CYTOGENETIC STUDIES ON NATURAL POPULATIONS OF *ACRIDA LATA*

I. LOCAL VARIATION IN THE FREQUENCY OF B-CHROMOSOMES*

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1. INTRODUCTION

VARIOUS frequencies of B (accessory or supernumerary) chromosomes among natural or cultivated populations within a geographic range have been reported in both plants and animals, *e.g. Centaurea scabiosa* (Fröst, 1958), *Clarkia elegans* (Lewis, 1951), *Festuca pratensis* (Bosemark, 1956*a*), *Lilium aulatum* (Ogihara, 1962), *Lilium callosum* (Kayano, 1962), *Lilium medeoloides* (Samejima, 1958), *Myrmeleotettix maculatus* (John and Hewitt, 1965; Barker, 1966), *Phleum phleoides* (Bosemark, 1956*b*, 1967), *Pseudococcus obscurus* (Nur, 1962), and *Secale cereale* (Müntzing, 1950, 1957; Lee and Min, 1965). Correlations between certain environmental factors and the frequency of B's have been found in *Centaurea scabiosa* (Fröst, 1958), in *Festuca pratensis* (Bosemark, 1956*a*), in *Phleum phleoides* (Bosemark, 1956*b*, 1967), in *Secale cereale* (Lee, 1966), and in *Myrmeleotettix maculatus* (Barker, 1966; Hewitt and John, 1967).

For the elucidation of the role of B's in population dynamics it is of fundamental importance to clarify whether the frequency of B's in a given population is stable through generations or whether it undergoes change. Reports on the frequency of B's analysed in successive generations of the same population are rare. Recently, Jackson and Cheung (1967) reported stable frequencies of B's over 9 years in a population of *Phaulacridium vittatum.*

The present paper deals with natural populations of *Acrida lata* Motschulsky (Acrididae, Orthoptera) sampled at 11 localities in the northern part of Kyushu, Japan, over periods of 3 to 9 years in an attempt to estimate the extent of variation in the frequency of B's in time and space. In many of the populations the frequencies of B's were not significantly different between years though different populations differed in their B-frequencies. In two populations, however, different frequencies of B's were found in different years.

2. MATERIALS AND METHODS

Acrida lata inhabits the vegetation dominated by grass species such as *Eragrostis ferruginea* Beauvois, *Pennisetum alopecuroides* Sprengel, and *Zoysia macrostachya* Franchet at Savatier, and has one generation a year. It hatches out in June, gives rise to the imago from late July to early August, and

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survives to early November. Samples of males of *A. lata* were collected from natural populations at 11 localities over 3- to 9-year periods. The years of collections and the numbers of males cytologically examined are shown in table 5. An additional sample consisting of 50 males and 32 females was collected in October 1967, on the campus of Kyushu University at a location other than the previous collections, made from 1957 to 1965, in order to compare frequencies of B's among males and females of the same population.

For examination of chromosomes in primary spermatocytes, testes *in toto* were fixed with the fluid devised by Newcomer (1953) and follicles of the testes were squashed in iron-acetocarmine. Some of the preparations of testes showed spermatogonial metaphases. For examination of somatic chromosomes of females, each individual was injected with 0·05 c.c. of 0·03 per cent. aqueous solution of demecolcine (K & K Laboratories Inc., New York) for 18-24 hours before dissecting out the ovarioles (White, Cheney and Key, 1963). Ovarioles were fixed with acetic alcohol (1 : 3) and squashed in iron-acetocarmine.

