sano-toge	Yamanashi	24	ach	—	98·9	
F. japonica						
(Uncertain)	Aichi	22+0−1B	ach	ch	—	
Niwano	Aichi	22+14−16B	ach	—	96·9	
Mt. Fujiwara-dake	Mie	22+5−26B	ach	ch	97·2	
F. muraiana						
Mt. Kotsu-zan	Tokushima	24+2−8B	ach	ch	—	
Mt. Otaki-yama	Tokushima	24+4−6B	—	ch	95·8	
Mt. Torigata-yama	Kochi	24+0−6B	ach	ch	96·6	
F. shikokiana						
Mt. Unpenji-yama	Kagawa	24	ach	ch	95·3	*F. amabilis*
Mt. Kajigamori-yama	Kochi	24+3−8B	ach	ch	98·6	
Nanokawa	Kochi	24+0−4B	—	ch	95·6	
F. amabilis						
Himehara	Okayama	22+0−1B	ach	ch	99·6	
Mt. Hiko-san	Fukuoka	22+0−6B	ach	ch	95·6	
Mizunashi	Fukuoka	22+0−2B	ach	ch	95·4	

and 3). The chiasmata are not detectable at these stages, even though they may actually exist. The nucleoli usually but not invariably remain attached to the well-defined organiser of the nucleolar chromosomes.

The synaptic plane appears along the length of each bivalent at early metaphase I (plate I, fig. 4). At this stage, the opening-out begins in the kinetochore region, as if the paired kinetochores repel each other. On the other hand, no repulsion occurs either in intercalary or distal chromosome segments, the paired arms being retained closely in parallel. The paired condition is maintained even when the chromatid structure of the bivalent becomes visible at metaphase or early anaphase I. The kinetochores co-orientate and gradually become separated and the paired segments are

consequently pulled apart towards the distal ends by the kinetochore movement (plate I, figs. 5 and 6). An akinetic fragment which is produced by spontaneous breakage in *F. kaiensis* remains firmly paired because of its independence from the kinetochore movement (plate II, fig. 10). With all three fixatives numerous fine stainable filaments are observed consistently in the very narrow slit in the synaptic planes. These appear to be fine matrical threads rather than chromonemata and they are considered to be caused by stickiness of the matrical substances and interfere, to some degree, with the separation of homologues at anaphase I.

No chiasma is usually found at metaphase I and the bivalents without any chiasma are maintained in parallel by lateral association, which acts against the kinetochore movement (plate I, fig. 6). A bridge between the homologues has occasionally been observed (plate III, fig. 13; a case of *F. amabilis*). Such a chiasma-like structure may be regarded as a concealed chiasma and has been observed in cryptochiasmate meiosis (White, 1965*a*).

Separation of the homologous chromosomes proceeds linearly along the horizontal plane of each bivalent at late metaphase I to early anaphase I (plate II, fig. 7). The loops at the kinetochore region enlarge and finally terminalise at the distal ends, the homologous chromosomes being pulled apart without pronounced attenuation toward the opposite poles. There is no indication of special terminal affinity between the distal ends of homologues. Usually, the association between sister chromatids in the half-bivalents lapses (plate II, figs. 7 and 8). In other cases, however, the half-bivalents appear as a single unit and their chromatid structures are not recognisable, as observed in most plants of *F. kaiensis* (plate II, fig. 10). There appears to be nothing unusual during the second division.

An achiasmate meiosis with 12 bivalents formed by parallel pairing was also observed in PMCs of the plants of *F. kaiensis*, *F. muraiana*, and *F. shikokiana* collected from six localities.

The chiasmate meiosis in EMCs observed in five local strains of *F. koidzumiana* and *F. shikokiana* proceeds typically in sharp contrast to the achiasmate meiosis in PMCs (plate II, fig. 9; cf. Noda, 1970). Twelve bivalents show opening-out at numerous points along the whole length of the chromosome at diplotene/diakinesis. At metaphase I, two to eight chiasmata per bivalent were formed at random; the mean chiasma frequency being 4·25 in *F koidzumiana*. After the tetrad stage, migration of one out of two nuclei at the micropylar side to the chalazal side of embryo-sac was observed, a feature typical of *Fritillaria* and *Lilium*.

