

Variation and Evolution in the Karyotype of *Lycoris* (Amaryllidaceae)

V. Chromosomal Variation in *L. sanguinea* Maxim.

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Abstract In 554 bulbs from 38 populations of *Lycoris sanguinea*, several chromosomal variations have been discovered. Most of the bulbs have a common karyotype consisting of 22 acrocentric (*A*) chromosomes. Though their frequencies are low, some rearranged chromosomes which are aberrant have been found. The aberrants are as follows: 1. Subtelocentrics (*ST*); 2. Telocentrics (*T'*); 3. Metacentrics (*M'*); 4. Very small acrocentrics (*a*); 5. Very small metacentrics (*m*); 6. Acentric fragments (*Ac*); and 7. Dicentrics (*Di*) chromosome. All can be easily suspected to be derived from *As*. Some aberrations of the satellite chromosomes have been observed also. In addition, a new karyotype composed of $2n=32=31A+1M'$ chromosomes has been found.

Key words: *Lycoris sanguinea*, Robertsonian fusion, chromosomal variation, structural rearrangement.

Almost all species of *Lycoris* have been studied cytologically by several authors, and it has been revealed that their comparatively large and distinctive chromosomes seem to furnish ideal materials for a study of karyotype evolution (Kurita, 1986).

Although Koyama (1959) and Kitamura et al. (1964) considered that *L. sanguinea* is distributed in China, Korea, and Japan, all reliable locality records of herbarium specimens are confined only to Japan. This species is distributed throughout Japan except for Hokkaido and Nansei Shoto (Ohwi, 1978) and is rather rare on the Pacific coast of Iwate and Aomori Prefectures. It occurs usually in the secondary broad-leaved deciduous forest, or at the margin of laurilignosa.

Nishiyama (1928) first counted the chromosome numbers for this species as $n=11$ and $2n=22$. Inariyama (1931, 1937, 1951) and Takemura (1961) observed 22 rod-shaped somatic chromosomes. Sato (1942), Koyama (1954, 1962), Yoshida (1972), and Nakamura (1978) also reported 22 subterminally or terminally constricted chromosomes including two satellite chromosomes. On the other hand, Bose and Flory (1963) observed four SATs in their diploid material. An inter-individual variation in the long-arm lengths of SATs was also reported by Yoshida (1972).

This paper deals with the intrapopulational and/or intraspecific chromosomal variations of *L. sanguinea*.

Materials and Methods

The karyotypes of 554 bulbs collected in 38 populations ranging from Aomori to Oita Prefectures were studied (Table 1). Bulbs collected by random sampling in each population were cultivated in pots at the experimental garden of Chiba University. The karyotype analyses were made on root-tip cells by using the same methods reported by Kurita (1986).

For the description of chromosome morphology the following symbols have been adopted; SAT for satellite chromosome, *A* for acrocentrics, *M'* for metacentrics, *T'* for telocentrics, *a* for very small acrocentrics, *m* for very small metacentrics, *Di* for dicentrics, *Ac* for acntrics, and *ST* for subtelocentrics. In addition *r* represents an arm ratio, and *Ll/SI* is the ratio of the longest long-arm length/the shortest long-arm length in a chromosome complement. Subtelocentrics (*ST*) mean the chromosomes with the arm ratio between 3.0 to 5.0 in this paper.

Chromosomes in the idiograms were alined according to the length of their long arm. Black-painted

chromosomes in idiograms excepting those of Fig. 10 are SATs and aberrant chromosomes such as M' , T' , a . As occasion demanded, the long arm length of each chromosome was added and the mean value (\bar{x}) with standard deviation (S) calculated. The complement was divided into three chromosome groups, LG , MG , and SG (vid. Kurita, 1987a).

Some statistical and technical problems in the measurement of chromosome length for the detection of the homologues have been pointed out by some authors (Matern and Simka, 1968, Benzer et al., 1971). In order to reduce the errors in determination of the structural change as much as possible, the author tried to measure and calculate the length of the long arms of two SATs considered homologous in 15 well-spread prometaphase and/or metaphase plates in root-tips within a single bulb. The greatest disparity in the length between two chromosomes considered homologues in a complement was $0.6 \mu\text{m}$, and the mean and standard deviation of the disparity was $0.22 \mu\text{m}$ and $0.19 \mu\text{m}$, respectively. The author took this result into account when measuring the complements of the other bulbs examined and took a disparity of more than $0.7 \mu\text{m}$ in any chromosome set as the significant numerical value as the standard for the detection of structural difference in the long arms, though a disparity of over $0.41 \mu\text{m}$ was significant statistically. In contrast, the aberration in the length of the short arms was rather easily detectable, because the length in the standard complements at prometaphase and/or metaphase was very stable.

Results

In the first place, 100 bulbs from the Noro population (Chiba Pref.) were studied (Table 1). Five bulbs were collected from 20 sites (S-1~S-20) which were selected randomly from a $400 \text{ m} \times 50 \text{ m}$ square. The karyotype observed in 65 percent of the bulbs from this population is shown in Figs. 1 and 10, and is designated as the standard. It consists of 22 As . Chromosome numbers 1 to 4, 21 and 22, and 5 to 20, belong to LG , SG , and MG , respectively. One pair of SATs (chromosomes 3 and 4), and two chromosomes with the smallest short arm (chromosomes 15 and 16), can be differentiated. The absolute arm length, the relative length and the r of the standard karyotype are shown in Table 2. Its Ll/SI , \bar{x} and S are 1.3, $10.1 \mu\text{m}$ and $0.7 \mu\text{m}$, respectively. One to two nucleoli at interphase were observed, two nucleoli being predominant.

