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Lampbrush Chromosomes of *Rana nigromaculata*, *R. brevipoda*, *R. plancyi chosenica*, *R. p. fukienensis* and their Reciprocal Hybrids

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(With 6 Text-figures)

CONTENTS

ABSTRACT

Landmarks and chiasmata of lampbrush chromosomes were observed in the oocytes of female *Rana nigromaculata*, (N)NN, *R. brevipoda*, (B)BB, *R. plancyi chosenica*, (C)CC, and *R. p. fukienensis*, (F)FF, and in those of 12 kinds of hybrids produced from these

species and subspecies. The lampbrush chromosomes of the three species and one subspecies are not always parallel to their mitotic chromosomes in morphological characters. The lampbrush chromosomes of *Rana plancyi chosenica* are peculiar in extreme scarcity of landmarks and remarkably differ from the conspecific *R. p. fukienensis* at nearly the same degree as the other two species.

(N)NN, (B)BB, (C)CC and (F)FF had all 13 bivalents in each of 50 oocytes and were 38.5, 38.7, 42.5 and 38.2, respectively, in the mean number of chiasmata of the 13 bivalents. When compared with the parental species and subspecies, all the 12 kinds of hybrids among them were fewer in the number of oocytes having 13 bivalents as well as in the mean number of chiasmata found in the 13 pairs of homologous chromosomes. These fewer numbers in bivalents and chiasmata are attributable to the differences between the lampbrush chromosomes of the two parental species or subspecies. On the other hand, the difference between reciprocal hybrids in the number of oocytes having 13 bivalents and the mean number of chiasmata in the 13 pairs of homologous chromosomes seems to be attributable to a difference in cytoplasm between the two parental species or subspecies.

INTRODUCTION

Lampbrush chromosomes found in the amphibian oocytes are characterized by their huge size and the presence of several landmarks, in contrast to mitotic chromosomes. As these landmarks are specific in position, number, figure and structure, the lampbrush chromosomes of various amphibians can be distinguished from one another.

The maps of lampbrush chromosomes have been drawn in various amphibians by many investigators. GALL (1954) has first drawn the map of urodelan species, *Notophthalmus viridescens*. CALLAN and LLOYD (1960) have observed lampbrush chromosomes in three subspecies of *Triturus cristatus*. The lampbrush chromosomes of *Triturus* were found to be remarkably different from those of *Notophthalmus* in having numerous landmarks in each of them. Maps of lampbrush chromosomes of urodeles have also been drawn by NARDI, RAGGHIANTI and MANCINO (1972) in *Triturus marmoratus,* by MANCINO (1965), MANCINO and BARSACCHI (1965) and RAGGHIANTI, NARDI and MANCINO (1972) in *T. alpestris apuanus,* by BARSACCHI, BUSSOTTI and MANCINO (1970) in *T. vulgaris meridionalis,* by MANCINO (1965) and MANCINO and BARSACCHI (1966) in *T. helveticus helveticus,* by MANCINO and BARSACCHI (1969) in *T. italicus,* by MANCINO, BARSACCHI and NARDI (1969) in *Salamandra salamandra,* by LACROIX (1968) in *Pleurodeles waltl* and *P. poireti,* and by CALLAN (1966) in *Ambystoma mexicanum.*

In anurans, MORESCALCHI and FILOSA (1965) have briefly reported on the lampbrush chromosomes of *Rana esculenta.* Each of the 13 lampbrush chromosomes of this species has been minutely described by GIORGI and GALLENI (1972). The lampbrush chromosomes of *Xenopus laevis* have been reported by MÜLLER (1974). The maps of lampbrush chromosomes in *Rana nigromaculata* and *R. brevipoda* have been drawn by the present author (1975). By making good use of morphologically different lampbrush chromosomes of these two sibling species, NISHIOKA, OHTANI and SUMIDA (1980, 1987) and NISHIOKA and OHTANI (1986)

have detected the chromosomes bearing the loci for various color mutations and proteins.

In the present study, the lampbrush chromosomes in *Rana nigromaculata* and *R. brevipoda* from Japan, *R. plancyi chosenica* from Korea and *R. p. fukienensis* from Taiwan and in 12 kinds of hybrids produced from them were observed in order to clarify the morphological and genetic differences among the lampbrush chromosomes of these three species and one subspecies.

MATERIALS AND METHODS

Lampbrush chromosomes were observed in female offspring of *Rana nigromaculata* HALLOWELL, *Rana brevipoda brevipoda* ITO, *Rana plancyi chosenica* OKADA and *Rana plancyi fukienensis* POPE which were originated in the suburbs of Hiroshima, in Konko-cho, Okayama Prefecture, in Suwon, Korea and in Changhura, Taiwan, respectively. They were also observed in 12 kinds of female reciprocal hybrids among these species and subspecies.

The abbreviations and the numbers of the female *R. nigromaculata, R. brevipoda, R. p. chosenica* and *R. p. fukienensis* used in observing lampbrush chromosomes are as follows: (N)NN, 10; (B)BB, 11; (C)CC, 8 and (F)FF, 8. The origins, abbreviations and numbers of hybrids used in the present study are shown in Table 1.

The preparations of lampbrush chromosomes were principally made in accordance to the method of GALL (1966). An isolated nucleus removed from an ovarian egg was put into saline solution which was contained in a hollow surrounded with a circular dike of paraffin wax on a slide glass. The nuclear membrane was gently torn and removed with two pairs of forceps. The saline solution used in dispersing the lampbrush chromosomes was a mixture of 5 parts of 75 mM KCl solution and 1 part of 75 mM NaCl solution, containing 0.08% formaldehyde. Thereafter, the preparation was placed overnight in a chamber

TABLE 1
Origins, abbreviations and numbers of female hybrids used in the present study

Origin	Abbreviation	Number
R. nigromaculata ♀ × *R. brevipoda* ♂	(N)NB	9
R. brevipoda ♀ × *R. nigromaculata* ♂	(B)BN	8
R. nigromaculata ♀ × *R. p. chosenica* ♂	(N)NC	9
R. p. chosenica ♀ × *R. nigromaculata* ♂	(C)CN	9
R. nigromaculata ♀ × *R. p. fukienensis* ♂	(N)NF	6
R. p. fukienensis ♀ × *R. nigromaculata* ♂	(F)FN	7
R. brevipoda ♀ × *R. p. chosenica* ♂	(B)BC	9
R. p. chosenica ♀ × *R. brevipoda* ♂	(C)CB	8
R. brevipoda ♀ × *R. p. fukienensis* ♂	(B)BF	5
R. p. fukienensis ♀ × *R. brevipoda* ♂	(F)FB	9
R. p. chosenica ♀ × *R. p. fukienensis* ♂	(C)CF	8
R. p. fukienensis ♀ × *R. p. chosenica* ♂	(F)FC	7

saturated with the fumes of formaldehyde.

OBSERVATION

I. General structures of lampbrush chromosomes in pond frogs

Thirteen pairs of lampbrush chromosomes in the oocyte nuclei of pond frogs were used in the present study. Each pair of the lampbrush chromosomes forms a bivalent by joining with each other through the mediation of a certain number of chiasmata and rarely of one or two terminal fusions in addition. Each lampbrush chromosome has a short segment covered by numerous lateral loops which are

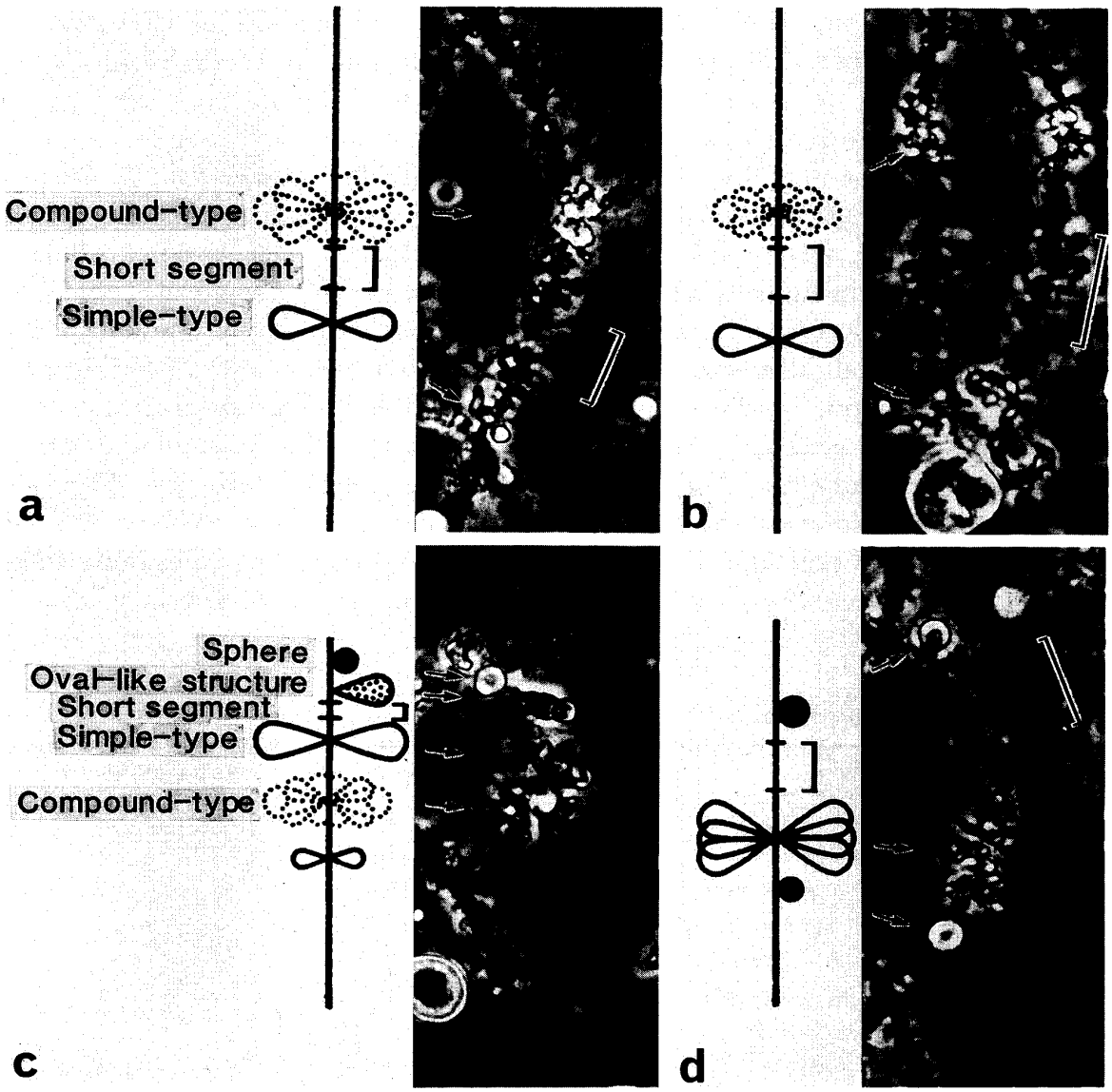

Fig. 1. Four types of landmarks and short segments in four kinds of lampbrush chromosomes from *Rana nigromaculata* females. ×800

a. Bivalent No. 2 b. Bivalent No. 5

c. Bivalent No. 9 d. Bivalent No. 11

distinctly larger than those of the other portions (Fig. 1). This short segment is always observed at a definite position which coincides with that of the centromere of the corresponding mitotic chromosome. Thus, the short segment seems to include the centromere of the lampbrush chromosome. Besides, there are one or more conspicuous giant loops and laterally attached lumpy objects in addition to numerous small lateral loops along the axes of the lampbrush chromosomes. These conspicuous giant loops and the lumpy objects are very useful landmarks in discriminating the lampbrush chromosomes from each other, as they are characteristic in number, shape and situation. Therefore, the 13 bivalents in each species and subspecies could be distinguished without fail from one another by their landmarks.

The numerical order of the 13 pairs of lampbrush chromosomes corresponds to that of the mitotic chromosomes of *R. nigromaculata* (NISHIOKA, 1972; NISHIOKA, OHTANI and SUMIDA, 1980). The numerical order of the 13 pairs of the lampbrush chromosomes in *R. brevipoda, R. p. chosenica* and *R. p. fukienensis* also coincides with that in *R. nigromaculata*.

In the lampbrush chromosomes of the four pond frog species and subspecies, there are four kinds of landmarks, simple-type giant loops, compound-type giant loops, spheres and oval-like structures (Fig. 1). The simple-type giant loop is regarded as a stiff loop covered with a large quantity of matrixes along its axis and has a smooth outline. The compound-type giant loop is an aggregation formed by fusion of two or more simple-type giant loops which are more slender than the independent simple-type giant loops and has a notched outline. The sphere is usually a round body with smooth outline. However, it resembles a comma-shaped bead in the early meiotic stage. The oval-like structure is ovoid with an uneven outline. The lampbrush chromosomes maps showing the position, kind and rough size of their landmarks are shown in Fig. 2. In these maps, the relative length of each of lampbrush chromosomes Nos. 1~13 is presented by a quotient of the total length of two homologous lampbrush chromosomes divided by the total length of the 13 pairs of lampbrush chromosomes. Measurements of the lampbrush chromosomes were made in 50 oocytes and then averaged. For the sake of convenience, each lampbrush chromosome is divided into eight equal portions and the respective portions are named from bottom as follows, under-terminal, under-subterminal, under-submedian, under-median, upper-median, upper-submedian, upper-subterminal and upper-terminal regions.

II. Lampbrush chromosomes in three Asian species and one subspecies of pond frogs

1. *Rana nigromaculata*

The lampbrush chromosome map of *R. nigromaculata* is shown in Fig. 2. This map was drawn on the basis of observations made on 50 oocytes of 10 females. These oocytes were 1.6~2.0 mm, 1.83 mm on the average, in diameter.

In bivalent No. 1, the two homologous chromosomes were 174~413 μm, 304.3

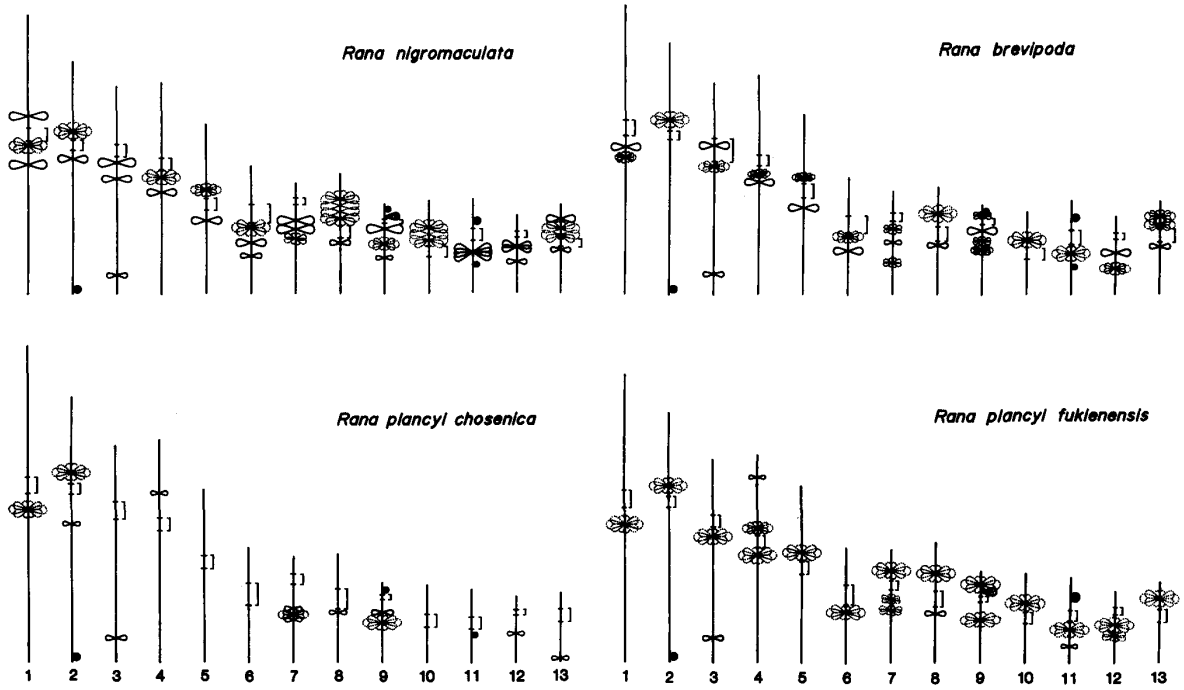

Fig. 2. Maps of the thirteen lampbrush chromosomes in three species and one subspecies of pond frogs.