3. Results

(i) *Mitotic stability of B's*

The basic chromosome complement of male *A. lata* consists of $2n = 22+XO$ in spermatogonia and 11 II+X in primary spermatocytes; that of females consists of $2n = 22+XX$ (plate I, figs. *a*, *c*, *e*). Some individuals were found to contain 1 to 4 B chromosomes in addition to the basic complement (plate I, figs. *b*, *d*, *f-h*). The B's were smaller than the

Table 1

Frequencies of mitotic aberrations in number of B's

Type of male	No. of males	No. of follicles	No. of primary spermatocytes					
			0B	1B	2B	3B	4B	Total
1B	15	154	—	4348	—	—	—	4348
	8	92	9	3097	6	—	—	3112
	1	8	—	112	15	—	—	127
Total	24	254	9	7557	21	—	—	7587
2B	16	176	—	—	4841	—	—	4841
	8	110	—	2	3412	14	1	3429
	1	18	—	42	507	—	—	549
Total	25	304	—	44	8760	14	1	8819
Grand total	49	558	9	7601	8781	14	1	16406

smallest A chromosomes and, like A and X chromosomes, acrocentric (the term " acrocentric " is used according to the view of White, 1954). The B's were heterochromatic adjacent to the kinetochore but euchromatic in their distal portion.

Using 24 males with 1 B and 25 males with 2 B's, a total of 16 406 primary spermatocytes from 558 follicles was analysed with respect to the stability of B's in germ line (table 1). Fifteen males with 1 B and 16 males with 2 B's were mitotically stable. One male contained an aberrant follicle in which all 15 primary spermatocytes contained 2 B's, while the other 7 follicles from this male had only 1 B. Another male contained an aberrant follicle which consisted of 42 cells with 1 B and 25 cells with 2 B's, while the other 17 follicles from this male were 2 B in type. Finally each of 26 among 202 follicles from 16 males (8 with 1 B and 8 with 2 B's) contained one or two aberrant cells, 32 aberrant cells in all (table 1). Therefore, aberrant primary spermatocytes occurred in 89 out of 16 406 cells (0·5 per cent.) and presumably resulted from non-disjunction in the pre-meiotic mitoses.

(ii) *Meiotic behaviour of B's and their distribution among males and females*

The B's were found to pair neither with A's nor with the X in primary spermatocytes. They did, however, pair amongst themselves and showed the following configurations at MI in spermatocytes: 1 II (18·9 per cent.)

TABLE 2

Distribution of B's in secondary spermatocytes

Type of male	Secondary spermatocytes					
	A's and X	0B	1B	2B	Total	B's per cell
1B	$n = 11$	114	108	—	222	0·486
	$n = 11+X$	111	107	—	218	0·491
Total		225	215	—	440	0·489
2B	$n = 11$	26	80	24	130	0·985
	$n = 11+X$	31	75	20	126	0·913
Total		57	155	44	256	0·946

and 2 I (81·1 per cent.) in the males with 2 B's (8760 cells), and 1 III (2 per cent.), 1 II+1 I (40 per cent.), and 3 I (58 per cent.) in the males with 3 B's (200 cells). Univalent B's lagged behind at AI in many cells, but they were rarely eliminated for B's were found in nearly half of the secondary spermatocytes in males with 1 B, the mean number of B's per secondary spermatocytes being 0·489 (table 2). In males with 2 B's, secondary spermatocytes contained no B, 1 B, or 2 B's, the mean number of B's per cell being 0·946 (table 2).

TABLE 3

Frequencies of B's in males and females in a population sample from Kyushu (Oct. 1967)

Sex	No. of individuals					% individuals with B's	Mean no. of B's per individual
	0B	1B	2B	3B	Total		
♂	41	7	1	1	50	18·0	0·24
♀	22	10	—	—	32	31·3	0·31
Total	63	17	1	1	82	23·2	0·27

The B's segregated from the X at random at AI, resulting in an equal distribution of B's among secondary spermatocytes with and without the X (table 2). This would be expected to result in an equal distribution of B's among males and females in the same population and in the one population where it was tested there was no significant difference between males and females ($0{\cdot}20 > \beta > 0{\cdot}10$), the mean B-numbers being 0·24 and 0·31 respectively (table 3).

(iii) *Frequencies of B's in natural populations*

Sample males collected from the Hk population in each year from 1961 through 1963 were used to compare frequencies of B's at different times in the same year. The frequencies of males with B's at different times were 37·0 and 50·0 per cent. in 1961, 45·0 and 32·0 per cent. in 1962, and 34·0 and 32·0 per cent. in 1963 (table 4). The results of a χ^2 test show no significant difference between the frequencies of B's at different times in the same year (table 4). The samples collected from the Tf population at different times in 1961 showed the frequencies of males with B's to be 11·0 and 8·0 per cent., which again are not significantly different (table 4). A couple of samples were collected in 1962 from the Tf population by dividing the sample area into two sections; here again the frequencies of males with B's, 10·0 and 14·0 per cent. respectively, were not significantly different (table 4).