(iii) *Meiosis in the species with x = 11*

Achiasmate meiosis in PMCs of *F. japonica* and *F. amabilis* from six localities is in precise agreement with that in the above-mentioned species with $x = 12$. Eleven pairs of homologous chromosomes are held together not by the chiasmata but by lateral association from early prophase to metaphase I (plate II, fig. 11; plate III, fig. 13; Noda, 1968*b*). Meiotic behaviour of chromosomes in EMCs of these two species is consistently of the same chiasmate type as that of the species with $x = 12$ (plate III, fig. 14). Mean chiasma frequency per bivalent was 3·20 in *F. japonica* and 2.45 in *F. amabilis* at metaphase I.

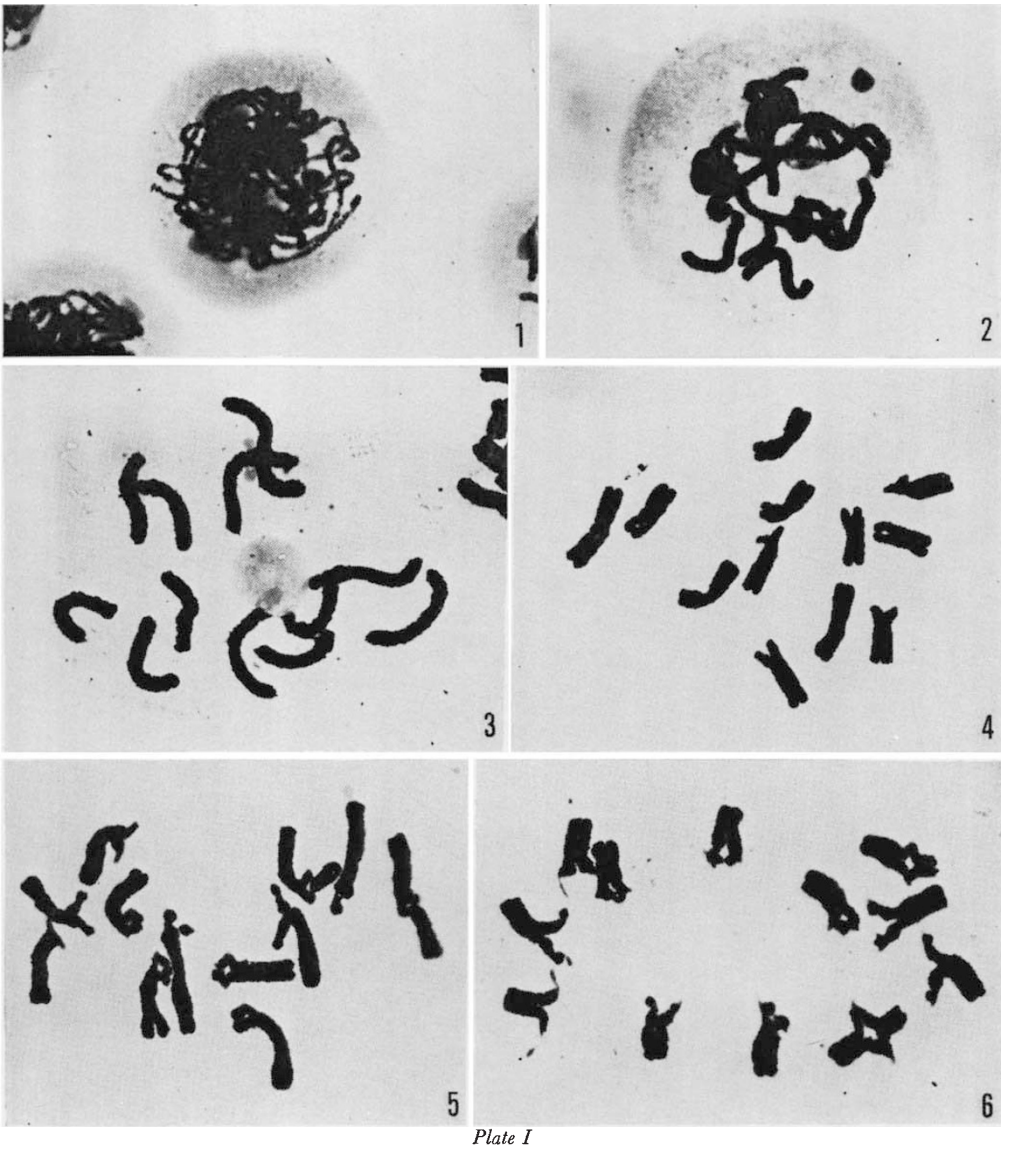


Plate I

Achiasmate meiosis in PMCs of *F. koidzumiana*