Marks drawn with a solid and a dotted line represent simple- and compound-type giant loops, respectively. A black spot and a speckled symbol indicate a sphere and an oval-like structure, respectively. A pair of short horizontal bars on each chromosome indicates the segement including the centromere.

μm on the average, in length. The short segment including the centromere was situated on the upper-median region (54.8~59.2%). Each of the homologous chromosomes was characterized by possession of two simple-type loops and a compound-type giant loop. One of the simple-type giant loops was located on the upper-submedian region (63.7%) of the short arm, while the other simple-type loop and the compound-type giant loops were located on the under-median (46.5%) and upper-median (53.3%) regions of the long arm, respectively. Of these landmarks, the two simple-type giant loops were observed in all the 50 oocytes, while the compound-type giant loop was not observed in two of the five oocytes from a female. The two homologous chromosomes were connected with each other by two, three, four, five, six and seven chiasmata in two, one, eight, 23, 14 and two oocytes, respectively. The chiasmata were 5.04 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 2, the two homologous chromosomes were 118~387 μm, 253.3 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (61.7~65.9%). Each of the homologous chromosomes possessed three kinds of landmarks, a compound-type giant loop, a simple-type giant loop and a sphere. The compound-type giant loop was located on the upper-submedian region (69.6%) of the short arm. The simple-type giant loop and the sphere were

TABLE 2
Number of chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from *Rana nigromaculata*

Chromosome no.	No. of bivalents								Total no. of chiasmata	Mean no. of chiasmata
	Total	No. of chiasmata								
		1	2	3	4	5	6	7		
1	50		2	1	8	23	14	2	252	5.04
2	50		1	3	17	29			224	4.48
3	50		4	16	21	7	2		187	3.74
4	50	1		7	20	16	6		218	4.36
5	50		3	21	19	7			180	3.60
6	50	4	31	12	3				114	2.28
7	50	1	25	24					123	2.46
8	50	3	28	18	1				117	2.34
9	50	9	30	11					102	2.04
10	50	4	41	5					101	2.02
11	50	4	42	4					100	2.00
12	50	3	38	9					106	2.12
13	50	2	44	4					102	2.04
Total									1926	38.5 (30~46)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

located on the upper-median (58.2%) and the under-terminal (2.3%) regions, respectively, of the long arm. Of these landmarks, the simple-type and compound-type giant loops were found in all the oocytes, while the sphere was not found in six of the 10 oocytes from two females. The two homologous chromosomes were connected with each other by two, three, four and five chiasmata in one, three, 17 and 29 oocytes, respectively. The chiasmata were 4.48 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 3, the two homologous chromosomes were 110~339 μm, 225.6 μm on the average, in length. The short segment including the centromere was situated on the upper-submedian region (66.2~71.8%). Each of the homologous chromosomes had three simple-type giant loops which were located on the upper-submedian (63.2%), upper-median (55.8%) and under-terminal (8.7%) regions of the long arm. While the two simple-type giant loops of upper-submedian and upper-median regions were observed in all the oocytes, the remaining one was not found in two of the nine oocytes from two females. The two homologous chromosomes were connected with each other by two, three, four, five and six chiasmata in four, 16, 21, seven and two oocytes, respectively. The chiasmata were 3.74 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 4, the two homologous chromosomes were 104~360 μm, 229.7 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian

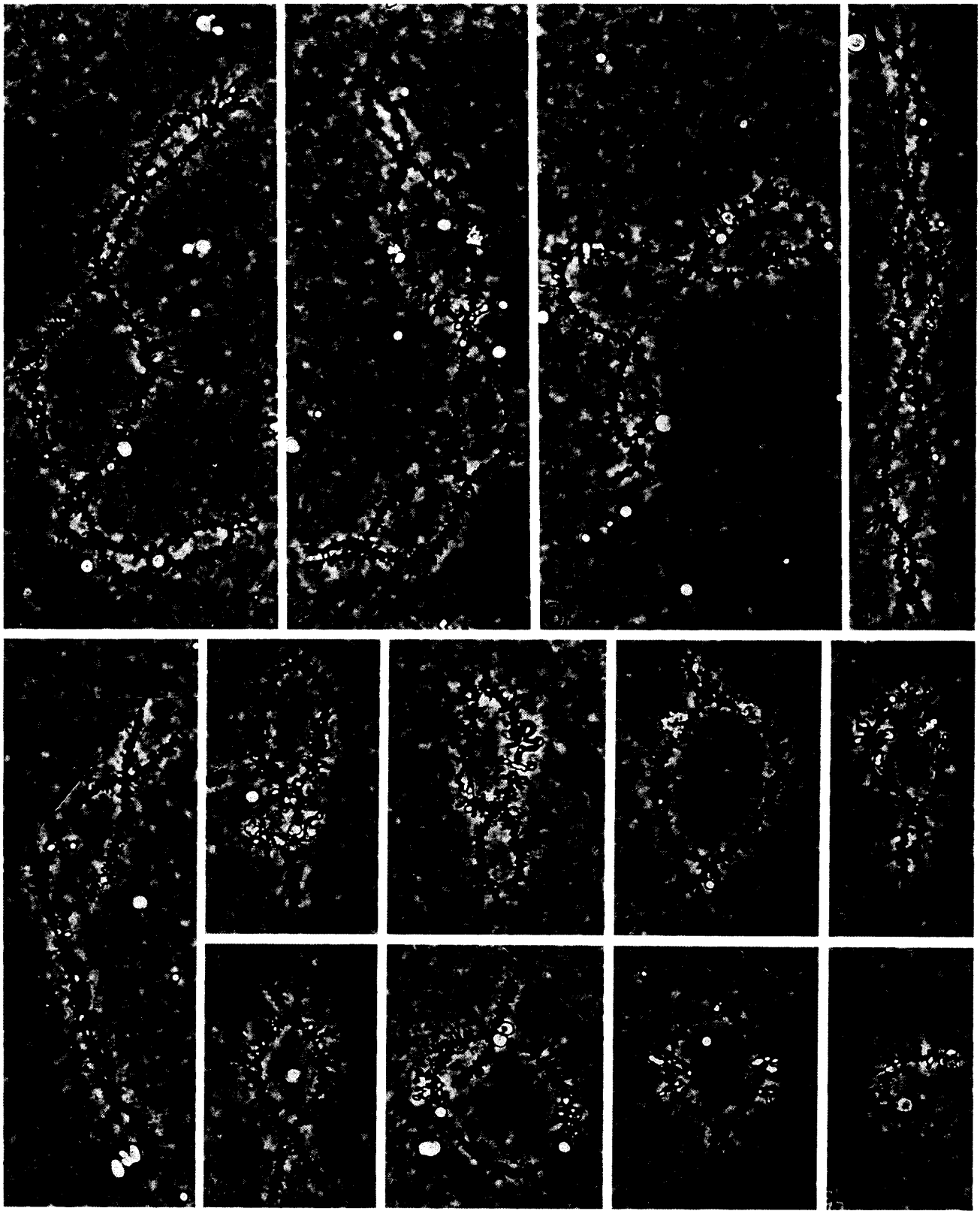

Fig. 3. Microphotographs of the thirteen lampbrush chromosomes in an oocyte of a female *Rana nigromaculata*, (N)NN♀, No. 1×(N)NN♂, No. 1. ×400

region (59.0~64.4%). Each of the homologous chromosomes had a compound-type loop and a simple-type giant loop located on the upper-median (55.4%) and the under-median (48.2%) regions, respectively, of the long arm in all the oocytes. The two homologous chromosomes were connected with each other by one, three, four, five and six chiasmata in one, seven, 20, 16 and six oocytes, respectively. The chiasmata were 4.36 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 5, the two homologous chromosomes were 84~321 μm, 183.9 μm on the average, in length. The short segment including the centromere was situated on the upper-median region (53.2~59.9%). Each of the homologous chromosomes had a compound-type loop and a simple-type giant loop. The compound-type giant loop was located on the upper-submedian region (65.5%) of the short arm, while the simple-type giant loop was located on the under-median region (46.5%) of the long arm. These landmarks were found in all the oocytes. The two homologous chromosomes were connected with each other by two, three, four and five chiasmata in three, 21, 19 and seven oocytes, respectively. The chiasmata were 3.60 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 6, the two homologous chromosomes were 73~210 μm, 139.3 μm on the average, in length. The short segment including the centromere occupied the position from the upper-median region to the upper-submedian region (55.1~69.3%). Each of the homologous chromosomes was characterized by possession of a compound-type loop and two simple-type giant loops. The compound-type giant loop was located on the upper-median region (51.1%) and the two simple-type giant loops were located on the under-median (39.9%) and the under-submedian (29.6%) regions of the long arm in all the oocytes. The simple-type giant loop on the under-median region was about two times larger in size than that on the under-submedian region. The two homologous chromosomes were connected with each other by one, two, three and four chiasmata in four, 31, 12 and three oocytes, respectively. The chiasmata were 2.28 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 7, the two homologous chromosomes were 62~186 μm, 119.7 μm on the average, in length. The short segment including the centromere was situated on the upper-subterminal region (80.7~86.8%). Each of the homologous chromosomes was characterized by possession of two simple-type loops and a compound-type giant loop. The compound-type giant loop was located on the upper-median region (54.2%) and the two simple-type giant loops were located on the upper-median (58.4%) and the upper-submedian (63.5%) regions of the long arm. The two simple-type giant loops were observed in all the oocytes, while the compound-type giant loop was not found in six of the 19 oocytes from four females. The two homologous chromosomes were connected with each other by one, two and three chiasmata in one, 25 and 24 oocytes, respectively. The chiasmata were 2.46 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 8, the two homologous chromosomes were 69~209 μm, 130.2 μm on the average. The short segment including the centromere was situated on the position from the under-median region to the upper-median region (46.5

~56.4%). Each of the homologous chromosomes possessed a compound-type loop and a simple-type giant loop in all the oocytes. The compound-type giant loop was located on the position from the upper-submedian region to the upper-subterminal region (62.5~78.0%) of the short arm. This giant loop was composed of very numerous constituent loops. The simple-type giant loop was located on the under-median region (41.9%) of the long arm. The two homologous chromosomes were connected with each other by one, two, three and four chiasmata in three, 28, 18 and one oocytes, respectively. The chiasmata were 2.34 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 9, the two homologous chromosomes were 55~142 μm, 97.0 μm on the average, in length. The short segment including the centromere was situated on the upper-subterminal region (78.4~82.2%). Each of the homologous chromosomes was characterized by possessing all the four kinds of landmarks, a sphere, an oval-like structure, two simple-type giant loops and a compound-type giant loop. The sphere and the oval-like structure were located on the upper-terminal (93.1%) and the upper-subterminal (85.5%) regions of the short arm, respectively. The two simple-type giant loops were located on the upper-submedian (71.6%) and the under-median (46.2%) regions of the long arm, while the compound-type giant loop was located on the upper-median region (55.1%) of the long arm. Of the two simple-type giant loops, the lower one was conspicuously smaller than the upper one. Of these landmarks, the sphere, the oval-like structure and the lower simple-type giant loop were not found in 17 of the 25 oocytes from five females, in six of the 14 oocytes from three females and in 16 of the 24 oocytes from five females, respectively. The remaining landmarks were observed in all the oocytes. The two homologous chromosomes were connected with each other by one, two and three chiasmata in nine, 30 and 11 oocytes, respectively. The chiasmata were 2.04 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 10, the two homologous chromosomes were 62~135 μm, 99.9 μm on the average, in length. The short segment including the centromere was situated on the position from the under-median region to the upper-median region (41.2~52.3%). Each of the homologous chromosomes had a compound-type giant loop located on the position from the upper-median region to the upper-submedian region (52.3~70.0%) of the short arm in all the oocytes. This giant loop was composed of very numerous constituent loops. The two homologous chromosomes were connected with each other by one, two and three chiasmata in four, 41 and five oocytes, respectively. The chiasmata were 2.02 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 11, the two homologous chromosomes were 55~141 μm, 102.2 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (55.2~67.8%). Each of the homologous chromosomes was characterized by possession of simple-type giant loops and two spheres. The simple-type giant loops were constructed with three giant loops and were located on the same

position of the under-median region (42.9%) in the long arm in all the oocytes. One of the two spheres was found on the upper-subterminal region (76.3%) of the short arm, while the other sphere was found on the under-submedian region (29.8%) of the long arm. While the sphere located on the upper-subterminal region was found in all the oocytes, that located on the under-submedian region was not observed in 24 of the 29 oocytes from six females. The two homologous chromosomes were connected with each other by one, two and three chiasmata in four, 42 and four oocytes, respectively. The chiasmata were 2.00 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 12, the two homologous chromosomes were 45~101 μm, 83.8 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-submedian region to the upper-subterminal region (72.9~79.8%). Each of the homologous chromosomes was characterized by possession of simple-type giant loops on the two sites of long arm in all the oocytes. The two sites were the upper-median (60.5%) and the under-median (40.8%) regions. The simple-type giant loops of the former were constructed with two giant loops, while that of the latter was single. The two homologous chromosomes were connected with each other by one, two and three chiasmata in three, 38 and nine oocytes, respectively. The chiasmata were 2.12 on the average in frequency (Table 2; Fig. 3).

In bivalent No. 13, the two homologous chromosomes were 52~157 μm, 95.4 μm on the average, in length. The short segment including the centromere was situated on the upper-median region (52.8~61.9%). Each of the homologous chromosomes was characterized by possession of two simple-type loops and a compound-type giant loop. One of the simple-type giant loops and the compound-type giant loop were located on the upper-subterminal (83.6%) and the upper-submedian (63.7~73.2%) regions, respectively, of the short arm. The other simple-type giant loop was located on the under-median region (49.6%) of the long arm. Of these landmarks, the simple-type giant loop located on the under-median region and the compound-type giant loop were not observed in 14 of the 24 oocytes from five females and in four oocytes from a female, respectively. The remaining landmark was observed in all the oocytes. The two homologous chromosomes were connected with each other by one, two and three chiasmata in two, 44 and four oocytes, respectively. The chiasmata were 2.04 on the average in frequency (Table 2; Fig. 3).

From the foregoing descriptions, it was found that the 13 bivalents can be distinguished without fail from one another by the chromosome length, the position of the short segment and the position, kind and number of landmarks. It was also found that all the 50 oocytes contained 13 bivalents whose homologous chromosomes were connected with each other by 30 to 46 chiasmata, 38.5 chiasmata on the average, in total (Table 2).

2. *Rana brevipoda*

The lampbrush chromosome map of *R. brevipoda* is shown in Fig. 2. This map

was drawn on the basis of observations on 50 oocytes of 11 females. These oocytes were 1.3~1.6 mm, 1.47 mm on the average, in diameter.