TABLE 4

Frequencies of B's in separate samples from particular populations at different times, I and II, in the same year, or in different sites, A and B, at the same locality

Locality, Year	Time or site	No. of males 0B	1B	2B	3B	Total	% males with B's	No. of B's per male	Date of collection	P value (χ^2 test)
Hk 1961	I	63	28	8	1	100	37·0	0·470	July 29, Aug. 5	0·10-0·05
	II	50	32	16	2	100	50·0	0·700	Aug. 17, 22	
Total		113	60	24	3	200	—	—	—	—
Mean		56·5	30·0	12·0	1·5	100	43·5	0·585	—	—
Hk 1962	I	55	35	10	—	100	45·0	0·550	Aug. 8	0·10-0·05
	II	68	21	9	2	100	32·0	0·450	Aug. 25	
Total		123	56	19	2	200	—	—	—	—
Mean		61·5	28·0	9·5	1·0	100	38·5	0·500	—	—
Hk 1963	I	66	29	5	—	100	34·0	0·390	Aug. 6	0·50-0·30
	II	68	23	9	—	100	32·0	0·410	Aug. 21	
Total		134	52	14	—	200	—	—	—	—
Mean		67	26	7	—	100	33·0	0·400	—	—
Tf 1961	I	89	11	—	—	100	11·0	0·110	Aug. 7	0·50-0·30
	II	92	7	1	—	100	8·0	0·090	Aug. 21	
Total		181	18	1	—	200	—	—	—	—
Mean		90·5	9·0	0·5	—	100	9·5	0·100	—	—
Tf 1962	A	90	9	1	—	100	10·0	0·110	Aug. 22	0·50-0·30
	B	86	14	—	—	100	14·0	0·140	Aug. 22	
Total		176	23	1	—	200	—	—	—	—
Mean		88·0	11·5	0·5	—	100	12·0	0·125	—	—

Among the samples from 11 populations over 3 to 9 years, the highest frequency of the mean number of B's per male was recorded in 1961 in the Hk population, in which the mean number of B's per male ranged from 0·350 to 0·585 over the 9-year period, 1957-65, with an overall mean of 0·443 (table 5). The lowest was recorded in 1963 in the Tf population, in which the mean number of B's per male ranged from 0·04 to 0·16 over the 5 years, 1959-63, with an overall mean of 0·099 (table 5). The lowest overall mean number of B's per male, 0·080, was found in the Ks population, in which the mean number of B's per male ranged from 0·07 to 0·11 over the 4 years, 1959-62 (table 5, fig. 1).

Differences in frequencies of B's among the 11 populations were statistically tested by an analysis of variance of the mean numbers of B's per male (*cf.* table 5). The result shows highly significant differences among the populations ($P < 0{\cdot}01$).

TABLE 5

Frequencies of B's over successive years in natural populations of A. lata

1. Gs (Gôshi-mura, Kikuchi-gun, Kumamoto-ken. 1959-63. 500 males)

Year of collection	Frequency (%) of males					Males obs.	% males with B's	Mean no. of B's per male	Date of collection
	0B	1B	2B	3B	4B				
1959	85	15	—	—	—	100	15·0	0·150	Aug. 17
1960	87	11	2	—	—	100	13·0	0·150	Aug. 14
1961	80	18	2	—	—	100	20·0	0·220	Aug. 19
1962	83	14	3	—	—	100	17·0	0·200	Aug. 19
1963	80	17	3	—	—	100	20·0	0·230	Aug. 18
Mean	83·0	15·0	2·0	—	—	—	17·0	0·190	—