Some slight but significant karyotypic variations have been detected in the remaining bulbs examined. Details are as follows. In the S-17 (Fig. 11), the long arm length of SATs (nos. 2 and 7) differ from each other. The SATs difference is $1.4 \mu\text{m}$. The shortest no. 22 chromosome with $r=6.2$ is distinct from the rest. The difference of length between nos. 22 and 21 is $1.2 \mu\text{m}$. Chromosome no. 10 has a somewhat larger short arm than that of any of the other chromosomes of the standard karyotype. Its r is 4.2 whereas the value of the standard with the largest short arm is 5.3. Its Ll/SI , \bar{x} , and S in this complement are 1.5, $10.0 \mu\text{m}$, and $0.9 \mu\text{m}$, respectively.

Only one SAT could be detected in both prometaphase and metaphase karyotypes of the S-11 (Fig. 13). Since one to two nucleoli can be observed at interphase, at least two NORs should be included in this complement. One aberrant ST chromosome with $r=3.9$, no. 12, was found. Its Ll/SI , \bar{x} , and S are 1.3, $10.6 \mu\text{m}$, and $0.9 \mu\text{m}$, respectively.

In the S-5 (Figs. 2 and 12), three SATs have been observed at metaphase (nos. 1, 4, and 8) and 1 to 3 nucleoli are observed at interphase. There is one aberrant ST , no. 6 with $r=4.1$. Its Ll/SI , \bar{x} , and S are 1.3, $8.9 \mu\text{m}$, and $0.9 \mu\text{m}$, respectively.

The S-10 has two medium-sized SATs (Fig. 15). Its ratio of Ll/SI is somewhat higher than that of the standard karyotype. Its \bar{x} and S are $8.8 \mu\text{m}$ and $0.8 \mu\text{m}$, respectively.

The S-12 has $2n=23$ including 22 As and one a chromosome (Figs. 3 and 16). The long and short arm lengths of a (no. 23) are $1.3 \mu\text{m}$ and $0.3 \mu\text{m}$, respectively, and it is totally euchromatic. Though two nucleoli are usually observed at interphase, only one SAT can be detected in prometaphase and/or metaphase karyotypes.

In the S-20, the long arm length of SATs differ from each other (Fig. 17). The difference is $1.1 \mu\text{m}$. Its Ll/SI , \bar{x} , and S are 1.4, $10.5 \mu\text{m}$, and $0.9 \mu\text{m}$, respectively. The satellite of chromosome no. 10 is larger than that of the standard, no. 2.

Two aberrations were found on SATs in site S-1 (Fig. 18), 1) tandem satellites and 2) the difference of the long arm length between the two SATs. In the latter case, their arm ratios are $r=6.1$ in no. 2 and $r=11.4$ in no. 10, respectively and the difference in the long arm length is $1.5 \mu\text{m}$. Its Ll/SI , \bar{x} , and S are 1.3, $10.5 \mu\text{m}$, and $0.8 \mu\text{m}$, respectively.

The frequency of various chromosomal aberrations in the Noro population are as follows. Plants with the two standard SATs comprise 65% of the

Table 1. Localities, the number of bulbs examined, and the percentage of bulbs having aberrant chromosomes.

Localities ¹⁾	Number of bulbs	Types of aberrant chromosomes (%)								
		Sum of aberrant SAT-chromosomes	T'	$2T'$	ST	M'	a	m	Di	Ac
Matsukami, Nishitsugaru-gun, Aomori Pref.	10	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Konoura, Yuri-gun, Akita Pref.	15	20.0	26.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kisakata, Yuri-gun, Akita Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Senami, Murakami-shi, Niigata Pref.	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kakudayama, Niigata-shi, Niigata Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kawauchi, Futaba-gun, Fukushima Pref.	7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orido, Suzu-shi, Ishikawa Pref.	10	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tamozawa, Nikko-shi, Tochigi Pref.	8	37.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Motodoriyama, Nagano-shi, Nagano Pref.	10	30.0	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0
Myogisan, Kanra-gun, Gunma Pref.	20	25.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tsukubasan, Tsukuba-gun, Tochigi Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ogano, Chichibu-gun, Saitama Pref.	14	50.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bukosan, Chichibu-gun, Saitama Pref.	10	30.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Inabe, Ina-shi, Nagano Pref.	5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Motono, Inba-gun, Chiba Pref.	6	33.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mitakesan, Oume-shi, Tokyo Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kamiange, Hachioji-shi, Tokyo Pref.	20	30.0	0.0	0.0	30.0	0.0	0.0	0.0	0.0	0.0
Kobotoke, Hachioji-shi, Tokyo Pref.	10	30.0	0.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0
Takaosan, Hachioji-shi, Tokyo Pref.	10	20.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Noro, Chiba-shi, Chiba Pref.	100	35.0	2.0	0.0	13.0	0.0	2.0	0.0	0.0	1.0
Sonno, Chiba-shi, Chiba Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Midorigaoka, Zama-shi, Kanagawa Pref.	5	20.0	0.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0
Suyama, Susono-shi, Shizuoka Pref.	15	26.7	0.0	0.0	13.3	0.0	0.0	0.0	0.0	0.0
Nakazato, Susono-shi, Shizuoka Pref.	20	15.0	0.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0
Imazato, Susono-shi, Shizuoka Pref.	10	30.0	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Iwanami, Susono-shi, Shizuoka Pref.	10	20.0	0.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0
Iriuda, Odawara-shi, Kanagawa Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nebukawa, Odawara-shi, Kanagawa Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kanaya, Haibara-gun, Shizuoka Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kurasawa, Ogasa-gun, Shizuoka Pref.	26	26.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tomoda, Ogasa-gun, Shizuoka Pref.	30	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Honjo, Ogasa-gun, Shizuoka Pref.	20	100.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0
Gomyo, Kakegawa-shi, Shizuoka Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kawasa, Fuchu-shi, Hiroshima Pref.	30	16.7	20.0	6.7	6.7	0.0	0.0	0.0	0.0	0.0
Shimokawabe, Fuchu-shi, Hiroshima Pref.	10	0.0	30.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0
Kudoyama, Ito-gun, Wakayama Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	0.0
Nakagawa, Chikushi-gun, Fukuoka Pref.	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Kuju, Naoiri-gun, Oita Pref.	10	30.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total number of bulbs	556	114	25	2	32	20	2	1	1	1
Mean (%)		20.50	4.50	0.36	5.76	3.60	0.36	0.18	0.18	0.18