FIG. 1.—Complete synapsis at pachytene. × 350.

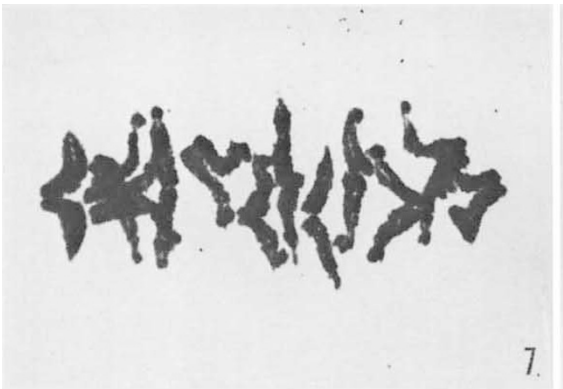
FIG. 2.—Mid post-pachytene showing no opening-out in the bivalents. × 350.

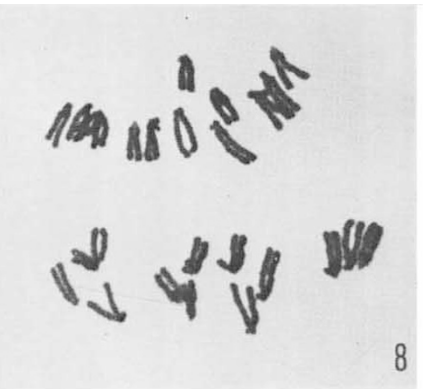
FIG. 3.—Late post-pachytene. Four out of diffused 12_{II} attach to the nucleoli. × 530.

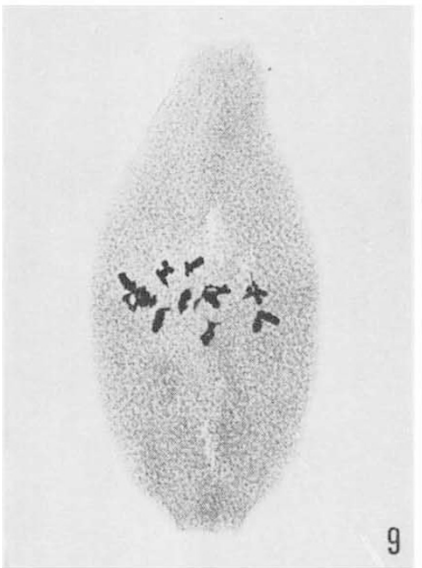
FIG. 4.—Early metaphase I showing achiasmate 12_{II}. The paired kinetochores of several bivalents begin to open out. × 530.

FIG. 5.—Subsequent stage to fig. 4. Loops at the kinetochore region become to enlarge. × 530.

FIG. 6.—Metaphase I showing achiasmate 12_{II}. × 530.







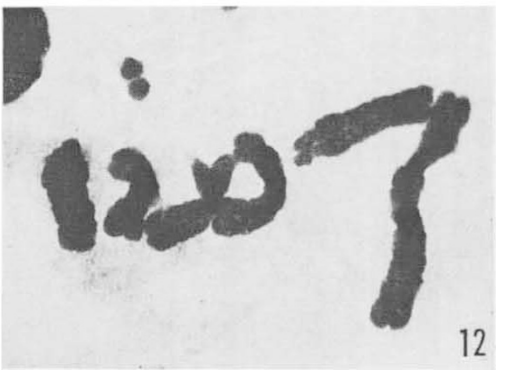


Plate II

FIG. 7.—Early anaphase I in PMC of *F. koidzumiana*. Half-bivalents show the chromatid structure. × 480.