2. Hk (Campus of Kyushu Univ., Hakozaki-machi, Fukuoka-shi, Fukuoka-ken. 1957-65. 1200 males)

Year of collection	Frequency (%) of males					Males obs.	% males with B's	Mean no. of B's per male	Date of collection
	0B	1B	2B	3B	4B				
1957	68	17	10	5	—	100	32·0	0·520	Aug. 8-Sept. 17
1958	66	29	3	2	—	100	34·0	0·410	Aug. 8-12
1959	70	25	5	—	—	100	30·0	0·350	July 23-Aug. 2
1960	64	28	6	2	—	100	36·0	0·460	Aug. 9-11
1961	56·5	30·0	12·0	1·5	—	200	43·5	0·585	July 29-Aug. 22
1962	61·5	28·0	9·5	1·0	—	200	38·5	0·500	Aug. 8-25
1963	67	26	7	—	—	200	33·0	0·400	Aug. 6-21
1964	66	28	6	—	—	100	34·0	0·400	Aug. 21
1965	72	23	3	1	1	100	28·0	0·360	Aug. 12-17
Mean	65·7	26·0	6·8	1·4	0·1	—	34·3	0·443	—

3. Ik (Ikushi, Ôita-shi, Ôita-ken. 1959-63. 500 males)

Year of collection	Frequency (%) of males					Males obs.	% males with B's	Mean no. of B's per male	Date of collection
	0B	1B	2B	3B	4B				
1959	70	19	10	1	—	100	30·0	0·420	Aug. 15-Sept. 23
1960	73	21	5	1	—	100	27·0	0·340	July 22-Aug. 5
1961	81	15	3	1	—	100	19·0	0·240	July 26-Aug. 6
1962	77	20	3	—	—	100	23·0	0·260	Aug. 15
1963	78	22	—	—	—	100	22·0	0·220	Aug. 13-15
Mean	75·8	19·4	4·2	0·6	—	—	24·2	0·296	—

TABLE 5 (*continued*)

4. Km (Vicinity of Kumamoto-jô, Kumamoto-shi, Kumamoto-ken. 1959-63. 500 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no. of B's per male	Date of collection
1959	77	15	8	—	—	100	23·0	0·310	Aug. 17-Sept. 17
1960	77	21	1	1	—	100	23·0	0·260	Aug. 14
1961	73	24	2	—	—	100	27·0	0·290	Aug. 18
1962	78	21	1	—	—	100	22·0	0·230	Aug. 18
1963	74	25	1	—	—	100	26·0	0·270	Aug. 19
Mean	75·8	21·4	2·6	0·2	—	—	24·2	0·272	—

5. Kr (Campus of Kumamoto Univ., Kurokami-chô, Kumamoto-shi, Kumamoto-ken. 1959-63. 500 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no.of B's per male	Date of collection
1959	76	19	5	—	—	100	24·0	0·290	Aug. 18
1960	81	16	2	1	—	100	19·0	0·230	Aug. 13
1961	76	22	2	—	—	100	24·0	0·260	Aug. 20
1962	85	13	2	—	—	100	15·0	0·170	Aug. 18
1963	85	12	3	—	—	100	15·0	0·180	Aug. 19
Mean	80·6	16·4	2·8	0·2	—	—	19·4	0·226	—

6. Ks (Kashii, Fukuoka-shi, Fukuoka-ken. 1959-62. 400 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no. of B's per male	Date of collection
1959	93	7	—	—	—	100	7·0	0·070	Aug. 7-11
1960	94	5	1	—	—	100	6·0	0·070	Aug. 11-15
1961	89	11	—	—	—	100	11·0	0·110	Aug. 8-12
1962	93	7	—	—	—	100	7·0	0·070	Aug. 11-25
Mean	92·25	7·50	0·25	—	—	—	7·75	0·080	—

7. Mt (Mitsusawa, Mikuni-mura, Mii-gun, Fukuoka-ken. 1959-63. 500 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no. of B's per male	Date of collection
1959	82	15	3	—	—	100	18·0	0·210	Aug. 5-10
1960	73	24	3	—	—	100	27·0	0·300	Aug. 10
1961	81	17	2	—	—	100	19·0	0·210	Aug. 9
1962	81	19	—	—	—	100	19·0	0·190	Aug. 11
1963	64	30	6	—	—	100	36·0	0·420	Aug. 15-22
Mean	76·2	21·0	2·8	—	—	—	23·8	0·266	—