1) Localities are arranged from north to south.

Table 2. Measurements of somatic chromosomes in a representative karyotype of *L. sanguinea*.

Chromosome	Length of arms (um)			Relative length	Arm ratio
	short	long	total		
1 (<i>LG</i>)	2.1	11.1	13.2	5.2	5.3
2 (<i>LG</i>)	2.1	11.1	13.2	5.2	5.3
3 (<i>LG</i>)*	0.3	2.1	11.1	5.2	5.3
4 (<i>LG</i>)*	0.3	1.8	11.1	5.1	6.2
5 (<i>MG</i>)	1.6	10.8	12.4	4.9	6.8
6 (<i>MG</i>)	1.4	10.8	12.2	4.8	7.7
7 (<i>MG</i>)	1.3	10.8	12.1	4.8	8.3
8 (<i>MG</i>)	1.6	10.5	12.1	4.8	6.6
9 (<i>MG</i>)	1.6	10.5	12.1	4.8	6.6
10 (<i>MG</i>)	1.6	10.3	11.9	4.7	6.4
11 (<i>MG</i>)	1.7	10.0	11.7	4.6	5.9
12 (<i>MG</i>)	1.6	10.0	11.6	4.6	6.3
13 (<i>MG</i>)	1.3	9.7	11.0	4.3	7.5
14 (<i>MG</i>)	1.3	9.7	11.0	4.3	7.5
15 (<i>MG</i>)	0.9	9.7	10.6	4.2	10.8
16 (<i>MG</i>)	0.9	9.7	10.6	4.2	10.8
17 (<i>MG</i>)	1.4	9.7	11.1	4.4	6.9
18 (<i>MG</i>)	1.3	9.5	10.8	4.2	7.3
19 (<i>MG</i>)	1.2	9.4	10.6	4.1	7.8
20 (<i>MG</i>)	1.1	9.4	10.5	4.1	8.5
21 (<i>SG</i>)	1.3	8.7	10.0	3.9	6.7
22 (<i>SG</i>)	1.3	8.7	10.0	3.9	6.7
Mean	1.48	10.1	11.58	4.56	7.15