In bivalent No. 1, the two homologous chromosomes were 163~530 μm, 310.9 μm on the average, in length. The short segment including the centromere was situated on the upper-median region (54.7~60.1%). Each of the homologous chromosomes was characterized by possession of a simple-type loop and a compound-type giant loop. These two giant loops were located on the upper-median (50.7%) and the under-median (47.5%) regions of the long arm, respectively, in all the 50 oocytes. While the short segment was situated almost at the same position as that of *R. nigromaculata,* the two giant loops differed in position from those of *R. nigromaculata.* The two homologous chromosomes were connected with each other by one, three, four, five, six, seven, eight and nine chiasmata in one, seven, 13, 15, nine, three, one and one oocytes, respectively. The chiasmata were 4.82 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 2, the two homologous chromosomes were 115~465 μm, 268.8 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (61.7~65.3%) like that of *R. nigromaculata.* Each of the homologous chromosomes was characterized by possession of a compound-type giant loop located on the upper-submedian region (69.7%) of the short arm and a sphere

TABLE 3
Number of chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from *Rana brevipoda*

Chromosome no.	No. of bivalents										Total no. of chiasmata	Mean no. of chiasmata
	Total	No. of chiasmata										
		1	2	3	4	5	6	7	8	9		
1	50	1		7	13	15	9	3	1	1	241	4.82
2	50		2	4	18	13	9	4			235	4.70
3	50		1	15	17	13	3	1			205	4.10
4	50		1	13	21	9	5	1			207	4.14
5	50		3	18	24	5					181	3.62
6	50		30	18	2						122	2.44
7	50	3	30	15	2						116	2.32
8	50	3	33	11	3						114	2.28
9	50	12	25	13							101	2.02
10	50	2	37	11							109	2.18
11	50	5	37	6	2						105	2.10
12	50	8	37	5							97	1.94
13	50	6	36	8							102	2.04
Total											1935	38.7 (31~53)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

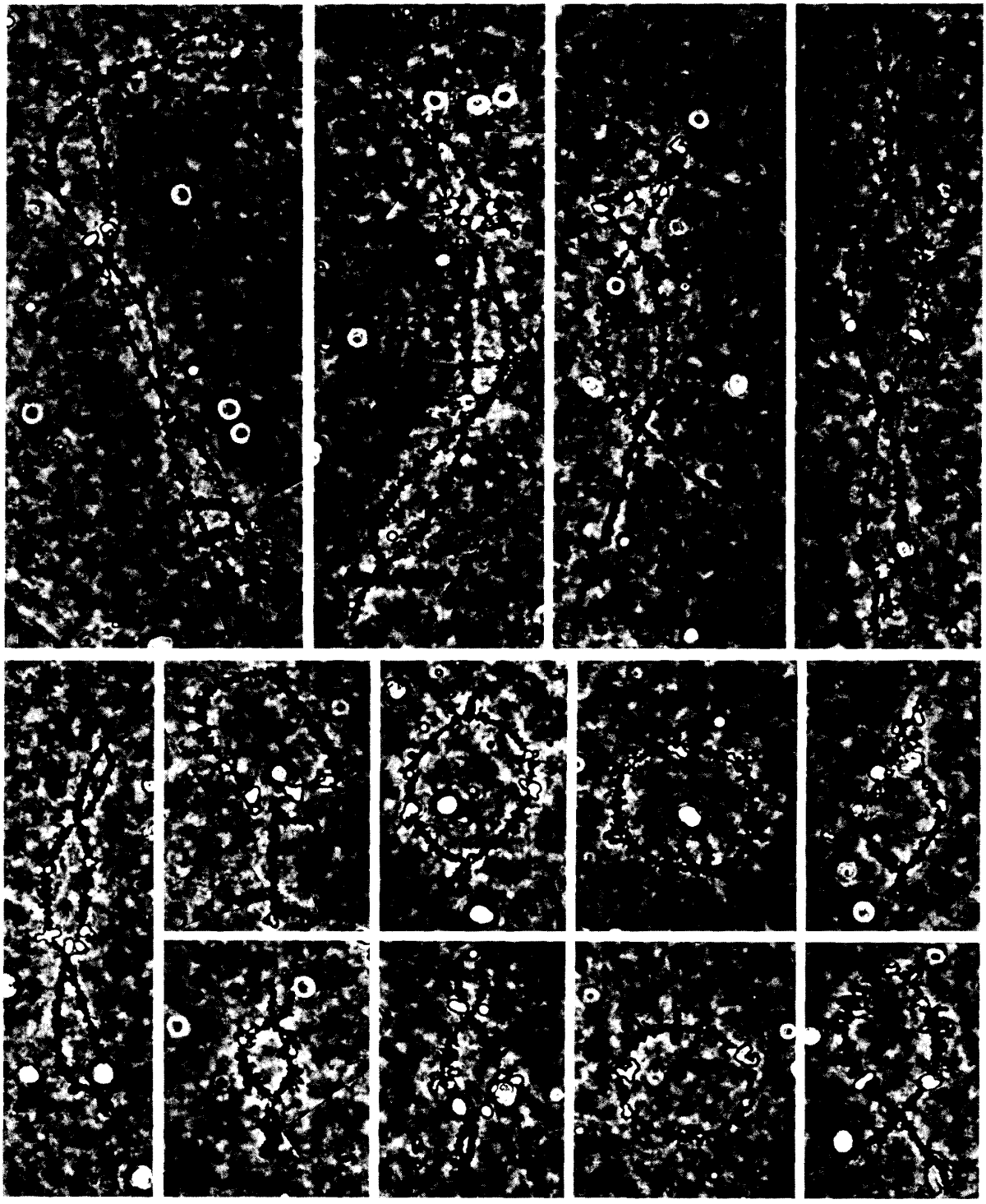

Fig. 4. Microphotographs of the thirteen lampbrush chromosomes in an oocyte of a female *Rana brevipoda*, (B) BB♀, No. 1×(B)BB♂, No. 1. ×400

located on the under-terminal region (2.3%) of the long arm. These two kinds of landmarks were similar in position to those of *R. nigromaculata*. The compound-type giant loop was found in all the oocytes, while the sphere was not found in two of the nine oocytes from two females. The two homologous chromosomes were connected with each other by two, three, four, five, six and seven chiasmata in

two, four, 18, 13, nine and four oocytes, respectively. The chiasmata were 4.70 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 3, the two homologous chromosomes were 108~372 μm, 227.1 μm on the average, in length. The short segment including the centromere was situated on the upper-submedian region (62.6~73.7%) like that of *R. nigromaculata*. Each of the homologous chromosomes possessed two simple-type loops and a compound-type giant loop. One of the simple-type giant loops was located on the upper-submedian region (70.5%) of the short arm and found in the range of the short segment. The compound-type giant loop was located on the upper-median region (60.8%) of the long arm, being adjacent to the short segment. These two giant loops were not observed on the same positions of *R. nigromaculata*. The other simple-type giant loop was located on the under-terminal region (9.6%) and seemed to be homologous with that of *R. nigromaculata*. While the simple-type giant loop located on the upper-submedian region and the compound-type giant loop were observed in all the oocytes, the remaining simple-type giant loop was not observed in two of the four oocytes of a female. The two homologous chromosomes were connected with each other by two, three, four, five, six and seven chiasmata in one, 15, 17, 13, three and one oocytes, respectively. The chiasmata were 4.10 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 4, the two homologous chromosomes were 118~377 μm, 234.5 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (58.9~64.2%) like that of *R. nigromaculata*. Each of the homologous chromosomes was characterized by possession of a compound-type loop and a simple-type giant loop near the short segment. These two giant loops were located on the upper-median region 55.1% and 50.9%, respectively, of the long arm. Bivalent No. 4 was very similar in feature to that of *R. nigromaculata*, although the compound-type giant loop was smaller in size and fewer in number of the constituent loops than that of *R. nigromaculata*. While the simple-type giant loop was located in all the oocytes, the compound-type giant loop was not found in six of the 28 oocytes from six females. The two homologous chromosomes were connected with each other by two, three, four, five, six and seven chiasmata in one, 13, 21, nine, five and one oocytes, respectively. The chiasmata were 4.14 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 5, the two homologous chromosomes were 97~284 μm, 192.0 μm on the average, in length. The short segment including the centromere was situated on the upper-median region (53.9~61.5%) like that of *R. nigromaculata*. Each of the homologous chromosomes was characterized by possession of a compound-type loop and a simple-type giant loop. These two giant loops were located on the upper-submedian region (65.0%) of the short arm and on the under-median region (48.1%) of the long arm, respectively. Bivalent No. 5 was

very similar in feature to that of *R. nigromaculata,* although the compound-type giant loop was smaller than that of *R. nigromaculata.* These two giant loops were observed in all the oocytes. The two homologous chromosomes were connected with each other by two, three, four and five chiasmata in three, 18, 24 and five oocytes, respectively. The chiasmata were 3.62 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 6, the two homologous chromosomes were 52~255 μm, 125.5 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (53.1~66.8%) like that of *R. nigromaculata.* Each of the homologous chromosomes possessed a compound-type loop and a simple-type giant loop. These two giant loops were located on the under-median regions, 49.7% and 39.1%, respectively, of the long arm in all the oocytes. They were similar in position to those of *R. nigromaculata.* The two homologous chromosomes were connected with each other by two, three and four chiasmata in 30, 18 and two oocytes, respectively. The chiasmata were 2.44 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 7, the two homologous chromosomes were 49~170 μm, 110.1 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-submedian region to the upper-subterminal region (71.8~79.0%). This position slightly differed from that of *R. nigromaculata.* There were two compound-type giant loops on the upper-median (60.8%) and the under-submedian (31.6%) regions and a simple-type giant loop on the upper-median region (51.0%) in each of the homologous chromosomes. This chromosome remarkably differed in feature from that of *R. nigromaculata.* Of the three giant loops, the compound-type giant loop in the under-submedian region and the simple-type giant loop were found in all the oocytes, while the remaining compound-type giant loop was not found in 25 of the 30 oocytes from seven females. The two homologous chromosomes were connected with each other by one, two, three and four chiasmata in three, 30, 15 and two oocytes, respectively. The chiasmata were 2.32 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 8, the two homologous chromosomes were 60~218 μm, 115.0 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (50.5~63.9%). This position was about the same as that of *R. nigromaculata.* Each of the homologous chromosomes was characterized by possession of a compound-type loop and a simple-type giant loop. These two giant loops were located on the upper-submedian region (74.8%) of the short arm and on the under-median region (46.8%) of the long arm, respectively. This chromosome was quite similar in feature to that of *R. nigromaculata,* although the compound-type

giant loop was composed of fewer constituent loops. While the compound-type giant loop was found in all the oocytes, the simple-type giant loop was not found in 22 of the 26 oocytes from six females. The two homologous chromosomes were connected with each other by one, two, three and four chiasmata in three, 33, 11 and three oocytes, respectively. The chiasmata were 2.28 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 9, the two homologous chromosomes were 44~161 μm, 96.1 μm on the average, in length. The short segment including the centromere was situated on the upper-subterminal region (79.4~83.9%) like that of *R. nigromaculata*. This chromosome possessed the largest number of landmarks in *R. brevipoda*. There were a sphere and a compound-type giant loop on the upper-terminal (92.3%) and the upper-subterminal (87.3%) regions, respectively, of the short arm. On the upper-median (61.0%) and the under-median (49.3%) regions of the long arm, there were two compound-type giant loops and, moreover, there was a simple-type giant loop on the upper-submedian region (72.1%) of the long arm. Of these landmarks, the sphere, simple-type giant loop and compound-type giant loop on the upper-median region were similar in position to those of *R. nigromaculata*. However, the constituent loops of the compound-type giant loop were fewer and more slender than those of *R. nigromaculata*. While the compound-type giant loop on the upper-median region and that on the upper-subterminal region were not found in six of the 12 oocytes from three females and in 10 of the 23 oocytes from five females, respectively, the remaining landmarks were always observed in all the oocytes. The two homologous chromosomes were connected with each other by one, two and three chiasmata in 12, 25 and 13 oocytes, respectively. The chiasmata were 2.02 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 10, the two homologous chromosomes were 40~155 μm, 89.1 μm on the average, in length. The short segment including the centromere was situated from the under-median region to the upper-median region (43.9~57.8%) like that of *R. nigromaculata*. Each of the homologous chromosomes was characterized by possession of a compound-type giant loop located on the upper-submedian region (66.0%) of the short arm. This compound-type giant loop was found in all the oocytes and very similar in position to that of *R. nigromaculata*, although the constituent loops were fewer than those of the latter species. The two homologous chromosomes were connected with each other by one, two and three chiasmata in two, 37 and 11 oocytes, respectively. The chiasmata were 2.18 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 11, the two homologous chromosomes were 51~190 μm, 101.4 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (54.1~68.8%) like that of *R. nigromaculata*. Each of the homologous

chromosomes was characterized by possession of a compound-type giant loop and two spheres. The compound-type giant loop was located on the under-median region (44.3%) of the long arm and the two spheres were located on the upper-subterminal region (79.8%) of the short arm and on the under-submedian region (30.1%) of the long arm. These landmarks were the same in position as those of *R. nigromaculata* except that the compound-type giant loop was replaced with the simple-type giant loops. While the compound-type giant loop and the sphere on the upper-subterminal region were found in all the oocytes, the remaining sphere was not found in 24 of the 32 oocytes from seven females. The two homologous chromosomes were connected with each other by one, two, three and four chiasmata in five, 37, six and two oocytes, respectively. The chiasmata were 2.10 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 12, the two homologous chromosomes were 50~156 μm, 84.0 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-submedian region to the upper-subterminal region (71.6~79.3%). This position was about the same as that of *R. nigromaculata*. Each of the homologous chromosomes was characterized by possession of a simple-type loop and a compound-type giant loop. These two giant loops were located on the upper-median (54.8%) and the under-submedian (33.5%) regions of the long arm, respectively, in all the oocytes. The two homologous chromosomes were connected with each other by one, two and three chiasmata in eight, 37 and five oocytes, respectively. The chiasmata were 1.94 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

In bivalent No. 13, the two homologous chromosomes were 50~186 μm, 99.2 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (56.9~70.8%) like that of *R. nigromaculata*. Each of the homologous chromosomes was characterized by possession of a compound-type loop and a simple-type giant loop. These two giant loops were located on the position from the upper-submedian region to the upper-subterminal region (73.9~84.5%) of the short arm and on the upper-median region (51.7%) of the long arm, respectively, in all the oocytes. They were similar in position to those of *R. nigromaculata*. The two homologous chromosomes were connected with each other by one, two and three chiasmata in six, 36 and eight oocytes, respectively. The chiasmata was 2.04 on the average in frequency. This mean value was statistically identical with that of *R. nigromaculata* at the 5% level (Table 3; Fig. 4).

From the foregoing descriptions, it was found that the 13 bivalents can be distinguished without fail from one another by the chromosome length, the position of the short segment and the position, kind and number of landmarks. It was also found that all the 50 oocytes contained 13 bivalents whose homologous chromosomes were connected with each other by 31 to 53 chiasmata, 38.7 chiasmata on the average, in total. This mean value was statistically identical

with that of *R. nigromaculata* at the 5% level (Table 3).

3. *Rana plancyi chosenica*

The lampbrush chromosome map of *R. p. chosenica* is shown in Fig. 2. This map was drawn on the basis of observations on 50 oocytes of eight females. These oocytes were 1.3~1.7 mm, 1.42 mm on the average, in diameter. The lampbrush chromosomes of *R. p. chosenica* possessed the fewest number of landmarks among those of the four pond frog species and subspecies.

In bivalent No. 1, the two homologous chromosomes were 195~406 μm, 311.1 μm on the average, in length. The short segment including the centromere was situated on the upper-median region (53.0~58.3%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes had only one compound-type giant loop on the under-median region (48.1%) of the long arm. This giant loop was similar in position to that of *R. brevipoda*, although its constituent loops were more numerous than those of the latter species. It was always found in the homologous chromosomes of bivalent No. 1 of all the oocytes. The two homologous chromosomes were connected with each other by four, five, six, seven and eight chiasmata in two, 13, 21, 12 and two oocytes, respectively. The chiasmata were 5.98 on the average in frequency. This mean value statistically differed from the 5.04 in *R. nigromaculata* and the 4.82 in *R. brevipoda* at the 5% level (Table 4; Fig. 5).