8. Ng (Tateyama, Nagasaki-shi, Nagasaki-ken. 1961-63. 300 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no. of B's per male	Date of collection
1961	79	19	2	—	—	100	21·0	0·230	Aug. 24
1962	65	31	4	—	—	100	35·0	0·390	Aug. 23
1963	67	25	8	—	—	100	33·0	0·410	Aug. 20
Mean	70·3	25·0	4·7	—	—	—	29·7	0·343	—

TABLE 5 (*continued*)

9. Om (Enmei-kôen, Ômuta-shi, Fukuoka-ken. 1961-63. 300 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no. of B's per male	Date of collection
1961	73	25	2	—	—	100	27·0	0·290	Aug. 10
1962	92	7	1	—	—	100	8·0	0·090	Aug. 9
1963	84	13	3	—	—	100	16·0	0·190	Aug. 13
Mean	83·0	15·0	2·0	—	—	—	17·0	0·190	—

10. Ot (Campus of Ooita Univ., Ôita-shi, Ôita-ken. 1959-63. 500 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no. of B's per male	Date of collection
1959	69	29	2	—	—	100	31·0	0·330	Aug. 15
1960	67	27	5	1	—	100	33·0	0·400	July 21-30
1961	58	35	7	—	—	100	42·0	0·490	July 26-Aug. 7
1962	59	33	8	—	—	100	41·0	0·490	Aug. 14
1963	21	10	1	—	—	100	32·0	0·320	Aug. 12-13
Mean	64·2	29·0	6·4	0·4	—	—	35·8	0·406	—

11. Tf (Tofurôato, Dazaifu-machi, Chikushi-gun, Fukuoka-ken. 1959-63. 700 males)

Year of collection	Frequency (%) of males 0B	1B	2B	3B	4B	Males obs.	% males with B's	Mean no. of B's per male	Date of collection
1959	93	7	—	—	—	100	7·0	0·070	Aug. 10
1960	85	14	1	—	—	100	15·0	0·160	Aug. 10
1961	90·5	9·0	0·5	—	—	200	9·5	0·100	Aug. 7-12
1962	88·0	11·5	0·5	—	—	200	12·0	0·125	Aug. 22
1963	96	4	—	—	—	100	4·0	0·040	Aug. 22
Mean	90·5	9·1	0·4	—	—	—	9·5	0·099	—

Differences among the values in different years were tested for each population by means of χ^2 test. The results of χ^2 tests show that only two populations, Mt and Om, differ over years. In 9 populations, Gs, Hk, Ik, Km, Kr, Ks, Ng, Ot, and Tf, the frequencies of B's are not significantly different over years.

4. DISCUSSION

In *A. lata* the combination of B's and the X in sperms appears to be random since there is no significant difference in the frequencies of B's between males and females. This is the case also in *Pyrgomorpha kraussi* (Lewis and John, 1959) and *Myrmeleotettix maculatus* (John and Hewitt, 1965; Hewitt and John, 1967). In *Pseudococcus obscurus* on the other hand B's are less frequent in the males than in the females (Nur, 1966, 1968). Jackson and Cheung (1967) find that in *Phaulacridium vittatum*, B chromosomes segregate preferentially from the X chromosome in primary spermatocytes and on this basis suggest a differential frequency of B's may well occur between the sexes in this species. This suggestion has not been tested by observation as yet.