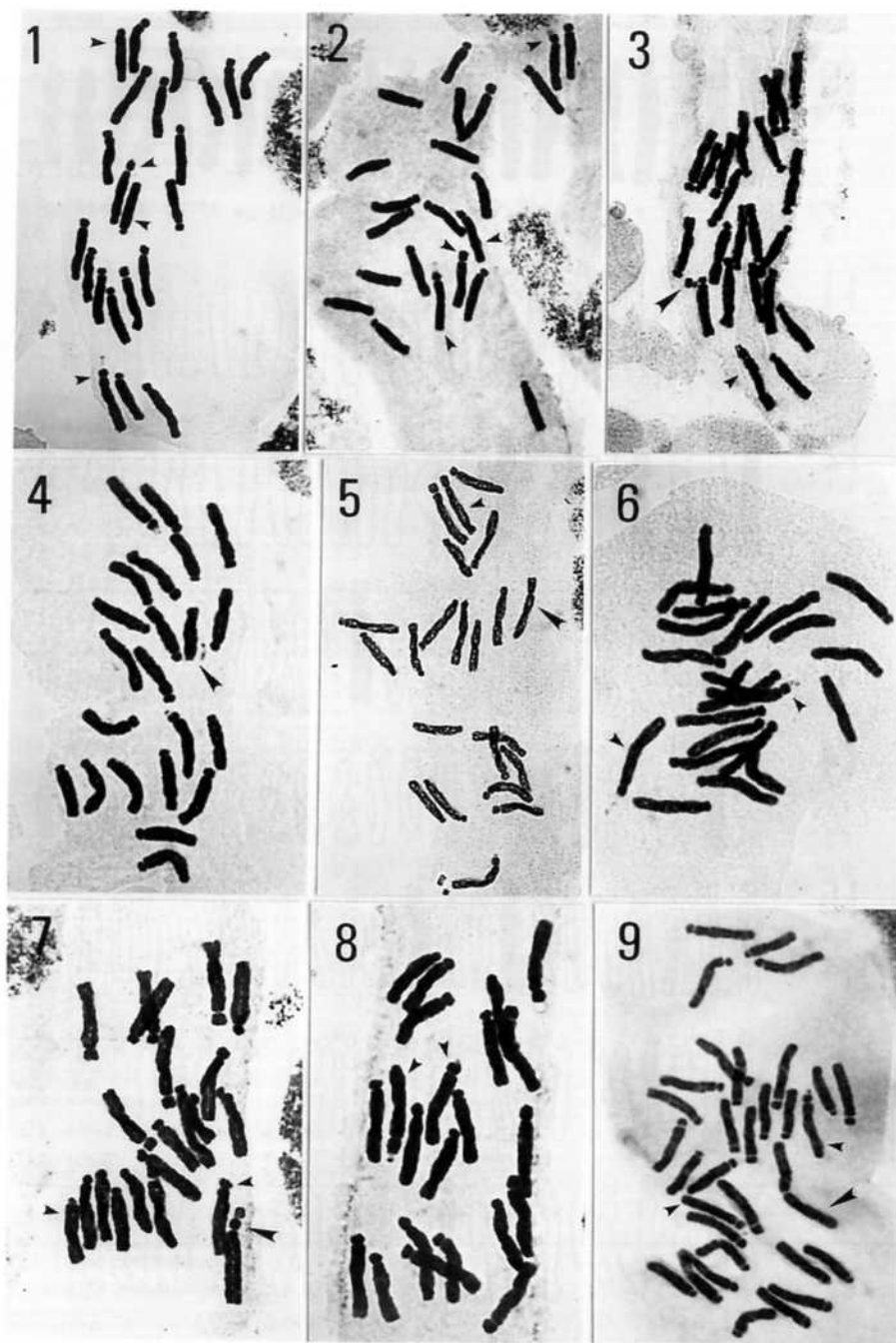
* Satellite chromosome.

population. The remaining 35% of the plants have various combinations of aberrant SATs. They are designated as "Aberrant SAT-chromosomes" in Table 1. The plants with two different SATs in their long arm (Fig. 11) have only a 5% share of the population. The plants with one tandem and one standard SAT have a 2% share, and the plants including one standard and one aberrant with a fairly large satellite a 3% share. While individuals having only one standard SAT and those having three standard SATs have a share of 23% and 2%, respectively. 84% of the bulbs from this population have a karyotype with 22 *As*. Their *rs* ranges from 5.0 to 13.0. The 13% individuals of this population have at least one aberrant *ST* with a lower arm ratio than 4.8. One *T'* and one *a* are found in 2% and 1% of the individuals from this population, respectively.

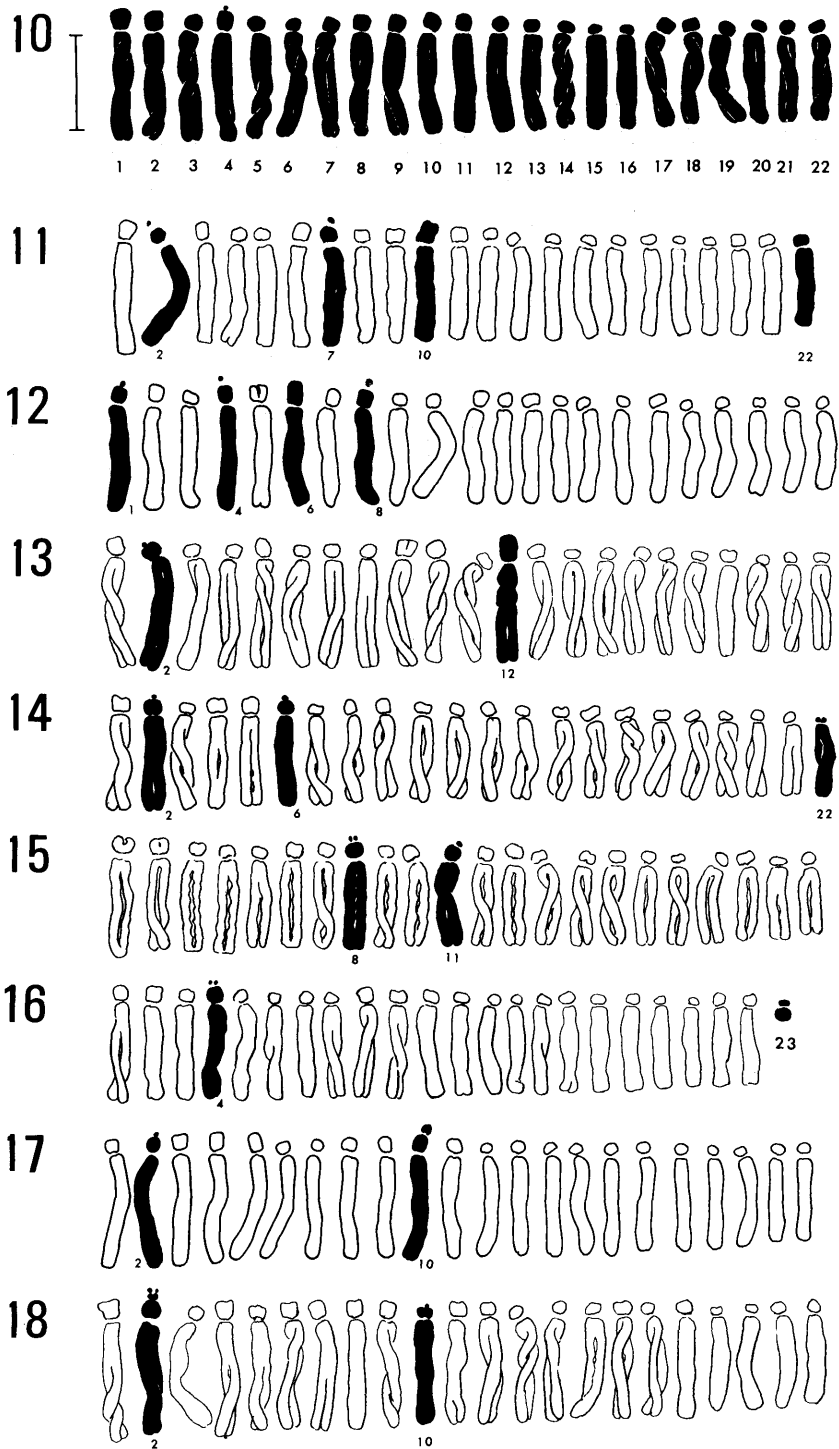
A similar trend of intrapopulation karyotype variation has been found in almost all the populations examined (Table 1).