TABLE 4
Number of chiasmata in each of the 13 pares of homologous chromosomes in 50 oocytes from *Rana plancyi chosenica*

Chromosome no.	No. of bivalents									Total no. of chiamata	Mean no. of chiasmata
	Total	No. of chiasmata									
		1	2	3	4	5	6	7	8		
1	50				2	13	21	12	2	299	5.98
2	50		1	2	11	21	12	3		250	5.00
3	50			10	21	14	4	1		215	4.30
4	50			1	21	23	5			232	4.64
5	50		1	7	26	15	1			208	4.16
6	50		26	21	2	1				128	2.56
7	50		17	29	4					137	2.74
8	50	1	36	12	1					113	2.26
9	50	2	23	25						123	2.46
10	50		48	2						102	2.04
11	50		46	4						104	2.08
12	50	2	33	15						113	2.26
13	50	3	41	6						103	2.06
Total										2127	42.5 (35~52)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

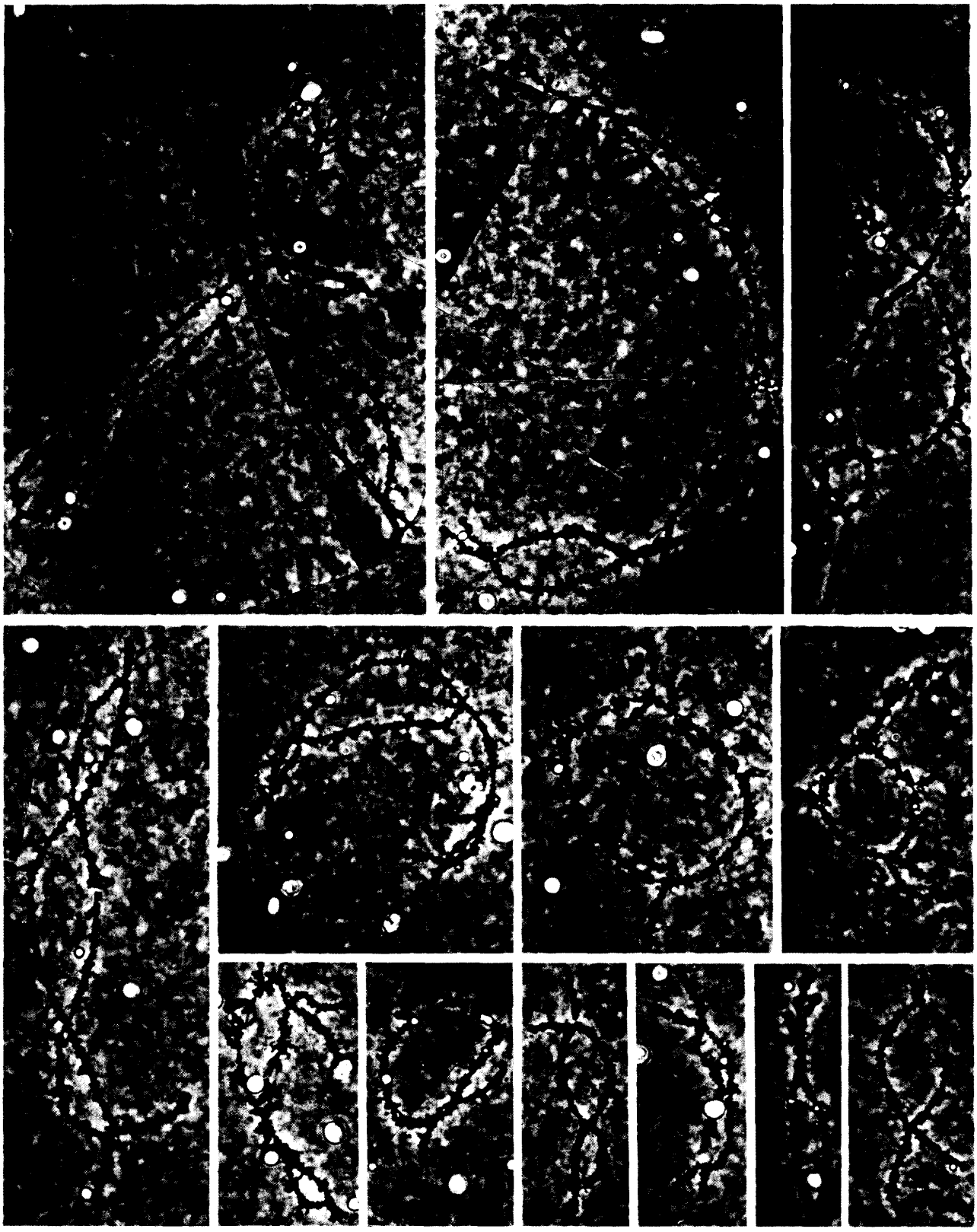

Fig. 5. Microphotographs of the thirteen lampbrush chromosomes in an oocyte of a female *Rana plancyi chosenica*, (C)CC♀, No. 1×(C)CC♂, No. 1. ×400

In bivalent No. 2, the two homologous chromosomes were 160~338 μm, 258.9 μm on the average, in length. The short segment including the centromere was situated on the upper-submedian region (63.5~67.4%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes was characterized by possession of a compound-type giant loop, a simple-type giant loop and a sphere. The compound-type giant loop was located on the upper-submedian region (71.7%) of the short arm. The simple-type giant loop and the sphere were located on the upper-median (52.2%) and the under-terminal (1.8%) regions of the long arm, respectively. The compound-type giant loop and the sphere were similar in position to those of *R. nigromaculata* and *R. brevipoda* and constituent loops of the former were the fewest among those of the four pond frog species and subspecies. These three landmarks were always observed in the homologous chromosomes of bivalent No. 2 of all the oocytes. The two homologous chromosomes were connected with each other by two, three, four, five, six and seven chiasmata in one, two, 11, 21, 12 and three oocytes, respectively. The chiasmata were 5.00 on the average in frequency. This mean value statistically differed from the 4.48 of *R. nigromaculata,* while it did not statistically differ from the 4.70 of *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 3, the two homologous chromosomes were 114~267 μm, 211.9 μm on the average, in length. The short segment including the centromere was situated on the upper-submedian region (65.8~73.6%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes was characterized by possession of a simple-type giant loop located on the under-terminal region (10.7%) of the long arm. This giant loop was similar in position to those of the foregoing two species and found in all the oocytes. The two homologous chromosomes were connected with each other by three, four, five, six and seven chiasmata in 10, 21, 14, four and one oocytes, respectively. The chiasmata were 4.30 on the average in frequency. This mean value statistically differed from the 3.74 of *R. nigromaculata,* while it was statistically equal to the 4.10 of *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 4, the two homologous chromosomes were 126~292 μm, 217.1 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (59.4~65.2%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes was characterized by possession of a simple-type giant loop located on the upper-subterminal region (77.8%) of the short arm. This landmark was not found in 19 of the 41 oocytes from six females. The two homologous chromosomes were connected with each other by three, four, five and six chiasmata in one, 21, 23 and five oocytes, respectively. The chiasmata were 4.64 on the average in frequency. This mean value differed from the 4.14 of *R. brevipoda,* while it was equal to the 4.36 of *R. nigromaculata* at a statistically significant level (Table 4; Fig. 5).

In bivalent No. 5, the two homologous chromosomes were 89~236 μm, 169.3 μm on the average, in length. The short segment including the centromere was

situated on the upper-median region (54.2~61.9%) like those of *R.nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes possessed no landmark. The two homologous chromosomes were connected with each other by two, three, four, five and six chiasmata in one, seven, 26, 15 and one oocytes, respectively. The chiasmata were 4.16 on the average in frequency. This mean value statistically differed from the 3.60 of *R. nigromaculata* and the 3.62 of *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 6, the two homologous chromosomes were 64~147 μm, 112.9 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (50.7~68.5%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes possessed no landmark like chromosome No. 5. The two homologous chromosomes were connected with each other by two, three, four and five chiasmata in 26, 21, two and one oocytes, respectively. The chiasmata were 2.56 on the average in frequency. This mean value statistically differed from the 2.28 of *R. nigromaculata,* while it did not statsitically differed from 2.44 of *R. breviponda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 7, the two homologous chromosomes were 57~139 μm, 103.8 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-submedian region to the upper-subterminal region (74.3~83.5%). This position was roughly the same as those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes was characterized by possession of two simple-type loops and a compound-type giant loop. The two simple-type giant loops were located on the under-median (41.0%) and the upper-median (52.4%) regions of the long arm, while the compound-type giant loop was located on the under-median region (47.0%) between the two simple-type giant loops. Of the three giant loops, the compound-type giant loop and the simple-type giant loop on the under-median region were found in all the oocytes, while the remaining simple-type giant loop was not found in 28 of the 50 oocytes. The two homologous chromosomes were connected with each other by two, three and four chiasmata in 17, 29 and four oocytes, respectively. The chiasmata were 2.74 on the average in frequency. This mean value statistically differed from the 2.46 of *R. nigromaculata* and the 2.32 of *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 8, the two homologous chromosomes were 66~147 μm, 105.9 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (50.4~67.6%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes possessed a simple-type giant loop on the under-median region (48.4%) of the long arm. The simple-type giant loop was a common landmark found in *R. nigromaculata* and *R. brevipoda,* too, although this was not found in 28 of the 39 oocytes from six females. The two homologous chromosomes were connected with each other by one, two, three and four chiasmata in one, 36, 12 and one oocytes, respectively. The chiasmata were 2.26 on the

average in frequency. This mean value did not statistically differ from those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 9, the two homologous chromosomes were 47~101 μm, 78.3 μm on the average, in length. The short segment including the centromere was situated on the upper-subterminal region (79.3~85.2%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes was characterized by possession of a sphere, a simple-type giant loop and a compound-type giant loop. The sphere was located on the upper-terminal region (89.4%) of the short arm and was similar in position to those of *R. nigromaculata* and *R. brevipoda*. The simple-type giant loop was located on the upper-submedian region (64.3%) of the long arm. The compound-type giant loop was located on the upper-median region (51.3%) of the long arm and was similar in position to that located on the under-median region in *R. brevipoda*. Of these landmarks, the sphere and the simple-type giant loop were not found in three and all of the seven oocytes from a female, respectively. Moreover, the simple-type giant loop was not found in one of the homologous chromosomes of all the 21 oocytes from three females. The compound-type giant loop was observed in all the oocytes. The two homologous chromosomes were connected with each other by one, two and three chiasmata in two, 23 and 25 oocytes, respectively. The chiasmata were 2.46 on the average in frequency. This mean value statistically differed from the 2.04 of *R. nigromaculata* and the 2.02 of *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 10, the two homologous chromosomes were 43~103 μm, 75.7 μm on the average, in length. The short segment including the centromere was situated on the position from the under-median region to the upper-submedian region (44.9~65.2%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes possessed no landmark. The two homologous chromosomes were connected with each other by two and three chiasmata in 48 and two oocytes, respectively. The chiasmata were 2.04 on the average in frequency. This mean value was statistically identical to those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 11, the two homologous chromosomes were 43~101 μm, 72.2 μm on the average, in length. The short segment including the centromere was situated on the position from the under-median region to the upper-submedian region (44.2~63.6%) and about the same in position as those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes was characterized by possession of a sphere located on the under-submedian region (36.9%) of the long arm. The sphere was similar in position to those of *R. nigromaculata* and *R. brevipoda*, although this was not found in seven of the 18 oocytes from three females. The two homologous chromosomes were connected with each other by two and three chiasmata in 46 and four oocytes, respectively. The chiasmata were 2.08 on the average in frequency. This mean value did not statistically differ from those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 4; Fig. 5).

In bivalent No. 12, the two homologous chromosomes were 38~90 μm, 65.3 μm

on the average, in length. The short segment including the centromere was situated on the position from the upper-submedian region to the upper-subterminal region (73.0~81.3%) like those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes possessed a simple-type giant loop on the under-median region (41.6%) in all the oocytes. This giant loop was similar in position to that located on the under-median region in *R. nigromaculata*. The two homologous chromosomes were connected with each other by one, two and three chiasmata in two, 33 and 15 oocytes, respectively. The chiasmata were 2.26 on the average in frequency. This mean value statistically differed from the 1.94 of *R. brevipoda*, while statistically identical to the 2.12 of *R. nigromaculata* at the 5% level (Table 4; Fig. 5).

In bivalent No. 13, the two homologous chromosomes were 39~94 μm, 68.7 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-subterminal region (59.2~77.0%). This position was nearly the same as those of *R. nigromaculata* and *R. brevipoda*. Each of the homologous chromosomes was characterized by possession of a simple-type giant loop located on the under-terminal region (3.8%). This giant loop was not found in 18 of the 50 oocytes. The two homologous chromosomes were connected with each other by one, two and three chiasmata in three, 41 and six oocytes, respectively. The chiasmata were 2.06 on the average in frequency. This mean value was statistically equal to those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 4; Fig. 5).

From the foregoing observations, it was found that the 13 bivalents can be discriminated without fail from one another by the chromosome length, the position of the short segment and the position, kind and number of landmarks. It was also found that all the 50 oocytes contained 13 bivalents whose homologous chromosomes were connected with each other by 35 to 52 chiasmata, 42.5 chiasmata on the average, in total. This chiasma frequency per oocyte statistically differed from the 38.5 of *R. nigromaculata* and the 38.7 of *R. brevipoda* at the 5% level (Table 4).

4. *Rana plancyi fukienensis*

The lampbrush chromosome map of *R. p. fukienensis* is shown in Fig. 2. This map was drawn on the basis of observations on 50 oocytes of eight females. These oocytes were 1.3~1.5 mm, 1.38 mm on the average, in diameter. Each of the lampbrush chromosomes of this species had one to three landmarks. There were 25 landmarks, consisting of 18 compound-type giant loops, four simple-type giant loops, two spheres and one oval-like structure in the 13 lampbrush chromosomes. In this species, the compound-type giant loops remarkably differed in character from those of the other species and subspecies. They were very often united with one another among the members of homologous and heterologous sites and were collected into some groups, although those of the other species and subspecies were never united among those of heterologous sites.

In bivalent No. 1, the two homologous chromosomes were 198~399 μm, 314.8

μm on the average, in length. The short segment including the centromere was situated on the upper-median region (53.8~59.5%) like those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of a compound-type giant loop. This giant loop was located on the under-median region (48.0%) of the long arm and was about the same in position as those of *R. brevipoda* and *R. p. chosenica*. However, its constituent loops were more abundant in number than those of *R. brevipoda* and *R. p. chosenica*. The two homologous chromosomes were connected with each other by four, five, six and seven chiasmata in 12, 20, 17 and one oocytes, respectively. The chiasmata were 5.14 on the average in frequency. This mean value statistically differed from the 5.98 of *R. p. chosenica*, while it was statistically identical to those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5; Fig. 6).

In bivalent No. 2, the two homologous chromosomes were 188~352 μm, 272.6 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (61.9~66.1%) like those of the other species and subspecies. Each of the homologous chromosomes possessed a compound-type giant loop on the upper-submedian region (70.3%) of the short arm and a sphere on the under-terminal region (2.2%) of the long arm. These landmarks were similar in position to those of the other species and subspecies. The two homologous chromosomes were connected with each other by three, four, five and six chiasmata in four, 18, 24 and four oocytes, respectively. The chiasmata were 4.56 on the average in frequency.