FIG. 8.—Regular separation at anaphase I in PMC of *F. koidzumiana*. × 360.

FIG. 9.—Metaphase I in EMC of *F. koidzumiana* showing 12_{II} with total 47 chiasmata. × 220.

FIG. 10.—Spontaneous breakage of a V-shaped bivalent at early anaphase I in PMC of *F. kaiensis*, in which an akinetic fragment remains paired. Arrow indicates a breakpoint. Chromatid structure in the half-bivalent is not recognisable. × 800.

FIG. 11.—Metaphase I in PMC of *F. japonica* showing achiasmate 11_{II}. × 600.

FIG. 12.—Parallely paired homologous B chromosomes B_2's at early metaphase I in PMC of *F. amabilis*. × 800.

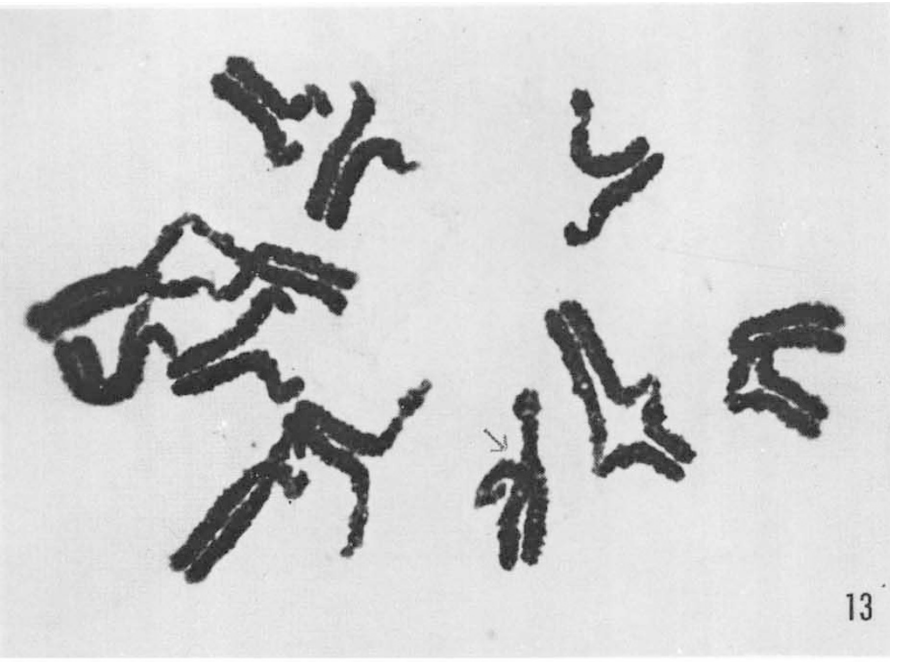


Plate III

Metaphase I in *F. amabilis*

FIG. 13.—PMC showing achiasmate 11_{II}. Arrow indicates a concealed chiasma which is disclosed by the separation of I-shaped homologous chromosomes. ×900.

FIG. 14.—EMC showing 11_{II} with total 22 chiasmata. ×1200.

(iv) *Pairing behaviour of B chromosomes*

The telocentric B_2 chromosome is found in all of the five species except for *F. kaiensis* which is without B chromosomes. The other types of B's are specific to a certain population or species (Noda, 1964, 1968*a*). The frequency of pairing in the homologous B_2's of *F. amabilis* varies from plant to plant in PMCs. The B_2's in bivalents and multivalents pair tightly or loosely, with varying degrees of connection, by the matrical stickiness at early post-pachytene. In a plant with $2n = 22 + 2B_2$ of *F. amabilis*, most of the cells show paired B_2's at late post-pachytene (table 2). The association

TABLE 2

Meiotic pairing of two telocentric B chromosomes, B_2, at the successive stages in PMCs of F. amabilis

Pairing configuration	Late post-pachytene	Early metaphase I	Metaphase I
1_{II}	78	7	2
2_I	3	30	30
Cell obs.	81	37	32
Bivalent (%)	96·3	18·9	8·7

in most B_2 bivalents tends to resolve progressively to univalents before metaphase I, when only a few of them remain paired. In 56 B_2 bivalents examined at metaphase I, a major portion, 62·5 per cent, showed adhesion by matrical stickiness. The remainder were sustained in juxtaposition by lateral association very similar to that found in the ordinary chromosomes (plate II, fig. 12). These two non-orientated types of B_2 bivalents were distributed on or around the metaphase plate.