One *T'* has been found in some bulbs of seven other populations as well as in the S-14 site of the Noro population. The percentage of individuals with this *T'* chromosome varied from 30% in the Simokawabe population to 10% in the Imazato. In the Kawasa population, 6.7% of the individuals carried two *T'*s (Fig. 20), but the remaining 13.3% of individuals had only one *T'* (Figs. 4 and 19) as was found in the other individuals in the remaining six populations.

Some aberrant *ST*s, as in the Noro population, were also found in eight other populations. The percentage of the individuals with this *ST* varied from 30% in the Kamiange population to 6.7% in the Kawasa. Two aberrant *ST*s were found in two bulbs from Suyama (Fig. 21). The *r* of no. 5 and no. 18 are 4.5 and 3.0, respectively. The chromosome complements in the remaining populations, however, have only one aberrant *ST* as shown in Figs. 22 and 23. The *r* of chromosome no. 17



Figs. 1-9. Photomicrographs of mitotic metaphase chromosomes of *L. sanguinea*, X ca. 850 except for Fig. 5. 1: Standard karyotype from the S-12 site in the Noro population. Arrow heads indicate nos. 3, 4, 15, and 16 in Fig. 10. 2: Karyotype from the S-5 site. Arrow heads indicate three satellites and one aberrant *ST* chromosome. 3: the S-12 site. Arrow heads indicate a satellite and an *a* chromosome. 4: the Kawasa population. One *T'* indicated by arrow head is included. 5: the Suyama population. Arrow heads indicate two *ST*s (X ca. 750). 6: the Tomoda population. Arrow heads indicate two tandem SATs. 7: the Myogisan population. Arrow heads indicate a heteromorphic pair of satellites and *T*'s. 8: the Bukosan population. Arrow heads indicate two SATs, of which one is the aberrant *ST*. 9: Triploid from the Honjo population. $2n=32 (31A+1M')$. Arrow heads indicate a *M'* and SATs.



Figs. 10–18. Variation of the karyotypes from the Noro population. Bar represents 10 μm. 10: Standard karyotype depicted from Fig. 1. Figs. 11–18: Aberrant karyotypes. Figs. 11, 12, 13, 14, 15, 16, 17, and 18 are from the S-17, S-5, S-11, S-14, S-10, S-20, and S-1, respectively (vid. text).

Table 3. Measurements of somatic chromosomes in a representative karyotype of triploid *L. sanguinea*.

Chromosome	Length of arms (um)			Relative length	Arm ratio	
	short	long	total			
1 (LG)*		7.6	9.2	16.8	5.7	1.2
2 (LG)		1.3	8.9	10.2	3.5	6.8
3 (LG)		1.3	8.9	10.2	3.5	6.8
4 (LG)		1.3	8.9	10.2	3.5	6.8
5 (LG)		1.3	8.7	10.0	3.4	6.7
6 (LG)**	0.3	1.2	8.7	9.9	3.4	7.3
7 (LG)**	0.3	1.2	8.7	9.9	3.4	7.3
8 (LG)		1.3	8.7	10.0	3.4	6.7
9 (MG)		1.3	8.4	9.7	3.3	6.5
10 (MG)		1.1	8.4	9.5	3.2	7.6
11 (MG)		1.2	8.4	9.6	3.3	7.0
12 (MG)		1.3	8.4	9.7	3.3	6.5
13 (MG)		1.3	8.2	9.5	3.2	6.3
14 (MG)		0.9	8.2	9.1	3.1	9.1
15 (MG)		0.9	8.2	9.1	3.1	9.1
16 (MG)		1.1	8.2	9.3	3.2	7.5
17 (MG)		1.2	8.2	9.4	3.2	6.8
18 (MG)		1.1	8.2	9.3	3.2	7.5
19 (MG)		0.8	7.9	8.7	3.0	9.9
20 (MG)		1.1	7.6	8.7	3.0	6.9
21 (MG)		0.8	7.6	8.4	2.9	9.9
22 (MG)		0.9	7.6	8.5	2.9	8.4
23 (MG)		0.7	7.6	8.3	2.8	10.9
24 (MG)		1.1	7.4	8.5	2.9	6.7
25 (MG)		1.1	7.1	8.2	2.8	6.5
26 (MG)		0.9	7.1	8.0	2.7	7.9
27 (MG)		0.9	7.1	8.0	2.7	7.9
28 (MG)		0.7	7.1	7.8	2.7	10.0
29 (SG)		0.8	6.8	7.5	2.6	8.5
30 (SG)		0.7	6.8	7.5	2.6	9.7
31 (SG)		0.8	6.8	7.6	2.6	8.5
32 (SG)		0.8	6.1	6.9	2.3	7.6
Mean		1.25	7.94	9.19	3.14	7.59

* *M'* type chromosome.