TABLE 5

Number of chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from *Rana plancyi fukienensis*

Chromosome no.	No. of bivalents								Total no. of chiasmata	Mean no. of chiasmata
	Total	No. of chiasmata								
		1	2	3	4	5	6	7		
1	50				12	20	17	1	257	5.14
2	50			4	18	24	4		228	4.56
3	50		3	18	25	4			180	3.60
4	50		1	8	25	16			206	4.12
5	50		1	22	22	5			181	3.62
6	50		38	12					112	2.24
7	50	2	28	20					118	2.36
8	50	2	41	7					105	2.10
9	50	1	30	19					118	2.36
10	50	3	37	9	1				108	2.16
11	50	4	41	5					101	2.02
12	50	3	42	5					102	2.04
13	50	9	39	2					93	1.86
Total									1909	38.2 (33~44)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

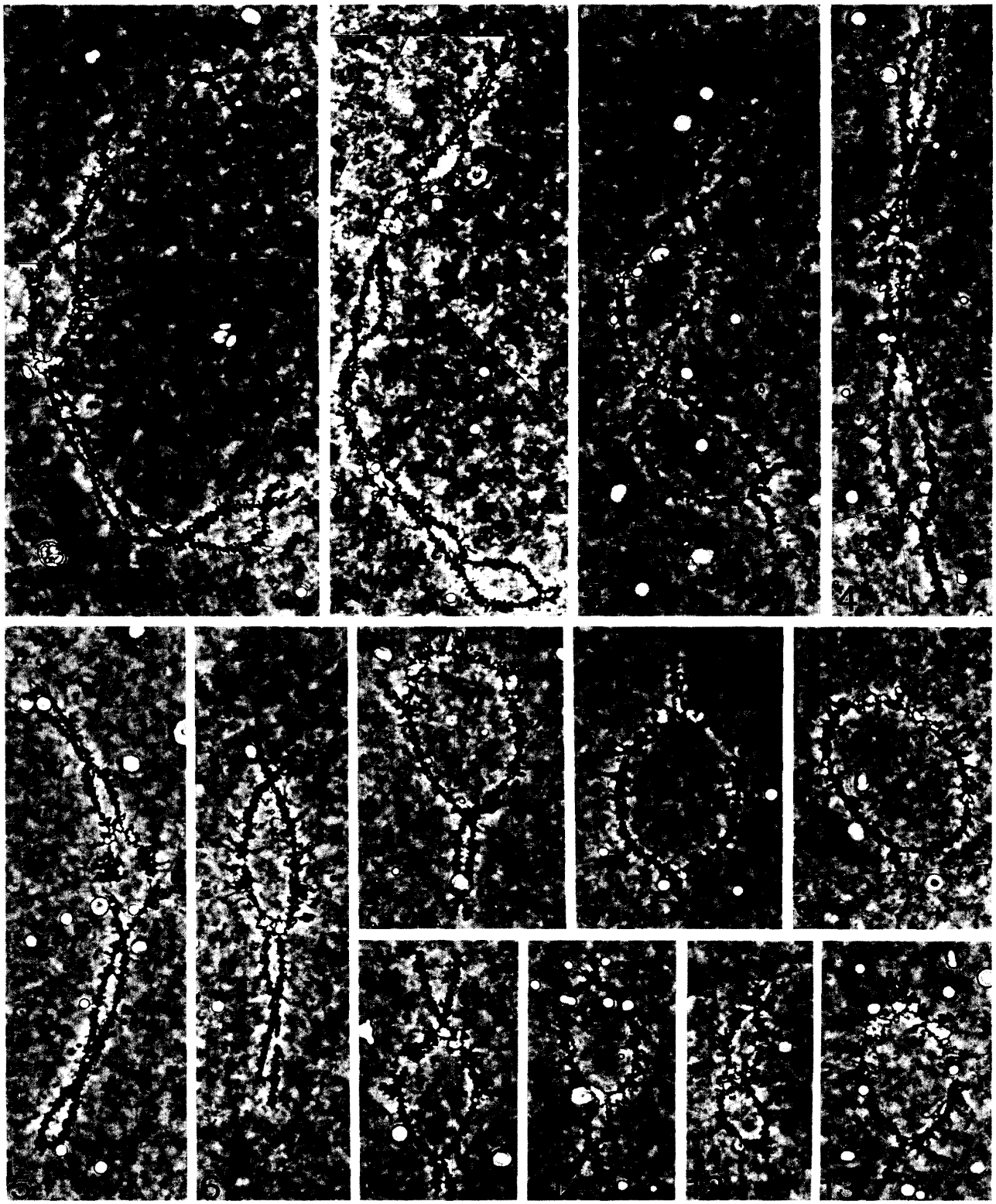

Fig. 6. Microphotographs of the thirteen lampbrush chromosomes in the oocytes of a female *Rana plancyi fukienensis*, (F)FF♀, No. 1×(F)FF♂, No. 1. ×350

This mean value statistically differed from the 5.00 of *R. p. chosenica*, while it was statistically identical with those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5; Fig. 6).

In bivalent No. 3, the two homologous chromosomes were 170~265 μm, 222.4 μm on the average, in length. The short segment including the centromere was situated on the upper-submedian region (66.6~72.5%) like those of the other species and subspecies. Each of the homologous chromosomes possessed a compound-type loop and a simple-type giant loop on the upper-median (61.7%) and the under-terminal (11.7%) regions, respectively, of the long arm. The compound-type giant loop was similar in position to that of *R. brevipoda* and the simple-type giant loop was similar in position to those of the other species and subspecies. The simple-type giant loop was not found in four of the 11 oocytes from two females. The two homologous chromosomes were connected with each other by two, three, four and five chiasmata in three, 18, 25 and four oocytes, respectively. The chiasmata were 3.60 on the average in frequency. This mean value statistically differed from the 4.10 of *R. brevipoda* and the 4.30 of *R. p. chosenica,* while it was statistically identical to that of *R. nigromaculata* at the 5% level (Table 5; Fig. 6).

In bivalent No. 4, the two homologous chromosomes were 165~334 μm, 226.5 μm on the average, in length. The short segment including the centromere was situated on the upper-median region (55.4~60.9%) like those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of a simple-type giant loop and two compound-type giant loops. The two compound-type giant loops were located on the upper-submedian region (64.7%) of the short arm and the upper-median region (51.6%) of the long arm. Of these two giant loops, the latter was similar in position to those of *R. nigromaculata* and *R. brevipoda.* The simple-type giant loop was located on the upper-subterminal region (84.6%) of the short arm. This simple-type giant loop was not found in two of the 13 oocytes from two females. The two homologous chromosomes were connected with each other by two, three, four and five chiasmata in one, eight, 25 and 16 oocytes, respectively. The chiasmata were 4.12 on the average in frequency. This mean value statistically differed from the 4.64 of *R. p. chosenica,* while it was statistically equal to those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5; Fig. 6).

In bivalent No. 5, the two homologous chromosomes were 117~234 μm, 192.4 μm on the average, in length. The short segment including the centromere was situated on the upper-median region (50.3~57.5%) like those of the other species and subspecies. Each of the homologous chromosomes possessed a compound-type giant loop on the upper-median region (62.1%) of the short arm. This giant loop was similar in position to those of *R. nigromaculata* and *R. brevipoda.* The two homologous chromosomes were connected with each other by two, three, four and five chiasmata in one, 22, 22 and five oocytes, respectively. The chiasmata were 3.62 on the average in frequency. This mean value statistically differed from the 4.16 of *R. p. chosenica,* while it was statistically equal to those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5; Fig. 6).

In bivalent No. 6, the two homologous chromosomes were 80~163 μm, 125.3 μm on the average, in length. The short segment including the centromere was

situated on the position from the upper-median region to the upper-submedian region (51.8~68.0%) like those of the other species and subspecies. Each of the homologous chromosomes possessed a compound-type giant loop on the under-median region (45.4%) of the long arm. This giant loop was similar in position to those of *R. nigromaculata* and *R. brevipoda*. The two homologous chromosomes were connected with each other by two chiasmata in 38 oocytes and by three chiasmata in the remaining 12 oocytes. The chiasmata were 2.24 on the average in frequency. This mean value statistically differed from the 2.56 of *R. p. chosenica*, while it was statistically identical with those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5; Fig. 6).

In bivalent No. 7, the two homologous chromosomes were 80~169 μm, 123.5 μm on the average, in length. The short segment including the centromere was situated on the upper-submedian region (65.0~72.5%). This position slightly differed from those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of three compound-type giant loops. One of these giant loops was located on the upper-subterminal region (81.0%) of the short arm, while the other two were located on the upper-median (56.4%) and the under-median (47.6%) regions of the long arm. Of these giant loops, the two compound-type giant loops in the upper-median and the under-median regions were similar in position to those of *R. brevipoda* and *R. p. chosenica*, respectively. The two homologous chromosomes were connected with each other by one, two and three chiasmata in two, 28 and 20 oocytes, respectively. The chiasmata were 2.36 on the average in frequency. This mean value statistically differed from the 2.74 of *R. p. chosenica*, while it was statistically identical with those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5; Fig. 6).

In bivalent No. 8, the two homologous chromosomes were 90~168 μm, 132.0 μm on the average, in length. The short segment including the centromere was situated on the position from the under-median region to the upper-median region (47.8~60.1%) like those of the other species and subspecies. Each of the homologous chromosomes possessed a compound-type giant loop and a simple-type giant loop. The compound-type giant loop was located on the upper-submedian region (73.2%) of the short arm and was very similar in position to those of *R. nigromaculata* and *R. brevipoda*. However, the loops constituting the compound-type giant loop were fewer in number than those of *R. nigromaculata* and more numerous than those of *R. brevipoda*. The simple-type giant loop was located on the under-median region (41.8%) of the long arm and was similar in position to those of the other species and subspecies. The two homologous chromosomes were connected with each other by one, two and three chiasmata in two, 41 and seven oocytes, respectively. The chiasmata were 2.10 on the average in frequency. This mean value statistically differed from the 2.34 of *R. nigromaculata*, while it was statistically identical with those of *R. brevipoda* and *R. p. chosenica* at the 5% level (Table 5; Fig. 6).

In bivalent No. 9, the two homologous chromosomes were 81~128 μm, 100.3 μm on the average, in length. The short segment including the centromere was

situated on the upper-submedian region (67.6~72.4%). This position slightly differed from those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of two compound-type giant loops and an oval-like structure. These two giant loops were located on the upper-subterminal region (84.9%) of the short arm and the under-median (48.3%) region of the long arm. The latter giant loop was similar in position to those of *R. brevipoda* and *R. p. chosenica*. The oval-like structure was located on the upper-subterminal region (78.2%) of the short arm and seemed to be homologous with that of *R. nigromaculata*. The two homologous chromosomes were connected with each other by one, two and three chiasmata in one, 30 and 19 oocytes, respectively. The chiasmata were 2.36 on the average in frequency. This mean value statistically differed from the 2.04 of *R. nigromaculata* and the 2.02 of *R. brevipoda*, while it was statistically identical with that of *R. p. chosenica* at the 5% level (Table 5; Fig. 6).

In bivalent No. 10, the two homologous chromosomes were 67~122 μm, 98.5 μm on the average, in length. The short segment including the centromere was situated on the position from the under-median region to the upper-median region (44.8~57.5%) like those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of a compound-type giant loop. This giant loop was located on the upper-submedian region (67.4%) of the short arm and was similar in position to those of *R. nigromaculata* and *R. brevipoda*. However, the constituent loops were intermediate in number between those of the latter two species. The two homologous chromosomes were connected with each other by one, two, three and four chiasmata in three, 37, nine and one oocytes, respectively. The chiasmata were 2.16 on the average in frequency. There was no statistical difference at the 5% level between this mean value and those of the other species and subspecies (Table 5; Fig. 6).

In bivalent No. 11, the two homologous chromosomes were 61~125 μm, 93.3 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (50.5~63.6%) like those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of a sphere, a compound-type giant loop and a simple-type giant loop. The sphere was located on the upper-subterminal region (77.0%) of the short arm and was similar in position to those of *R. nigromaculata* and *R. brevipoda*. The compound-type giant loop was located on the under-median region (38.8%) of the long arm and was similar in position to that of *R. brevipoda*. The simple-type giant loop was located on the under-subterminal region (19.6%) of the long arm and was not found in 19 of the 31 oocytes from five females. The two homologous chromosomes were connected with each other by one, two and three chiasmata in four, 41 and five oocytes, respectively. The chiasmata were 2.02 on the average in frequency. Between this mean value and those of the other species and subspecies, there was no statistical difference at the 5% level (Table 5; Fig. 6).

In bivalent No. 12, the two homologous chromosomes were 56~114 μm, 78.6

μm on the average, in length. The short segment including the centromere was situated on the position from the upper-submedian region to the upper-subterminal region (69.6~78.3%) like those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of two compound-type giant loops located on the upper-median (52.5%) and the under-submedian (37.0%) regions of the long arm. The latter giant loop was similar in position to that of *R. brevipoda.* The two homologous chromosomes were connected with each other by one, two and three chiasmata in three, 42 and five oocytes, respectively. The chiasmata were 2.04 on the average in frequency. This mean value statistically differed from the 2.26 of *R. p. chosenica,* while it was statistically identical with those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5; Fig. 6).

In bivalent No. 13, the two homologous chromosomes were 61~123 μm, 88.3 μm on the average, in length. The short segment including the centromere was situated on the position from the upper-median region to the upper-submedian region (50.7~66.6%) like those of the other species and subspecies. Each of the homologous chromosomes was characterized by possession of a compound-type giant loop located on the upper-subterminal region (79.3%) of the short arm. This giant loop was similar in position to those of *R. nigromaculata* and *R. brevipoda.* The two homologous chromosomes were connected with each other by one, two and three chiasmata in nine, 39 and two oocytes, respectively. The chiasmata were 1.86 on the average in frequency. This mean value statistically differed from the 2.04 of *R. nigromaculata* and the 2.06 of *R. p. chosenica,* while it was statistically identical with that of *R. brevipoda* at the 5% level (Table 5; Fig. 6).

From the foregoing observations, it was found that the 13 bivalents can be distinguished without fail from one another by chromosome length, the position of the short segment including the centromere and the position, kind and number of landmarks. It was also found that all the 50 oocytes contained 13 bivalents whose homologous chromosomes were connected with each other by 33 to 44 chiasmata, 38.2 chiasmata on the average, in total. This chiasma frequency per oocyte statistically differed from the 42.5 of *R. p. chosenica,* while it was identical with those of *R. nigromaculata* and *R. brevipoda* at the 5% level (Table 5).

III. Comparison of the landmarks of lampbrush chromosomes in three species and one subspecies

When *R. nigromaculata, R. brevipoda, R. p. chosenica* and *R. p. fukienensis* were compared with one another in kind and number of landmarks situated on the lampbrush chromosomes of the 13 bivalents, *R. p. chosenica* was peculiar in having a distinctly small number of landmarks. In this subspecies, chromosomes Nos. 5, 6 and 10 had no landmarks, while all the lampbrush chromosomes of the other species and subspecies had one to five landmarks. The landmarks of the lampbrush chromosomes of *R. p. chosenica* were only 16 in total number, including four compound-type giant loops, nine simple-type giant loops and three spheres, in

contrast to 25~35 landmarks in lampbrush chromosomes of each of the other species and subspecies. It was also remarkable that the lampbrush chromosomes of the other subspecies *R. p. fukienensis* had 25 landmarks in total, including 18 compound-type giant loops, four simple-type giant loops, two spheres and an oval-like structure. The lampbrush chromosomes of *R. nigromaculata* had 35 landmarks in total, including 10 compound-type giant loops, 20 simple-type giant loops, four spheres and an oval-like structure, while those of *R. brevipoda* had 31 landmarks in total, including 16 compound-type giant loops, 11 simple-type giant loops and four spheres.

The landmarks situated on the lampbrush chromosomes of the 13 bivalents were compared with one another among the three species and one subspecies. In bivalent No. 1, *R. brevipoda, R. p. chosenica* and *R. p. fukienensis* were similar to one another in having a compound-type giant loop on the long arm near the centromere. *R. nigromaculata* was peculiar in having two simple-type giant loops on the short and long arms and a compound-type giant loop which was adjacent to the short segment on the long arm.

In bivalent No. 2, *R. nigromaculata, R. brevipoda, R. p. chosenica* and *R. p. fukienensis* were very similar to one another in having a compound-type giant loop on the short arm and a sphere at the end of the long arm. However, *R. nigromaculata* and *R. p. chosenica* were peculiar in having a simple-type giant loop on the long arm in addition, although those of the two species differed from each other in size and position.

In bivalent No. 3, *R. nigromaculata, R. brevipoda, R. p. chosenica* and *R. p. fukienensis* were very similar to one another in having a small simple-type giant loop near the end of the long arm. In addition, *R. nigromaculata* had two simple-type giant loops on the long arm, *R. brevipoda* had a simple-type giant loop and a compound-type giant loop near the centromere, and *R. p. fukienensis* had a compound-type giant loop similar to that of *R. brevipoda* on the long arm near the centromere.