Whatever the precise role of B chromosomes in natural populations, and this role certainly appears to differ in different species (*cf.* Kimura and Kayano, 1961; Nur, 1966; Hewitt and John, 1967), equilibrium frequencies of B's have been found in several cases, at least on a short-term basis. This applies, for example, to *Aiolopus* species B (Ray-Chaudhury and Guha, 1955), *Pseudococcus obscurus* (Nur, 1966), *Phaulacridium vittatum* (Jackson and Cheung, 1967), *Lilium callosum* (Kimura and Kayano, 1961), and *Myrmeleotettix maculatus* (Hewitt and John, 1967). In the present study no *A. lata*

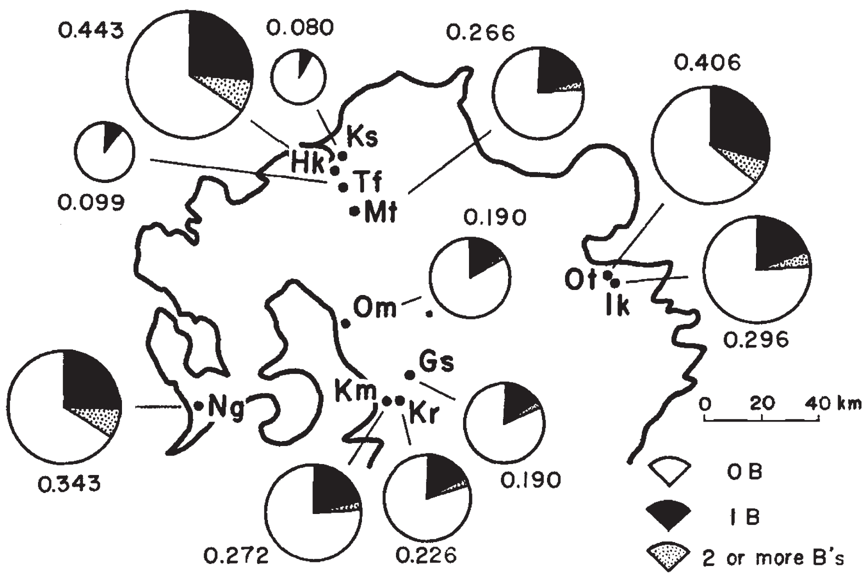


FIG. 1.—Map of the northern part of Kyushu showing 11 localities where natural populations of *A. lata* were sampled. Sizes of circles are relative to the frequencies of B-chromosomes. Sectors in circles show percentages of males of respective types, 0B, 1B, and 2 or more B's. Mean numbers of B's per male in the populations are shown alongside the circles.

population lost its B chromosomes during the period of observation. Nevertheless the different equilibria present suggests that the populations examined are more or less isolated from each other and that the exchange of genetic material between them is restricted. The populations are probably under differing environmental conditions and they may be different in their genotypes. Therefore, the fitness of the individuals with B's may be different from population to population. The year-to-year change in the frequency of B's found in two populations of *A. lata* are probably due to disturbance of the habitats by man's activities, for these populations were found on roadsides and in a park respectively.

5. SUMMARY

1. In natural populations of *Acrida lata* ($2n♂ = 22+XO+0\sim4$ B, $2n♀ = 22+XX+0\sim1$ B) at 11 localities in the northern part of Kyushu, Japan, individuals with B chromosomes were found in various frequencies. The B's were smaller than the smallest A's, and they were mitotically rather stable in germ line. The B's paired neither with A's nor with the X, but

Plate I

(All figs. × 1000)

Chromosomes of *A. lata*. The B-chromosomes are indicated by arrows.