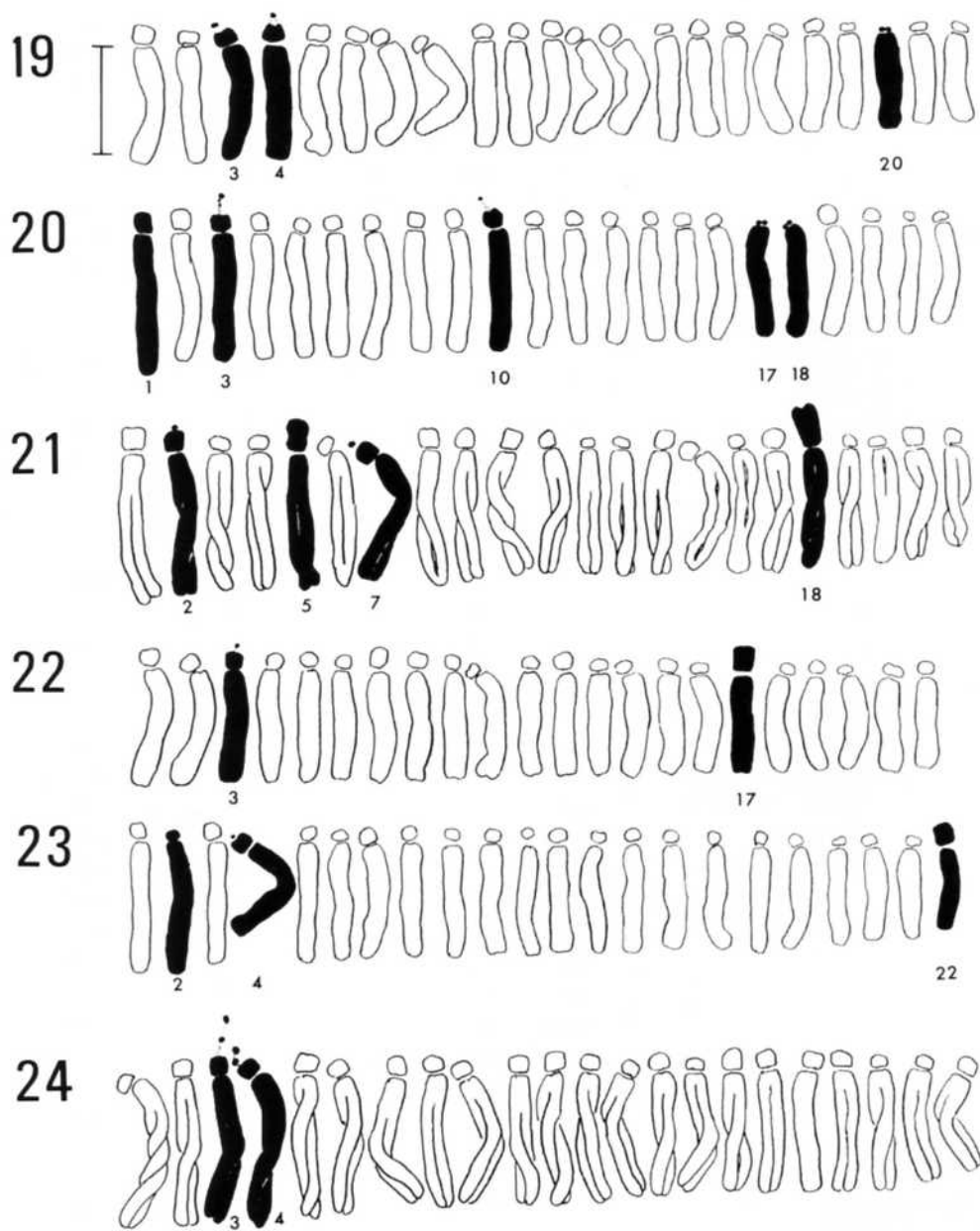
** Satellite chromosome.

from Kawasa (Fig. 22) is 3.7 and that of the no. 22 from Simokawabe (Fig. 23) is 4.0. Chromosome no. 2 from Simokawabe has a fairly small short arm in which $r=12.9$.