In bivalent No. 4, *R. nigromaculata* and *R. brevipoda* resembled each other in having a compound-type loop and a simple-type giant loop on the long arm, although the compound-type giant loop of *R. nigromaculata* was considerably larger in size than that of *R. brevipoda*. *R. p. chosenica* and *R. p. fukienensis* were somewhat similar to each other in having a small simple-type giant loop on the short arm, although those of the two subspecies fairly differed in position. *R. p. fukienensis* was peculiar in having a compound-type giant loop on the short arm near the centromere in addition to a compound-type giant loop similar to those of *R. nigromaculata* and *R. brevipoda* which were situated on the long arm near the centromere.

In bivalent No. 5, *R. nigromaculata, R. brevipoda* and *R. p. fukienensis* were similar to one another in having a compound-type giant loop on the short arm near the centromere. The former two species, moreover, resembled each other in having a simple-type giant loop on the long arm near the centromere. *R. p. chosenica* differed from the other species and subspecies in having no landmarks.

In bivalent No. 6, *R. nigromaculata, R. brevipoda* and *R. p. fukienensis* were similar

to one another in having a compound-type giant loop on the long arm near the centromere. The former two species, moreover, were similar to each other in having a simple-type giant loop contiguous to the compound-type giant loop on the long arm. *R. nigromaculata* had a small simple-type giant loop in addition on the long arm. *R. p. chosenica* was peculiar in having no landmarks.

In bivalent No. 7, *R. nigromaculata, R. brevipoda, R. p. chosenica* and *R. p. fukienensis* remarkably differed from one another in shape and situation of giant loops. *R. nigromaculata* had two simple-type giant loops and a small compound-type giant loop on the long arm. *R. brevipoda* had two small compound-type giant loops and a small simple-type giant loop on the long arm. *R. p. chosenica* had a compound-type giant loop and two small simple-type giant loops on the long arm, while *R. p. fukienensis* had three compound-type giant loops, of which one large and two small loops were situated on the short and long arms, respectively. One of the latter two compound-type giant loops was the same as that of *R. brevipoda*, while the other was similar to that of *R. p. chosenica*.

In bivalent No. 8, *R. nigromaculata, R. brevipoda, R. p. chosenica* and *R. p. fukienensis* were similar to one another in having a small simple-type giant loop on the long arm near the centromere. In addition, *R. nigromaculata, R. brevipoda* and *R. p. fukienensis* had a compound-type giant loop on the short arm, although the compound-type giant loops of these species and subspecies distinctly differed from one another in size.

In bivalent No. 9, *R. nigromaculata,* and *R. brevipoda* were similar to one another in having a sphere on the short arm and a simple-type giant loop and a compound-type giant loop on the long arm. *R. p. chosenica* had the same sphere on the short arm. *R. nigromaculata* and *R. p. chosenica* were similar in having a small simple-type giant loop on the long arm. *R. brevipoda, R. p. chosenica* and *R. p. fukienensis* were similar in having a compound-type giant loop on the long arm. *R. p. fukienensis* was similar to *R. nigromaculata* in having an oval-like structure on the short arm.

In bivalent No. 10, *R. nigromaculata, R. brevipoda* and *R. p. fukienensis* were similar to one another in having a compound-type giant loop on the short arm near the centromere. *R. p. chosenica* was peculiar in having no landmarks.

In bivalent No. 11, *R. nigromaculata* and *R. brevipoda* were very similar to each other in having two spheres on the short and long arms. *R. p. chosenica* was similar to these two species in having a sphere on the long arm, while *R. p. fukienensis* was similar to the same two species in having a sphere on the short arm. In addition, *R. nigromaculata* had three simple-type giant loops protruding from one position on the long arm near the centromere, while *R. brevipoda* and *R. p. fukienensis* had a compound-type giant loop on the same position. *R. p. fukienensis* had another small simple-type giant loop on the long arm.

In bivalent No. 12, *R. nigromaculata* and *R. p. chosenica* were similar to each other in having a small simple-type giant loop on the long arm. *R. nigromaculata* had two other simple-type giant loops protruding from one position on the long arm near the centromere. *R. brevipoda* and *R. p. fukienensis* were similar to each other in

having a compound-type giant loop on the long arm. Besides, *R. brevipoda* and *R. p. fukienensis* were peculiar in having a simple-type giant loop and a compound-type giant loop in addition on the long arm, respectively.

In bivalent No. 13, *R. nigromaculata, R. brevipoda* and *R. p. fukienensis* were similar to one another in having a compound-type giant loop on the short arm near the centromere. The former two species were similar to each other in having a small simple-type giant loop in addition on the long arm near the centromere. *R. nigromaculata* was peculiar in having another simple-type giant loop on the short arm. *R. p. chosenica* was also peculiar in having a simple-type giant loop at the end of the long arm.

The foregoing observations on the landmarks situated on the 13 lampbrush chromosomes showed that *R. nigromaculata, R. brevipoda, R. p. chosenica* and *R. p. fukienensis* had various number of common landmarks in kind and situation. There were 19 common landmarks between *R. nigromaculata* and *R. brevipoda,* 12 common landmarks between *R. nigromaculata* and *R. p. fukienensis,* and seven common landmarks between *R. nigromaculata* and *R. p. chosenica.* On the other hand, there were 17 common landmarks between *R. brevipoda* and *R. p. fukienensis,* eight common landmarks between *R. brevipoda* and *R. p. chosenica,* and seven common landmarks between *R. p. chosenica* and *R. p. fukienensis.*

IV. Lampbrush chromosomes in interspecific and intersubspecific hybrids

The interspecific and intersubspecific hybrids among *R. nigromaculata, R. brevipoda, R. plancyi chosenica* and *R. p. fukienensis* were nearly normal in viability and attained sexual maturity in the late autumn of the following year after fertilization. Females of all kinds of hybrids had as many oocytes as those of the maternal species. When the lampbrush chromosomes of their oocytes were observed, it was found that two homologous chromosomes formed a bivalent connected with each other by chiasmata or terminal fusions. However, if there was neither chiasma nor terminal fusion between the two homologous chromosomes, the latter did not form a bivalent and remained as univalents. When a terminal fusion existed between the homologous chromosomes, a bivalent was formed, even if there was no chiasma.

While most of the oocytes were diploids, a few of them were tetraploids. In the tetraploid oocytes, there were two genomes derived from the maternal species and two genomes derived from the paternal species. Each quadruplet usually formed two bivalents, each of which consisted of two homologous chromosomes derived from one species. In some cases, the quadruplet formed a quadrivalent. In this chapter, only the lampbrush chromosomes of diploid oocytes are described.

1. Reciprocal hybrids between *Rana nigromaculata* and *R. brevipoda*

The lampbrush chromosomes were observed in 50 oocytes of nine female (N)NB hybrids between two female *R. nigromaculata* and two male *R. brevipoda* and in 50 oocytes of eight female (B)BN hybrids between two female *R. brevipoda* and two

male *R. nigromaculata*. The oocytes of the (N)NB and (B)BN hybrids were 1.5~1.8 mm, 1.68 mm on the average, and 1.4~1.8 mm, 1.62 mm on the average, in diameter, respectively. The lampbrush chromosomes of these oocytes were nearly at the same stage as those of the parental species observed previously.

In reciprocal hybrids between *R. nigromaculata* and *R. brevipoda*, most of the lampbrush chromosomes formed bivalents connected with each other by chiasmata and occasionally by one or two terminal fusions in addition (Table 6). A few bivalents were formed by only terminal fusions without the participation of chiasmata. In each of the bivalents, one of the two homologous chromosomes was the same in appearance as that of *R. nigromaculata*, and the other was the same in appearance as that of *R. brevipoda*. The lampbrush chromosomes of the (N)NB hybrids were the same in appearance as those of the reciprocal hybrids. The landmarks located on *R. nigromaculata* chromosomes did not fuse with those located on *R. brevipoda* chromosomes.

In bivalent No. 1, the two homologous chromosomes in all the 50 oocytes of (N)NB hybrids and the 50 oocytes of (B)BN hybrids were connected with each other by one to seven chiasmata. The mean numbers of chiasmata were 3.44 and 3.74, respectively. There was no statistical difference at the 5% level between these mean numbers (Table 7).

In bivalent No. 2, the two homologous chromosomes in all the 50 oocytes of (N)NB hybrids and the 50 oocytes of (B)BN hybrids were connected with each other by one to five chiasmata or terminal fusions alone. The mean numbers of

TABLE 6

Number of different combinations of bivalents and univalents in 50 oocytes from each of the four parental species and subspecies and the 12 hybrids among them

No. of univalents	0	2	4	6	8	10	12	14	16	18	20	22	24	26	Total
No. of bivalents	13	12	11	10	9	8	7	6	5	4	3	2	1	0	
(N)NN	50														50
(B)BB	50														50
(C)CC	50														50
(F)FF	50														50
(N)NB	47	3													50
(B)BN	48	2													50
(N)NC	47	3													50
(C)CN	47	2	1												50
(N)NF	36	9	5												50
(F)FN	31	10	3	3	1	1	1								50
(B)BC	32	10	6	1		1									50
(C)CB						1		2	1				3	43	50
(B)BF	13	14	5	6	3	2	1						1	5	50
(F)FB	2	2	6	3	3	6	2	4	2	1	2	3	2	12	50
(C)CF	36	6	4	1	1		2								50
(F)FC	44	4	1	1											50

TABLE 7

Numbers of univalents, bivalents and chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from reciprocal hybrids between *R. nigromaculata* and *R. brevipoda*

Kind	Chromosome no.	No. of univalents	No. of bivalents								Total no. of chiasmata	Mean no. of chiasmata
			Total	No. of chiasmata								
				0	1	2	3	4	5	6	7	
(N)NB	1		50			7	23	13	5	2		172	3.44
	2		50		11	17	16	6				117	2.34
	3		50		3	18	25	4				130	2.60
	4		50		3	14	17	14	2			148	2.96
	5		50	1	6	14	19	8	2			133	2.66
	6		50	2	10	27	10	1				98	1.96
	7		50	1	17	28	4					85	1.70
	8		50		13	30	7					94	1.88
	9	2	49	1	20	27	1					77	1.54
	10	2	49		11	37	1					88	1.76
	11		50	3	15	32						79	1.58
	12		50	3	19	24	4					79	1.58
	13	2	49		17	31	1					82	1.64
	Total	6	647									1382	27.6 (22～36)
(B)BN	1		50		2	7	13	14	9	4	1	187	3.74
	2		50	2	12	15	14	6	1			113	2.26
	3		50		7	21	12	9	1			126	2.52
	4		50	1	1	12	22	11	3			150	3.00
	5		50		8	21	15	6				119	2.38
	6		50		5	26	16	3				117	2.34
	7		50	1	20	18	11					89	1.78
	8		50	2	5	35	7	1				100	2.00
	9	4	48	4	14	24	6					80	1.60
	10		50		12	32	6					94	1.88
	11		50		11	36	3					92	1.84
	12		50		14	34	2					88	1.76
	13		50	2	10	34	4					90	1.80
	Total	4	648									1445	28.9 (20～40)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

chiasmata were 2.34 and 2.26, respectively. There was no statistical difference between these mean numbers (Table 7).

In bivalents Nos. 3, 4 and 5 of the 50 oocytes of (N)NB hybrids, the two homologous chromosomes of each bivalent were connected with each other by one to five chiasmata or a terminal fusion alone. The mean numbers of chiasmata were 2.60, 2.96 and 2.66, respectively. On the other hand, in bivalents Nos. 3, 4 and 5 of the 50 oocytes of (B)BN hybrids, the two homologous chromosomes of

each bivalent were connected with each other by one to five chiasmata or a terminal fusion alone. The mean numbers of chiasmata were 2.52, 3.00 and 2.38, respectively. There was no statistical difference between the mean chiasma numbers of the (N)NB and (B)BN hybrids in each of bivalents Nos. 3, 4 and 5 (Table 7).

In bivalent No. 6, the two homologous chromosomes in all the 50 oocytes of (N)NB hybrids and the 50 oocytes of (B)BN hybrids were connected with each other by one to four chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.96 and 2.34, respectively. There was a statistical difference between these mean numbers (Table 7).

In bivalent No. 7, the two homologous chromosomes in all the 50 oocytes of (N)NB hybrids and the 50 oocytes of (B)BN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.70 and 1.78, respectively. There was no statistical difference between these mean numbers (Table 7).

In bivalent No. 8, the two homologous chromosomes in all the 50 oocytes of (N)NB hybrids and the 50 oocytes of (B)BN hybrids were connected with each other by one to four chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.88 and 2.00, respectively. There was no statistical difference between these mean numbers (Table 7).

In bivalent No. 9, the two homologous chromosomes in 49 of the 50 oocytes of (N)NB hybrids and 48 of the 50 oocytes of (B)BN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining one and two oocytes, they did not form a bivalent and remained as univalents. The mean numbers of chiasmata were 1.54 and 1.60 in the (N)NB and (B)BN hybrids, respectively. There was no statistical difference between these mean numbers (Table 7).

In bivalent No. 10, the two homologous chromosomes in 49 of the 50 oocytes of (N)NB hybrids and all the 50 oocytes of (B)BN hybrids were connected with each other by one to three chiasmata, while those in the other oocyte remained as univalents. The mean numbers of chiasmata were 1.76 and 1.88 in the (N)NB and (B)BN hybrids, respectively. There was no statistical difference between these mean numbers (Table 7).

In bivalent No. 11, the two homologous chromosomes in all the 50 oocytes of (N)NB hybrids and the 50 oocytes of (B)BN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.58 and 1.84, respectively. A statistical difference was observed between these mean numbers (Table 7).

In bivalent No. 12, the two homologous chromosomes in all the 50 oocytes of (N)NB hybrids and the 50 oocytes of (B)BN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.58 and 1.76, respectively. There was no statistical difference between these mean numbers (Table 7).

In bivalent No. 13, the two homologous chromosomes in 49 of the 50 oocytes of

(N)NB hybrids and all the 50 oocytes of (B)BN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining oocyte, they remained as univalents. The mean numbers of chiasmata were 1.64 and 1.80 in the (N)NB and (B)BN hybrids, respectively. There was no statistical difference between these mean numbers (Table 7).

The chiasmata of bivalents Nos. 1~13 in each of the 50 oocytes from the (N)NB hybrids ranged in number from 22 to 36 with average of 27.6, while those of the 13 bivalents in each of the 50 oocytes from the (B)BN hybrids ranged in number from 20 to 40 with average of 28.9. There was no statistical difference at the 5% level between the mean chiasma numbers of the reciprocal hybrids. Generally speaking, larger bivalents were more numerous in chiasma number than smaller bivalents. The five large bivalents in each of the (N)NB and (B)BN hybrids were 2.34~3.44 and 2.26~3.74 in mean chiasma number, respectively, while the eight small bivalents in each of the (N)NB and (B)BN hybrids were 1.54~1.96 and 1.60~2.34 in mean chiasma number, respectively. In contrast to the oocytes of *R. nigromaculata* and *R. brevipoda* which had no univalents, there were six univalents in three of the 50 oocytes from the (N)NB hybrids and four univalents in two of the 50 oocytes from the (B)BN hybrids (Tables 6, 7).

2. Reciprocal hybrids between *Rana nigromaculata* and *R. plancyi chosenica*

The lampbrush chromosomes were observed in 50 oocytes of nine female (N)NC hybrids between a female *R. nigromaculata* and a male *R. p. chosenica* and in 50 oocytes of nine female (C)CN hybrids between a female *R. p. chosenica* and a male *R. nigromaculata*. The oocytes of the (N)NC and (C)CN hybrids were 1.4~1.7 mm, 1.56 mm on the average, and 1.4~1.8 mm, 1.60 mm on the average, in diameter, respectively. The lampbrush chromosomes of these oocytes were nearly at the same stage as those of the parental species. As the lampbrush chromosomes derived from *R. nigromaculata* and *R. p. chosenica* possessed their own landmarks at the same position as those of the parental species, the origin of the lampbrush chromosomes in the hybrids was able to be identified without difficulty. The lampbrush chromosomes of the (N)NC hybrids were the same in appearance as those of the reciprocal hybrids. The landmarks located on *R. nigromaculata* chromosomes did not fuse with those located on *R. p. chosenica* ones. Most of the homologous lampbrush chromosomes in the reciprocal hybrids formed bivalents connected with each other by chiasmata and occasionally by one or two terminal fusions in addition (Table 6). A few bivalents were formed by terminal fusions alone without participation of chiasmata.