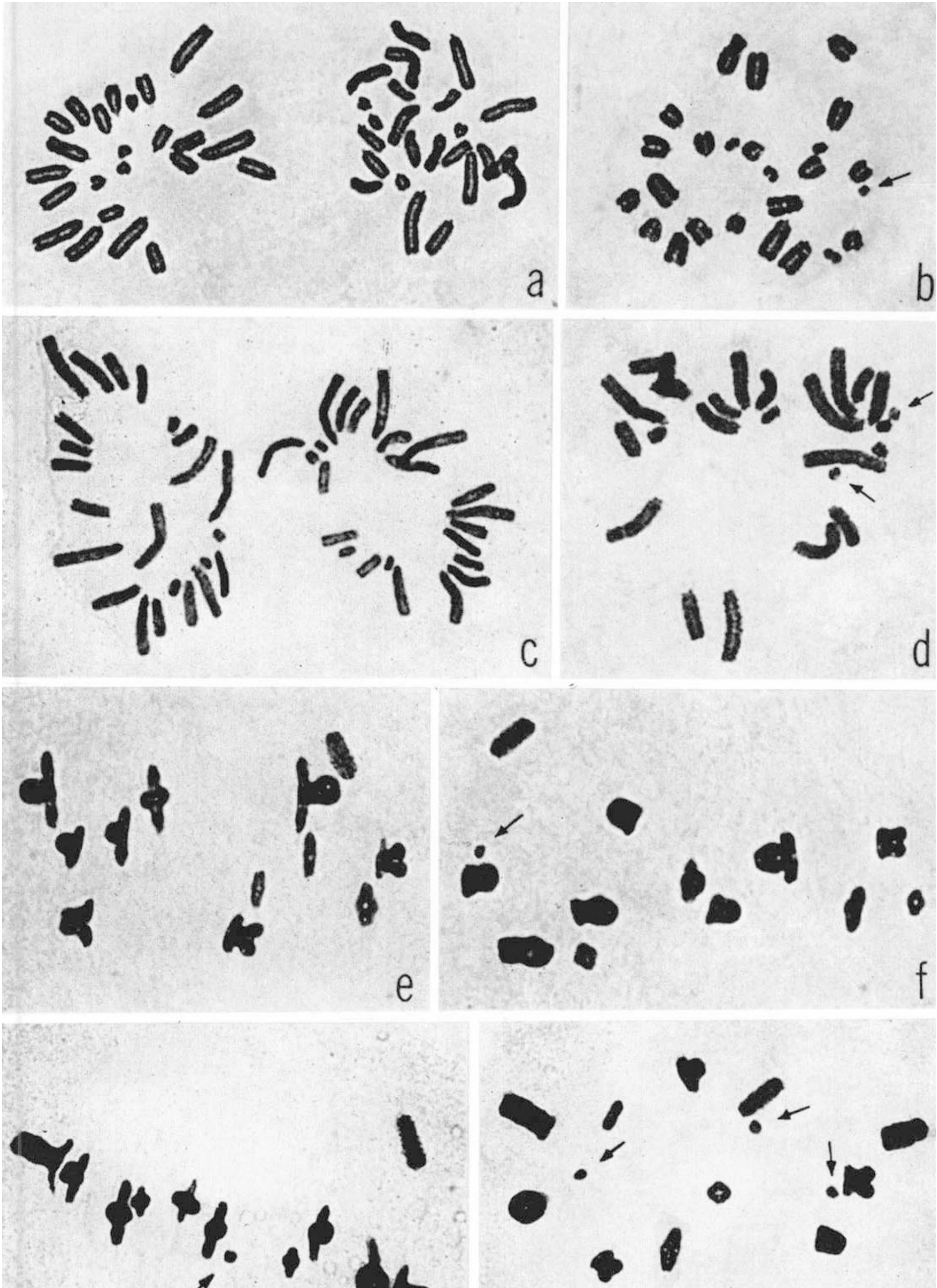
(*a*) Wall cells of an ovariole ($2n = 22+XX$).

(*b*) A wall cell of an ovariole ($2n = 22+XX+1B$).

(*c*) Spermatogonial cells ($2n = 22+XO$).

(*d*) A spermatogonial cell ($2n = 22+XO+2B$).

(*e*)-(*h*) Primary spermatocytes without a B and with 1 B, 2 B's, and 3 B's, respectively.


a
b
c
d
e
f
g
h

they paired between themselves in primary spermatocytes. The B's were rarely eliminated during spermatogenesis.

2. The B's segregated from the X at random in spermatogenesis and in the one natural population where it was tested B's were equally frequent in both males and females.

3. The frequency of B chromosomes was significantly different between populations, the overall mean number of B's per male among the populations ranging from 0·08 to 0·44. This suggests that the populations are more or less isolated from each other. The different frequencies of B's between populations might be due to different environmental conditions of the habitats and/or to different genotypes comprising the populations, which affect variously the fitness of the individuals with B's.

4. Year-to-year change in frequencies of B's was found in two populations. The changes are probably due to disturbance of the habitats by man's activities. Nine other populations showed no change in B-frequency between years.

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