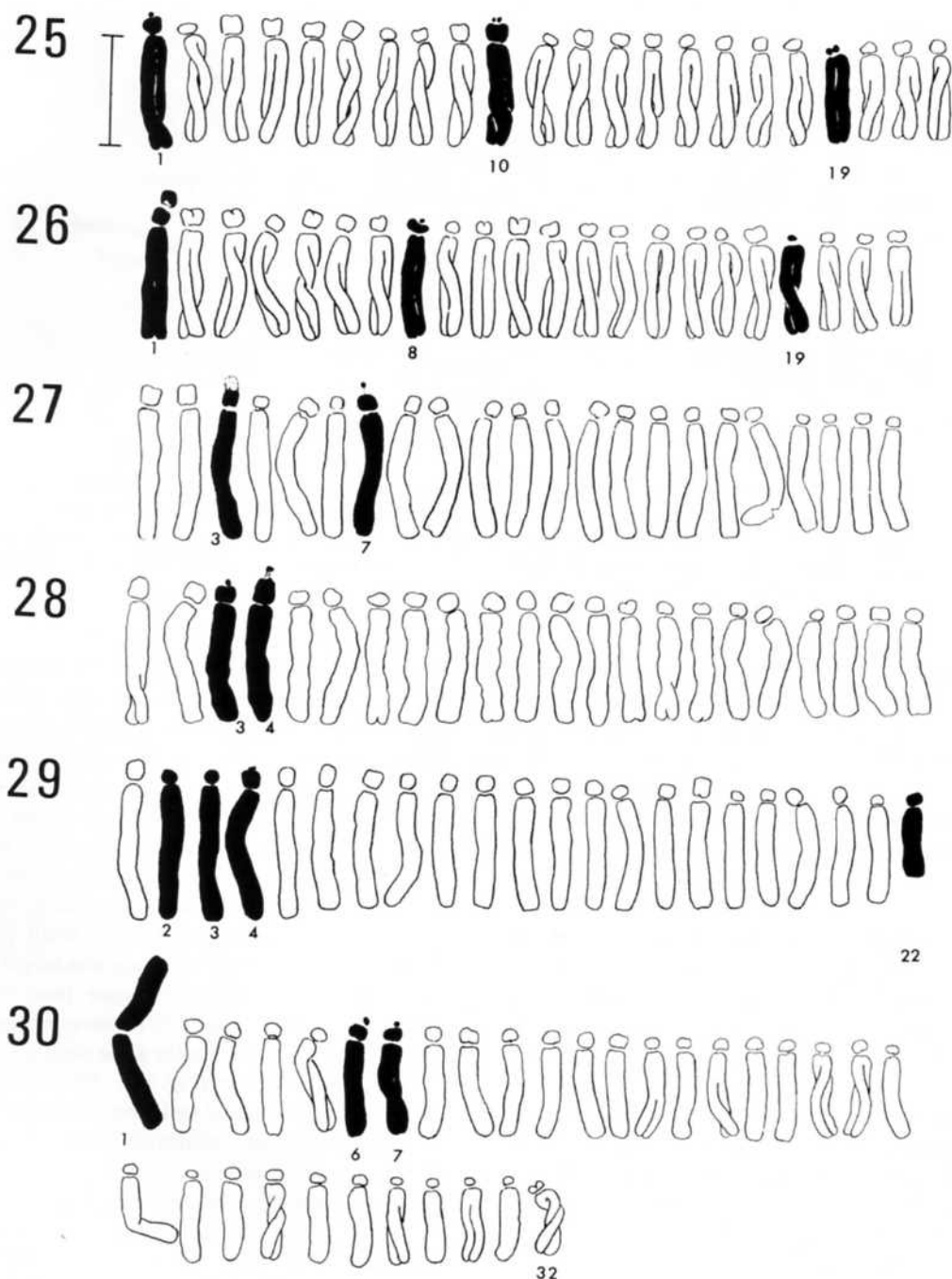
The heterogeneous SATs constitution as shown in Fig. 11 was also found in the Imazato (Fig. 25), Suyama, Iwanami, and Myogisan populations (Fig. 26). Tandem satellites were found in the bulbs from Matsukami, Suyama, and Tomoda. Ten percent of

bulbs from Matsukami and 13.3% from Suyama have one tandem SAT. On the other hand, 3.3% of the bulbs from Tomoda carry two tandem SATs (Figs. 6 and 24)

A very large satellite, almost the same size as the short arm, was observed in the complement of 25% of bulbs from the Myogisan population (Figs. 7 and 26). The r value of this SAT is 7.5. A similar large satellite was also found in the Kuju population.