In EMCs of *F. amabilis* the pairing behaviour of homologous B_2's at each stage is similar to that in PMCs, in which failure of pairing is very conspicuous. Co-orientated B_2 bivalents joined by probable chiasmata were rarely observed.

4. DISCUSSION

Numerous kinds of conjunctive mechanisms between the homologous chromosomes have been found or presumed in various organisms (cf. Cooper, 1964). Hughes-Schrader (1943*a*) pointed out three main factors on the maintenance of association of homologues at the later stages of meiosis; lateral attraction, terminal attraction, and chiasmata. The synapsed homologous chromosomes in PMCs of the *Fritillaria japonica* group are sustained by the lateral attraction alone. Furthermore, the homologous chromosomes at late prophase are embedded in a common diffused matrical substance. The persistence of bivalents at this stage, therefore, is aided by the chromosome matrix which is non-specific. Such an atypical meiotic behaviour of chromosomes is very similar to achiasmate meiosis in male insects such as *Callimantis antillarum*, mantids (White, 1938; Hughes-Schrader, 1943*b*), *Panorpa*, *Mecoptera* (Ullerich, 1961), and many species of *Diptera* comprising *Tipula caesia* (Bauer, cited from figs. 35-40 in John and Lewis, 1965), *Phryne* (Bauer, 1946; Wolf, 1950), *Thaumalea testacea* (Wolf, 1941), *Calliphoridae* (Ullerich, 1963), and so forth. The achiasmate meiosis in the *Fritillaria japonica* group as well in the above insects is considered to

correspond to the non-chiasmate type 1 categorised by John and Lewis (1957).

Achiasmate meiosis is assumed to have evolved from the chiasmate process. This is clearly proved phylogenetically in *Diptera* (White, 1949), mantids (Hughes-Schrader, 1950, 1953; White, 1965*b*), and *Enchytraeid* worms (Christensen, 1961). In these cases the primitive group has chiasmate meiosis while the achiasmate meiotic system has been established in the higher groups. In a conversion from chiasmate to achiasmate meiosis during the evolution of meiotic systems the prolongation of lateral association must theoretically be antecedent to complete suppression of chiasma formation. If it were not the species would not achieve regular assortment of homologous chromosomes at anaphase I. Indeed, such a change in the nature of synapsis seems to be realised in cryptochiasmate meiosis as found in the spermatocytes of two groups *Orthoptera*, *i.e.* various families of mantids (Hughes-Schrader, 1943*a*, 1950, 1953) and the subfamily *Thericleinae* of grasshoppers (White, 1965*a*).

In cryptochiasmate meiosis, which is regarded as an atypical chiasmate meiosis, numerous chiasmata are concealed between closely synapsed homologues by the prolongation of lateral association (White, 1965*a*) These are disclosed eventually by the pre-metaphase stretch in the mantids and by delayed opening-out of chromatids or anaphase I separation in the grasshoppers. Thus the concealed chiasmata in either case are apparently not responsible for, or have merely a subsidiary role in, maintaining the bivalent up to later meiotic stages. Their role is replaced by the lateral association. This is an additional mechanism contributing to chromosome conjugation which is assumed to have originated independently of the suppression of chiasma formation. When the prolongation of lateral association coincides with the suppression of chiasma formation the conversion of a cryptochiasmate meiosis into an achiasmate one becomes possible. The conclusion is that the establishment of prolongation of lateral association is a prerequisite for the evolution to achiasmate meiosis, as emphasised by White (1965*a*). The fact that the mantids and grasshoppers mentioned above comprise various species having chiasmate, cryptochiasmate, and achiasmate meioses are compatible with this view.