In bivalent No. 1, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and the 50 oocytes of (C)CN hybrids were connected with each other by one to seven chiasmata. The mean numbers of chiasmata were 3.76 and 4.24, respectively. There was no statistical difference at the 5% level between these mean numbers (Table 8).

In bivalent No. 2, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and the 50 oocytes of (C)CN hybrids were connected with each

TABLE 8
Numbers of univalents, bivalents and chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from reciprocal hybrids between *R. nigromaculata* and *R. p. chosenica*

Kind	Chromosome no.	No. of univalents	No. of bivalents								Total no. of chiasmata	Mean no. of chiasmata
			Total	No. of chiasmata								
				0	1	2	3	4	5	6	7	
(N)NC	1		50		2	4	13	20	7	4		188	3.76
	2		50		2	11	17	13	6	1		163	3.26
	3		50		5	10	17	13	4	1		154	3.08
	4		50		1	11	17	11	9	1		169	3.38
	5		50		4	17	20	7	2			136	2.72
	6	2	49		11	23	12	3				105	2.10
	7	2	49		18	23	6	2				90	1.80
	8		50	1	10	29	10					98	1.96
	9	2	49	4	12	30	3					81	1.62
	10		50	2	13	30	5					88	1.76
	11		50		6	36	8					102	2.04
	12		50	3	20	26	1					75	1.50
	13		50	3	14	30	3					83	1.66
	Total	6	647									1532	30.6 (21～41)
(C)CN	1		50		1	3	7	20	12	5	2	212	4.24
	2		50		1	5	11	19	13	1		191	3.82
	3		50		2	7	20	17	4			164	3.28
	4		50		2	8	24	11	4	1		160	3.20
	5	2	49		2	13	17	14	3			150	3.00
	6	2	49		7	26	15	1				108	2.16
	7		50	2	12	30	6					90	1.80
	8		50		11	35	4					93	1.86
	9		50	1	18	26	5					85	1.70
	10		50	1	13	30	6					91	1.82
	11		50	1	11	34	4					91	1.82
	12	4	48	1	18	27	2					78	1.56
	13		50	1	15	31	3					86	1.72
	Total	8	646									1599	32.0 (22～39)

The parentheses show the range of chiasma numbers in teh 13 pairs of homologous chromosomes.

other by one to six chiasmata. The mean numbers of chiasmata were 3.26 and 3.82, respectively. There was a statistical difference between these mean numbers (Table 8).

In bivalent No. 3, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and the 50 oocytes of (C)CN hybrids were connected with each other by one to six chiasmata. The mean numbers of chiasmata were 3.08 and

3.28, respectively. There was no statistical difference between these mean numbers (Table 8).

In bivalent No. 4, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and the 50 oocytes of (C)CN hybrids were connected with each other by one to six chiasmata. The mean numbers of chiasmata were 3.38 and 3.20, respectively. Between these mean numbers, there was no statistical difference (Table 8).

In bivalent No. 5, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and 49 of the 50 oocytes of (C)CN hybrids were connected with each other by one to five chiasmata, while those in the remaining oocyte from the (C)CN hybrids remained as univalents. The mean numbers of chiasmata were 2.72 and 3.00 in the (N)NC and (C)CN hybrids, respectively. These mean numbers did not statistically differ from each other (Table 8).

In bivalent No. 6, the two homologous chromosomes in 49 of the 50 oocytes of (N)NC hybrids and 49 of the 50 oocytes of (C)CN hybrids were connected with each other by one to four chiasmata. In the remaining two oocytes, they did not form a bivalent and remained as univalents. The mean numbers of chiasmata were 2.10 and 2.16 in the (N)NC and (C)CN hybrids, respectively. There was no statistical difference between these mean numbers (Table 8).

In bivalent No. 7, the two homologous chromosomes in 49 of the 50 oocytes of (N)NC hybrids and all the 50 oocytes of (C)CN hybrids were connected with each other by one to four chiasmata or terminal fusions alone. In the remaining oocyte from the (N)NC hybrid, they remained as univalents. The mean numbers of chiasmata were 1.80 and 1.80 in the (N)NC and (C)CN hybrids, respectively (Table 8).

In bivalent No. 8, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and the 50 oocytes of (C)CN hybrids were connected with each other by one to three chiasmata or a terminal fusion alone. The mean numbers of chiasmata were 1.96 and 1.86, respectively. There was no statistical difference between these mean numbers (Table 8).

In bivalent No. 9, the two homologous chromosomes in 49 of the 50 oocytes of (N)NC hybrids and all the 50 oocytes of (C)CN hybrids were connected with each other by one to three chiasmata or terminal fusions alone, while those in the remaining oocyte from the (N)NC hybrid remained as univalents. The mean numbers of chiasmata were 1.62 and 1.70 in the (N)NC and (C)CN hybrids, respectively. There was no statistical difference between these mean numbers (Table 8).

In each of bivalents Nos. 10 and 11, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids were connected with each other by one to three chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.76 and 2.04 in bivalents Nos. 10 and 11, respectively. On the other hand, the two homologous chromosomes in all the 50 oocytes of (C)CN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.82 and 1.82 in bivalents Nos. 10 and 11, respectively.

There were no statistical difference between the mean chiasma numbers in bivalents Nos. 10 and 11 of the (N)NC and (C)CN hybrids (Table 8).

In bivalent No. 12, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and 48 of the 50 oocytes of (C)CN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining two oocytes from the (C)CN hybrids, they remained as univalents. The mean numbers of chiasmata were 1.50 and 1.56 in the (N)NC and (C)CN hybrids, respectively. There was no statistical difference between these mean numbers (Table 8).

In bivalent No. 13, the two homologous chromosomes in all the 50 oocytes of (N)NC hybrids and the 50 oocytes of (C)CN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. The mean numbers of chiasmata were 1.66 and 1.72, respectively. There was no statistical difference between these mean numbers (Table 8).

The chiasmata of bivalents Nos. 1~13 in the 50 oocytes from the (N)NC hybrids ranged in number from 21 to 41 with average of 30.6, while those of the 13 bivalents in the 50 oocytes from the (C)CN hybrids ranged in number from 22 to 39 with average of 32.0. There was no statistical difference at the 5% level between the mean chiasma numbers of the reciprocal hybrids. The five large bivalents in each of the (N)NC and (C)CN hybrids were 2.72~3.76 and 3.00~4.24 in mean chiasma number, respectively, while the eight small bivalents in each of the (N)NC and (C)CN hybrids were 1.50~2.10 and 1.56~2.16 in mean chiasma number, respectively. In contrast to the oocytes of *R. nigromaculata* and *R. p. chosenica* which had no univalents, there were six univalents in three of the 50 oocytes from the (N)NC hybrids and eight univalents in three of the 50 oocytes from the (C)CN hybrids (Tables 6, 8).

3. Reciprocal hybrids between *Rana nigromaculata* and *R. plancyi fukienensis*

The lampbrush chromosomes were observed in 50 oocytes of six female (N)NF hybrids between a female *R. nigromaculata* and a male *R. p. fukienensis* and in 50 oocytes of seven female (F)FN hybrids between a female *R. p. fukienensis* and a male *R. nigromaculata*. The oocytes of the (N)NF and (F)FN hybrids were 1.3~1.7 mm, 1.50 mm on the average, and 1.3~1.6 mm, 1.40 mm on the average, in diameter, respectively. The lampbrush chromosomes of these oocytes were nearly at the same stage as those of the parental species. They had their own landmarks at the same positions as those of the parental species. The lampbrush chromosomes of the (N)NF hybrids were the same in appearance as those of the reciprocal hybrids. Most of the homologous lampbrush chromosomes in the reciprocal hybrids formed bivalents connected with each other by chiasmata and occasionally by one or two terminal fusions in addition (Table 6). A few bivalents were formed by terminal fusions alone without participation of chiasmata.

TABLE 9

Numbers of univalents, bivalents and chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from reciprocal hybrids between *R. nigromaculata* and *R. p. fukienensis*

Kind	Chromosome no.	No. of univalents	No. of bivalents							Total no. of chiasmata	Mean no. of chiasmata
			Total	No. of chiasmata							
				0	1	2	3	4	5		
(N)NF	1		50		1	13	13	16	7	165	3.30
	2	12	44	5	16	10	11	2		77	1.54
	3	2	49		10	14	11	11	3	130	2.60
	4		50		5	9	17	12	7	157	3.14
	5		50		6	20	17	7		125	2.50
	6	2	49		13	31	4	1		91	1.82
	7	6	47	1	19	23	4			77	1.54
	8	2	49		13	33	3			88	1.76
	9		50	4	21	19	6			77	1.54
	10	4	48	3	16	27	2			76	1.52
	11		50	1	10	37	2			90	1.80
	12	4	48	4	18	25	1			71	1.42
	13	6	47	2	21	21	3			72	1.44
	Total	38	631							1296	25.9 (18~35)
(F)FN	1	6	47		4	11	18	10	4	140	2.80
	2	14	43	1	14	14	10	4		88	1.76
	3	4	48	1	9	15	15	7	1	117	2.34
	4	4	48		5	14	14	7	8	143	2.86
	5	4	48		9	25	11	3		104	2.08
	6	2	49	1	18	23	7			85	1.70
	7	2	49	1	21	21	6			81	1.62
	8	2	49	1	16	27	5			85	1.70
	9	10	45	1	25	13	6			69	1.38
	10	6	47	2	13	27	3	2		84	1.68
	11	4	48	2	14	30	2			80	1.60
	12	12	44	4	17	22	1			64	1.28
	13	10	45	4	21	20				61	1.22
	Total	80	610							1201	24.0 (11~33)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

In bivalent No. 1, the two homologous chromosomes in all the 50 oocytes of (N)NF hybrids and 47 of the 50 oocytes of (F)FN hybrids were connected with each other by one to five chiasmata, while those in the remaining three oocytes remained as univalents. The mean numbers of chiasmata were 3.30 and 2.80 in the (N)NF and (F)FN hybrids, respectively. Between these mean numbers, there was a statistical difference (Table 9).

In bivalent No. 2, the two homologous chromosomes in 44 of the 50 oocytes of (N)NF hybrids and 43 of the 50 oocytes of (F)FN hybrids were connected with each other by one to four chiasmata or terminal fusions alone. In the remaining 13 oocytes, they remained as univalents. The mean numbers of chiasmata were 1.54 and 1.76 in the (N)NF and (F)FN hybrids, respectively. Between these mean numbers, there was no statistical difference (Table 9).

In bivalent No. 3, the two homologous chromosomes in 49 of the 50 oocytes of (N)NF hybrids and 48 of the 50 oocytes of (F)FN hybrids were connected with each other by one to five chiasmata or a terminal fusion alone. In the remaining three oocytes, they remained as univalents. The mean numbers of chiasmata were 2.60 and 2.34 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 4, the two homologous chromosomes in all the 50 oocytes of (N)NF hybrids and 48 of the 50 oocytes of (F)FN hybrids were connected with each other by one to five chiasmata, while those in the remaining two oocytes remained as univalents. The mean numbers of chiasmata were 3.14 and 2.86 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 5, the two homologous chromosomes in all the 50 oocytes of (N)NF hybrids and 48 of the 50 oocytes of (F)FN hybrids were connected with each other by one to four chiasmata, while those in the remaining two oocytes remained as univalents. The mean numbers of chiasmata were 2.50 and 2.08 in the (N)NF and (F)FN hybrids, respectively. There was a statistical difference between these mean numbers (Table 9).

In bivalent No. 6, the two homologous chromosomes in 49 of the 50 oocytes of (N)NF hybrids and 49 of the 50 oocytes of (F)FN hybrids were connected with each other by one to four chiasmata or a terminal fusion alone. Those in the remaining two oocytes remained as univalents. The mean numbers of chiasmata were 1.82 and 1.70 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 7, the two homologous chromosomes in 47 of the 50 oocytes of (N)NF hybrids and 49 of the 50 oocytes of (F)FN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. Those in the remaining four oocytes remained as univalents. The mean numbers of chiasmata were 1.54 and 1.62 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 8, the two homologous chromosomes in 49 of the 50 oocytes of (N)NF hybrids and 49 of the 50 oocytes of (F)FN hybrids were connected with each other by one to three chiasmata or a terminal fusion alone. In the remaining two oocytes, they remained as univalents. The mean numbers of chiasmata were 1.76 and 1.70 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 9, the two homologous chromosomes in all the 50 oocytes of (N)NF hybrids and 45 of the 50 oocytes of (F)FN hybrids were connected with

each other by one to three chiasmata or terminal fusions alone. In the remaining five oocytes, they remained as univalents. The mean numbers of chiasmata were 1.54 and 1.38 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 10, the two homologous chromosomes in 48 of the 50 oocytes of (N)NF hybrids and 47 of the 50 oocytes of (F)FN hybrids were connected with each other by one to four chiasmata or terminal fusions alone. In the remaining five oocytes, they remained as univalents. The mean numbers of chiasmata were 1.52 and 1.68 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 11, the two homologous chromosomes in all the 50 oocytes of (N)NF hybrids and 48 of the 50 oocytes of (F)FN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining two oocytes, they remained as univalents. The mean numbers of chiasmata were 1.80 and 1.60 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 12, the two homologous chromosomes in 48 of the 50 oocytes of (N)NF hybrids and 44 of the 50 oocytes of (F)FN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining eight oocytes, they remained as univalents. The mean numbers of chiasmata were 1.42 and 1.28 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

In bivalent No. 13, the two homologous chromosomes in 47 of the 50 oocytes of (N)NF hybrids and 45 of the 50 oocytes of (F)FN hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining eight oocytes, they remained as univalents. The mean numbers of chiasmata were 1.44 and 1.22 in the (N)NF and (F)FN hybrids, respectively. There was no statistical difference between these mean numbers (Table 9).

The chiasmata of bivalents Nos. 1~13 in each of the 50 oocytes from the (N)NF hybrids ranged in number from 18 to 35 with average of 25.9, while those of the 13 bivalents in each of the 50 oocytes from the (F)FN hybrids ranged in number from 11 to 33 with average of 24.0. There was no statistical difference at the 5% level between these mean chiasma numbers of the reciprocal hybrids. The five large bivalents in each of the (N)NF and (F)FN hybrids were 1.54~3.30 and 1.76~2.86 in mean chiasma number, respectively, while the eight small bivalents in each of the (N)NF and (F)FN hybrids were 1.42~1.82 and 1.22~1.70 in mean chiasma number, respectively. In contrast to the oocytes of *R. nigromaculata* and *R. p. fukienensis,* there were 38 univalents in 14 of the 50 oocytes from the (N)NF hybrids and 80 univalents in 18 of the 50 oocytes from the (F)FN hybrids (Tables 6, 9).