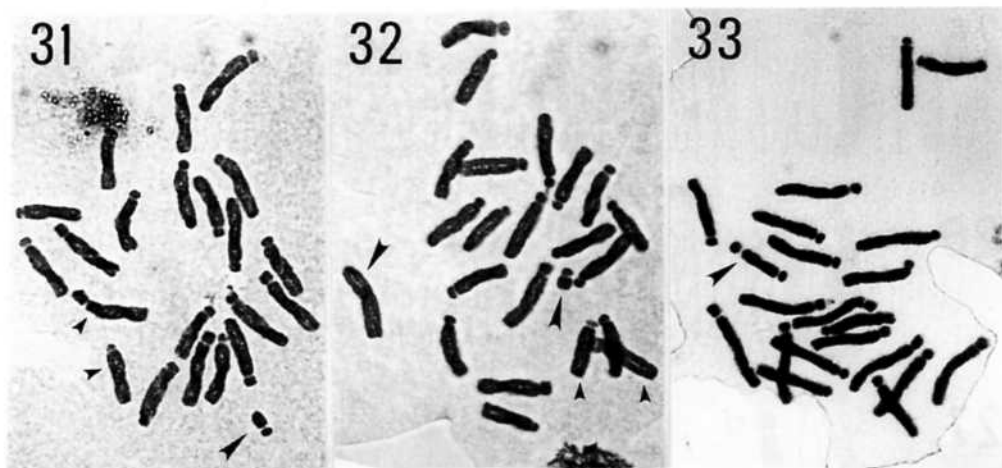
Figs. 19–30. Aberrant karyotypes from other populations. Bar represents 10 μm . 19: Karyogram based on Fig. 4, including one T' , no. 20. 20: the Kawasa population. Note two T' , nos. 17 and 18. 21: Karyogram depicted from Fig. 5, the Suyama population. Note two ST s, nos. 5 and 18. 22: the Kawasa population, including one ST , no. 17. 23: the Shimokawabe population. Note chromosome nos. 2 and 22. 24: the Tomoda population, depicted from Fig. 6. Note two tandem SAT s, nos. 3 and 4. 25: the Imazato population. Note a heteromorphic pair of SAT s and one T' , nos. 1, 10, and 19. 26: the Myogisan population, depicted from Fig. 7. Note a heteromorphic pair of SAT s, nos. 1 and 8, and one T' , no. 19. 27: the Motono population. Note chromosome no. 3 with a diffused satellite. 28: the Bukosan population, depicted from Fig. 8. Note a subtelocentric SAT , no. 4. 29: the kamiange population. Note both chromosomes have rather high r values, nos. 2 and 3, and a small A , no. 22. 30: the Honjo population, depicted from Fig. 9. Note the M' type chromosome, no. 1.



The no. 3 chromosome with a large heterochromatic satellite block (Fig. 27) was found in two bulbs from the Motono population. This satellite block is almost the same length as the short arm of this chromosome. One aberrant subtelocentric SAT was found in three bulbs from Mt. Bukosan (Figs. 8 and 28). Its r is 4.8.

A small A was observed in one bulb from Kamiange (Fig. 29). Its long arm length is $6.2 \mu\text{m}$. Its $L1/S1$, \bar{x} and S are 2.0, $10.4 \mu\text{m}$ and $1.4 \mu\text{m}$, respectively. This complement includes nos. 2 and 3 chromosomes with a high arm ratio of 10.4.

Only one satellite chromosome was found in the following populations: in 100% of the individuals ex-



Figs. 31–33. Photomicrographs of chimeral aberrant karyotypes. X ca. 850. 31: Metaphase in a root tip from the S-4 site. Large arrow head indicates an *a* and small one indicates the marker chromosomes. 32: the same root tip. Large arrow heads indicate an *a* and an acentric chromosome. Small ones indicate the markers. 33: the Kudoyama population. Note a presumed *Di* indicated by an arrow head.

amed in the Orido, 30% in the Motodoriyama, 50% in the Ogano, 20% in the Takaosan, 10% in the Sonno, 30% in the Kamiange (Fig. 29), 30% in the Kobotoke, 20% in the Midorigaoka, 15% in the Nakazato, 19.2% in the Kurasawa, 16.7% in the Kawasa (Fig. 22), 20% in the Shimokawabe (Fig. 23), and 20% in the Kuju. These individuals have two nucleoli at interphase, so they should have two NORs in their chromosome complements.

The somatic chromosome number of all bulbs collected from the Honjo population is 32 as shown in Figs. 9, 30 and Table 3. This complement consists of one metacentric and 31 acrocentrics: $1M' + 31A$. The M' may be derived from Robertsonian fusion of two *As*. This plant is regarded as a triploid. The number of SATs is two, instead of three, while the maximum number of nucleoli at interphase is three. Its Ll/SI , \bar{x} , and S are 1.5, $7.9 \mu\text{m}$, and $0.8 \mu\text{m}$, respectively. These triploids can be distinguished from the diploids by some external characters: the stomata which are $65(\pm 2) \mu\text{m}$ in length in the triploid but only $51(\pm 2) \mu\text{m}$ in length in the diploid. The shape and size of the flowers of the triploid, however, does not differ greatly from the diploid.

In some bulbs from four populations, intra-individual variation for chromosomal rearrangements was observed.

The common karyotype in site S-4 from the Noro population consists of 22 chromosomes including one SAT, one *ST*, and one *A* with a fairly small

short arm (Fig. 34). Two aberrant karyotypes were found in root tips with the karyotype mentioned above. One of them consists of 22 chromosomes including one *a* (Figs. 31 and 35), and the other consists of 23 chromosomes including one large *Ac* and one *a* (Figs. 32 and 36). These *as* are similar to that in site S-12 by their shape and euchromatic nature.

Among the cells with a standard karyotype in one bulb from the Motodoriyama population, one cell had the aberrant complement with a small *ST* (Fig. 37, no. 22). Its r is 3.5. The long arm length of the no.1 chromosome is much longer than that of chromosome no. 2. The Ll/SI of this complement is 2.5. In another bulb from the same population, one cell has 21 *As* and one *m* (Fig. 38). The r of this *m* is 1.3. An intra-individual variation for chromosomal interchange was also observed in the bulb from Kudoyama. This aberrant cell has $2n=21$ with one *Di* (Figs. 33 and 39). An extremely aberrant complement was found in one cell of the bulb from Nakazato. It has $2n=28$ including four chromosomes with a peculiar short arm. These short arms are heteropycnotic in contrast to the rest of chromosomes, including their long arms (Fig. 40, nos. 7, 13, 22, and 25). No SAT was observed in this complement.

Discussion

About 65% of the bulbs examined have the stand-