Achiasmate meiosis has been found independently among phylogenetically remote groups in various kinds of animals from Protozoa to Metazoa. This points to a multiple origin of this type of meiosis (Wolf, 1950; Hughes-Schrader, 1950, 1953; Christensen, 1961). The evidence from the plant kingdom offered in the present study gives further support to this view. It may justifiably be said, therefore, that the achiasmate meiotic system occurs widely throughout the plant and animal kingdoms. The prolongation of lateral association may be considered to have an adaptive significance in evolution, when chiasmata are lost.

Achiasmate animals are usually dioecious and the achiasmate modification of meiosis is restricted either to the male or female, predominantly the male (see table 4 in John and Lewis, 1965). The exceptional cases of achiasmate meiosis in both sexes have been reported only in several species of hermaphrodite *Enchytraeid* worms such as *Buchholzia fallax* and *Marionina subterranea* (Christensen, 1961). In *Fritillaria*, with hermaphrodite flowers, achiasmate meiosis is confined to the male sporocytes within a single genotype; that is, there is intra-individual differentiation in the meiotic

system. Sexual differentiation in respect of chiasma formation in higher plants is detectable in the frequency and distribution pattern (see table 4 in Ved Brat, 1964 and tables 5 and 6 in John and Lewis, 1965). It has been suggested that the general tendency toward a lower chiasma frequency on the male than on the female side would have some correlation with the differentiation of the cellular environment between two sex mother cells which controls the pairing behaviour relating to chiasma frequency (Fogwill, 1958; Wilson, 1960). In contrast, the B chromosomes appear to be free from such control or incompletely controlled under such a genetic system.

The genus *Fritillaria* growing in Japan consists of *F. camschatcensis* (L.) Ker-Gawler with $x = 12$ and the *F. japonica* group. The former, with chiasmate meiosis on the male side, belongs to the section *Liliorhiza* which is widely distributed, from Japan to Canada and the state of Washington in the United States via Kamtschatka and Alaska (Bentham and Hooker, 1883; Matsura, 1935; Beetle, 1944). In contrast, all the species of the latter which are interpretable as being among the constitutive members of the " Sino-Japanese region ", have achiasmate meiosis on the male side without exception. No close relationship in phylogeny and geographical distribution exists between them. In conclusion, it is highly probable that the achiasmate meiotic system was established in an unknown ancestral species common to the *F. japonica* group in the evolution of genus *Fritillaria*. Differentiation in morphological characters and the reduction in basic chromosome number occurred at subsequent stages.

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5. References

BAUER, H. 1946. Gekoppelte Vererbung bei *Phryne fenestralis* und die Beziehung zwischen Faktorenaustausch und Chiasmabildung. *Biol. Zbl., 65,* 108-115.

BEETLE, D. E. 1944. A monograph of the North American species of *Fritillaria*. *Madrono, 7,* 133-159.

BENTHAM, G., AND HOOKER, J. D. 1883. Fritillaria. *Genera Plantarum, 3,* 817-818.

CAVE, M. S. 1970. Chromosomes of the California Liliaceae. *Univ. California Pub. Bot., 57,* 1-48.

CHRISTENSEN, B. 1961. Studies on cyto-taxonomy and reproduction in the Enchytraeidae with notes on parthenogenesis and polyploidy in the animal kingdom. *Hereditas, 47,* 387-450.

COOPER, K. W. 1964. Meiotic conjunctive elements not involving chiasmata. *Proc. Nat. Acad. Sci., 52,* 1248-1255.

DARLINGTON, C. D. 1934. Anomalous chromosome pairing in the male *Drosophila pseudoobscura*. *Genetics, 19,* 95-118.

DARLINGTON, C. D., AND WYLIE, A. P. 1955. *Chromosome Atlas of Flowering Plants,* 2nd ed. George Allen and Unwin, London.

FOGWILL, H. 1958. Differences in crossing-over and chromosome size in the sex cells of *Lilium* and *Fritillaria*. *Chromosoma, 9,* 493-504.

HARA, H., AND KANAI, H. 1958. *Distribution Maps of Flowering Plants in Japan,* Part I. Inoue, Tokyo.

HUGHES-SCHRADER, S. 1943*a*. Polarization, kinetochore movements, and bivalent structure in the meiosis of male mantids. *Biol. Bull., 85,* 265-300.

HUGHES-SCHRADER, S. 1943*b*. Meiosis without chiasmata in diploid and tetraploid spermatocytes of the mantid *Callimantis antillarum* Saussure. *J. Morph., 73,* 111-140.

HUGHES-SCHRADER, S. 1950. The chromosomes of mantids (*Orthoptera: Manteidae*) in relation to taxonomy. *Chromosoma, 4*, 1-55.

HUGHES-SCHRADER, S. 1953. Supplementary notes on the cytotaxonomy of mantids (*Orthoptera: Mantoidea*). *Chromosoma, 6*, 79-90.

JOHN, B., AND LEWIS, K. R. 1957. Studies on *Periplaneta americana*. I. Experimental analysis on male meiosis. *Heredity, 11*, 1-9.

JOHN, B., AND LEWIS, K. R. 1965. *The Meiotic System*. Protoplasmatologia, 6, Fl. Springer-Verlag, Wien and New York.

MATSUURA, H. 1935. On karyotypes of *Fritillaria camschatcensis* (L.) Ker-Gawler. *J. Fac. Sci. Hokkaido Imp. Univ.*, Ser. 5, *5*, 121-198.

NARUHASHI, N., AND NODA, S. 1971. Relationship between six species of *Fritillaria japonica* group. II. Morphology and distribution. *Abst. at 36th Meet. Bot. Soc. Japan, 1971.*

NEWCOMER, E. H. 1953. A new cytological and histological fixing fluid. *Science, 118*, 161.

NODA, S. 1964. Cytology in the genus *Fritillaria*. I. Variations in karyotypes and B-chromosomes in *F. amabilis*. *Bull. Osaka Gakuin Univ., 2*, 125-132.

NODA, S. 1968*a*. Cytology in the genus *Fritillaria*. II. Karyotypes and B-chromosomes in *F. japonica* var. *japonica* and var. *koidzumiana*. *Bull. Osaka Gakuin Univ., 10*, 127-141.

NODA, S. 1968*b*. Achiasmate bivalent formation by parallel pairing in PMCs of *Fritillaria amabilis*. *Bot. Mag., Tokyo, 81*, 344-345.

NODA, S. 1970. Meiotic process in EMC of *Fritillaria amabilis*. *Bull. Osaka Gakuin Univ., 14*, 107-116.

OHWI, J. 1965. *Flora of Japan*, rev. ed. Shibundo, Tokyo.

ULLERICH, F.-H. 1961. Achiasmatische Spermatogenese bei der Skorpionfliege *Panorpa* (Mecoptera). *Chromosoma, 12*, 215-232.

ULLERICH, F.-H. 1963. Geschlechtschromosomen und Geschlechtsbestimmung bei einigen Calliphorinen (Calliphoridae, Diptera). *Chromosoma, 14*, 45-110.

VED BRAT, S. 1964. Genetic systems in *Allium*. II. Sex differences in meiosis. In: *Chromosome Today* (eds. C. D. Darlington and K. R. Lewis), vol. 1, pp. 31-40. Oliver and Boyd, Edinburgh and London.

WHITE, M. J. D. 1938. A new and anomalous type of meiosis in a mantid, *Callimantis antillarum* Saussure. *Proc. Roy. Soc.*, Ser. B, *125*, 516-523.

WHITE, M. J. D. 1949. Cytological evidence on the phylogeny and classification of the Diptera. *Evolution, 3*, 252-261.

WHITE, M. J. D. 1965*a*. Chiasmatic and achiasmatic meiosis in African Eumastacid grasshoppers. *Chromosoma, 16*, 271-307.

WHITE, M. J. D. 1965*b*. Sex chromosomes and meiotic mechanisms in some African and Australian mantids. *Chromosoma, 16*, 521-547.

WILSON, J. Y. 1960. Chiasma frequency in the two sex mother-cells of hermaphrodite. *Chromosoma, 11*, 433-440.

WOLF, B. E. 1941. Die Chromosomen in der Spermatogenese einiger Nematoceren. *Chromosoma, 2*, 192-246.

WOLF, B. E. 1950. Die Chromosomen in der Spermatogenese der Dipteren *Phryne* und *Mycetobia*. *Chromosoma, 4*, 148-204.