4. Reciprocal hybrids between *Rana brevipoda* and *R. plancyi chosenica*

The lampbrush chromosomes were observed in 50 oocytes of nine female (B)BC hybrids between a female *R. brevipoda* and a male *R. p. chosenica* and in 50 oocytes of eight female (C)CB hybrids between a female *R. p. chosenica* and a male *R.*

TABLE 10
Numbers of univalents, bivalents and chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from reciprocal hybrids between *R. brevipoda* and *R. p. chosenica*

Kind	Chromosome no.	No. of univalents	No. of bivalents								Total no. of chiasmata	Mean no. of chiasmata
			Total	No. of chiasmata								
				0	1	2	3	4	5	6	7	
(B)BC	1	4	48		2	3	15	15	6	5	2	187	3.74
	2	6	47	2	6	11	17	8	2	1		127	2.54
	3		50		5	14	18	9	4			143	2.86
	4	2	49			12	14	12	9	2		171	3.42
	5	16	42	1	9	13	15	3	1			97	1.94
	6	4	48		14	19	14	1				98	1.96
	7	6	47		11	23	11	2				98	1.96
	8	2	49	1	18	19	9	2				91	1.82
	9	4	48	2	23	20	3					72	1.44
	10	2	49	2	14	30	3					83	1.66
	11	8	46		15	28	3					80	1.60
	12	4	48		20	23	5					81	1.62
	13	2	49	1	35	12	1					62	1.24
	Total	60	620									1390	27.8 (14~35)
(C)CB	1	98	1						1			5	0.10
	2	96	2	1	1							1	0.02
	3	92	4		1	2	1					8	0.16
	4	90	5	2	1	2						5	0.10
	5	98	1		1							1	0.02
	6	98	1			1						2	0.04
	7	92	4		3	1						5	0.10
	8	98	1					1				4	0.08
	9	98	1		1							1	0.02
	10	92	4			3	1					9	0.18
	11	94	3		2	1						4	0.08
	12	100										—	—
	13	98	1		1							1	0.02
	Total	1244	28									46	0.9 (0~14)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

brevipoda. The oocytes of the (B)BC and (C)CB hybrids were 1.3~1.5 mm, 1.38 mm on the average, and 1.3~1.5 mm, 1.39 mm on the average, in diameter, respectively. The lampbrush chromosomes of these oocytes were nearly at the same stage as those of the parental species. In the (B)BC and (C)CB hybrids, one of the two homologous chromosomes was completely of the same appearance as that of the paternal species, while the other was completely of the same

appearance as that of the maternal species. The (B)BC hybrids were identical with the (C)CB hybrids in appearance of lampbrush chromosomes, although the former remarkably differed from the latter in formation of bivalents (Table 6). The landmarks located on *R. brevipoda* chromosomes did not fuse with those located on *R. p. chosenica* chromosomes.

In bivalent No. 1, the two homologous chromosomes in 48 of the 50 oocytes of (B)BC hybrids were connected with each other by one to seven chiasmata. Each of the other two oocytes contained two univalents. The mean number of chiasmata was 3.74. In the reciprocal (C)CB hybrids, the two homologous chromosomes in 49 of the 50 oocytes remained as univalents without forming a bivalent. In the remaining oocyte, the two homologous chromosomes formed a bivalent connected by five chiasmata (Table 10).

In bivalent No. 2, the two homologous chromosomes in 47 of the 50 oocytes of (B)BC hybrids were connected with each other by one to six chiasmata or terminal fusions alone. In the other three oocytes, they remained as univalents. The mean number of chiasmata was 2.54. In the reciprocal (C)CB hybrids, the two homologous chromosomes in 48 of the 50 oocytes were not connected with each other and remained as univalents, while those in the remaining two oocytes formed a bivalent connected with each other by a chiasma or a terminal fusion (Table 10).

In bivalent No. 3, the two homologous chromosomes in all the 50 oocytes of (B)BC hybrids were connected with each other by one to five chiasmata. The mean number of chiasmata was 2.86. The two homologous chromosomes in 46 of the 50 oocytes of (C)CB hybrids were not connected with each other and remained as univalents. In the remaining four oocytes, they were connected with each other by one to three chiasmata (Table 10).

In bivalent No. 4, the two homologous chromosomes in 49 of the 50 oocytes of (B)BC hybrids were connected with each other by two to six chiasmata, while in the other oocyte they remained as univalents. The mean number of chiasmata was 3.42. The two homologous chromosomes in 45 of the 50 oocytes of (C)CB hybrids remained as univalents. Those in the remaining five oocytes were connected with each other by one or two chiasmata or terminal fusions alone (Table 10).

In bivalent No. 5, the two homologous chromosomes in 42 of the 50 oocytes of (B)BC hybrids were connected with each other by one to five chiasmata or a terminal fusion alone, while those in the remaining eight oocytes remained as univalents. The mean number of chiasmata was 1.94. The two homologous chromosomes in 49 of the 50 oocytes of (C)CB hybrids remained as univalents, while those in the remaining oocyte formed a bivalent connected by a chiasma (Table 10).

In bivalent No. 6, the two homologous chromosomes in 48 of the 50 oocytes of (B)BC hybrids were connected with each other by one to four chiasmata, while those in the remaining two oocytes remained as univalents. The mean number of chiasmata was 1.96. In contrast, the two homologous chromosomes in 49 of the 50 oocytes of (C)CB hybrids remained as univalents, while those in the remaining

oocyte formed a bivalent connected by two chiasmata (Table 10).

In bivalent No. 7, the two homologous chromosomes in 47 of the 50 oocytes of (B)BC hybrids were connected with each other by one to four chiasmata, while in the remaining three oocytes they remained as univalents. The mean number of chiasmata was 1.96. In contrast, the two homologous chromosomes in 46 of the 50 oocytes of (C)CB hybrids were not connected with each other and remained as univalents. In the remaining four oocytes, they formed a bivalent connected by one or two chiasmata (Table 10).

In bivalent No. 8, the two homologous chromosomes in 49 of the 50 oocytes of (B)BC hybrids were connected with each other by one to four chiasmata or a terminal fusion alone, while in the remaining oocyte they remained as univalents. The mean number of chiasmata was 1.82. In contrast, the two homologous chromosomes in 49 of the 50 oocytes of (C)CB hybrids remained as univalents. In the remaining oocyte, they formed a bivalent connected by four chiasmata (Table 10).

In bivalent No. 9, the two homologous chromosomes in 48 of the 50 oocytes of (B)BC hybrids were connected with each other by one to three chiasmata or terminal fusions alone, while those in the other two oocytes remained as univalents. The mean number of chiasmata was 1.44. In contrast, the two homologous chromosomes in 49 of the 50 oocytes of (C)CB hybrids remained as univalents. In the remaining oocyte, they formed a bivalent connected by a chiasma (Table 10).

In bivalent No. 10, the two homologous chromosomes in 49 of the 50 oocytes of (B)BC hybrids were connected with each other by one to three chiasmata or terminal fusions alone, while those in the remaining oocyte remained as univalents. The mean number of chiasmata was 1.66. In contrast, the two homologous chromosomes in 46 of the 50 oocytes of (C)CB hybrids remained as univalents. In the remaining four oocytes, they formed a bivalent connected by two or three chiasmata (Table 10).

In bivalent No. 11, the two homologous chromosomes in 46 of the 50 oocytes of (B)BC hybrids were connected with each other by one to three chiasmata, while those in the remaining four oocytes remained as univalents. The mean number of chiasmata was 1.60. In contrast, the two homologous chromosomes in 47 of the 50 oocytes of (C)CB hybrids remained as univalents. In the remaining three oocytes, they formed a bivalent connected by one or two chiasmata (Table 10).

In bivalent No. 12, the two homologous chromosomes in 48 of the 50 oocytes of (B)BC hybrids were connected with each other by one to three chiasmata, while those in the remaining two oocytes remained as univalents. The mean number of chiasmata was 1.62. The two homologous chromosomes in all the 50 oocytes of (C)CB hybrids remained as univalents without forming a bivalent (Table 10).

In bivalent No. 13, the two homologous chromosomes in 49 of the 50 oocytes of (B)BC hybrids were connected with each other by one to three chiasmata or a terminal fusion alone, while those in the other oocyte remained as univalents. The mean number of chiasmata was 1.24. In contrast, the two homologous

chromosomes in 49 of the 50 oocytes of (C)CB hybrids did not form a bivalent and remained as univalents. In the remaining oocyte, they formed a bivalent connected by a chiasma (Table 10).

There was an extremely large difference in number of chiasmata in bivalents Nos. 1~13 between the (B)BC and (C)CB hybrids. The chiasmata of bivalents Nos. 1~13 in each of the 50 oocytes from the (B)BC hybrids ranged in number from 14 to 35 with average of 27.8, while those of the 13 bivalents in each of the 50 oocytes from the (C)CB hybrids ranged in number from 0 to 14 with average of 0.9. The five large bivalents in each of the (B)BC and (C)CB hybrids were 1.94~3.74 and 0.02~0.16 in mean chiasma number, respectively, while the eight small bivalents in each of the (B)BC and (C)CB hybrids were 1.24~1.96 and 0~0.18 in mean chiasma number, respectively. In contrast to the oocytes of *R. brevipoda* and *R. p. chosenica,* there were 60 univalents in 18 of the 50 oocytes from the (B)BC hybrids and 1244 univalents in all the 50 oocytes from the (C)CB hybrids (Tables 6, 10).

5. Reciprocal hybrids between *Rana brevipoda* and *R. plancyi fukienensis*

The lampbrush chromosomes were observed in 50 oocytes from five female (B)BF hybrids between a female *R. brevipoda* and a male *R. p. fukienensis* and in 50 oocytes from nine female (F)FB hybrids between a female *R. p. fukienensis* and a male *R. brevipoda.* The oocytes of the (B)BF and (F)FB hybrids were 1.3~1.6 mm, 1.37 mm on the average, and 1.2~1.5 mm, 1.35 mm on the average, in diameter, respectively. The lampbrush chromosomes of these oocytes were about the same stage as those of the parental species. In the (B)BF and (F)FB hybrids, one of the two homologous chromosomes was of the same appearance as that of the paternal species, while the other was of the same appearance as that of the maternal species. The lampbrush chromosomes of (B)BF hybrids were identical with those of (F)FB hybrids in appearance, although the former differed from the latter in formation of bivalents (Table 6).

In each of bivalents Nos. 1 and 2, the two homologous chromosomes in 43 and 39 of the 50 oocytes of (B)BF hybrids were connected with each other by one to five chiasmata or a terminal fusion alone. In the remaining seven and 11 oocytes, they did not form a bivalent. The mean numbers of chiasmata were 2.32 and 1.50 in bivalents Nos. 1 and 2, respectively. In contrast, the two homologous chromosomes in 24 and 15 of the 50 oocytes of (F)FB hybrids were connected with each other by one to five chiasmata. In the remaining 26 and 35 oocytes, they did not form a bivalent. The mean numbers of chiasmata were 0.98 and 0.48 in bivalents Nos. 1 and 2, respectively. These mean numbers in bivalents Nos. 1 and 2 statistically differed between the (B)BF and (F)FB hybrids (Table 11).

In bivalent No. 3, the two homologous chromosomes in 41 of the 50 oocytes of (B)BF hybrids were connected with each other by one to five chiasmata or terminal fusions alone, while those in the other nine oocytes remained as univalents. The mean number of chiasmata was 1.72. In (F)FB hybrids, the two homologous chromosomes in 28 of the 50 oocytes were connected with each other

TABLE 11

Numbers of univalents, bivalents and chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from reciprocal hybrids between *R. brevipoda* and *R. p. fukienensis*

Kind	Chromosome no.	No. of univalents	No. of bivalents							Total no. of chiasmata	Mean no. of chiasmata
			Total	No. of chiasmata							
				0	1	2	3	4	5		
(B)BF	1	14	43		9	12	8	11	3	116	2.32
	2	22	39	1	11	17	10			75	1.50
	3	18	41	2	14	11	7	6	1	86	1.72
	4	20	40		9	14	10	6	1	96	1.92
	5	28	36		11	15	9	1		72	1.44
	6	24	38	3	22	11	2			50	1.00
	7	26	37	4	20	12	1			47	0.94
	8	24	38	1	19	14	4			59	1.18
	9	26	37	1	17	16	2	1		59	1.18
	10	18	41	4	21	15	1			54	1.08
	11	22	39	2	24	13				50	1.00
	12	30	35	2	18	15				48	0.96
	13	22	39	3	26	10				46	0.92
	Total	294	503							858	17.2 (0~30)
(F)FB	1	52	24		11	5	5	2	1	49	0.98
	2	70	15		10	2	2	1		24	0.48
	3	44	28		11	11	3	3		54	1.08
	4	52	24		5	9	8	2		55	1.10
	5	62	19		9	7	1	2		34	0.68
	6	62	19		10	7	2			30	0.60
	7	56	22	5	14	1	2			22	0.44
	8	50	25		12	10	2	1		42	0.84
	9	62	19		13	6				25	0.50
	10	50	25	3	14	5	3			33	0.66
	11	52	24	1	14	8	1			33	0.66
	12	60	20	1	13	5	1			26	0.52
	13	54	23	4	13	5	1			26	0.52
	Total	726	287							453	9.1 (0~29)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

by one to four chiasmata, while those in the other 22 oocytes did not form a bivalent. The mean number of chiasmata was 1.08. These mean numbers of the reciprocal hybrids statistically differed from each other (Table 11).

In bivalents Nos. 4 and 5, the two homologous chromosomes in 40 and 36 of the 50 oocytes of (B)BF hybrids were connected with each other by one to five chiasmata. In the remaining 10 and 14 oocytes, they remained as univalents.

The mean numbers of chiasmata were 1.92 and 1.44 in bivalents Nos. 4 and 5, respectively. In (F)FB hybrids, the two homologous chromosomes in 24 and 19 of the 50 oocytes were connected with each other by one to four chiasmata. In the remaining 26 and 31 oocytes, they remained as univalents. The mean numbers of chiasmata were 1.10 and 0.68 in bivalents Nos. 4 and 5, respectively. These mean numbers in bivalents Nos. 4 and 5 statistically differed between the (B)BF and (F)FB hybrids (Table 11).

In each of bivalents Nos. 6, 7 and 8, the two homologous chromosomes in 38, 37 and 38 of the 50 oocytes of (B)BF hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining 12, 13 and 12 oocytes, they did not form a bivalent. The mean numbers of chiasmata were 1.00, 0.94 and 1.18 in bivalents Nos. 6, 7 and 8, respectively. In (F)FB hybrids, the two homologous chromosomes in 19, 22 and 25 of the 50 oocytes were connected with each other by one to four chiasmata or terminal fusions alone. In the remaining 31, 28 and 25 oocytes, they did not form a bivalent. The mean numbers of chiasmata were 0.60, 0.44 and 0.84 in bivalents Nos. 6, 7 and 8, respectively. These mean numbers in bivalents Nos. 6 and 7 statistically differed between the (B)BF and (F)FB hybrids, while those in bivalent No. 8 did not differ between the reciprocal hybrids (Table 11).

In bivalent No. 9, the two homologous chromosomes in 37 of the 50 oocytes of (B)BF hybrids were connected with each other by one to four chiasmata or a terminal fusion alone, while those in the other 13 oocytes remained as univalents. The mean number of chiasmata was 1.18. The two homologous chromosomes in 19 of the 50 oocytes of (F)FB hybrids were connected with each other by one or two chiasmata, while those in the remaining 31 oocytes remained as univalents. The mean number of chiasmata was 0.50. There was a statistical difference between these mean numbers (Table 11).

In each of bivalents Nos. 10 and 11, the two homologous chromosomes in 41 and 39 of the 50 oocytes of (B)BF hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining nine and 11 oocytes, they remained as univalents. The mean numbers of chiasmata were 1.08 and 1.00 in bivalents Nos. 10 and 11, respectively. In (F)FB hybrids, the two homologous chromosomes in 25 and 24 of the 50 oocytes were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining 25 and 26 oocytes, they did not form a bivalent. The mean numbers of chiasmata were 0.66 and 0.66 in bivalents Nos. 10 and 11, respectively. In each of bivalents Nos. 10 and 11, there was a statistical difference between the mean chiasma numbers of the (B)BF and (F)FB hybrids (Table 11).

In each of bivalents Nos. 12 and 13, the two homologous chromosomes in 35 and 39 of the 50 oocytes of (B)BF hybrids were connected with each other by one or two chiasmata or terminal fusions alone. In the remaining 15 and 11 oocytes, they remained as univalents. The mean numbers of chiasmata were 0.96 and 0.92 in bivalents Nos. 12 and 13, respectively. In (F)FB hybrids, the two homologous chromosomes in 20 and 23 of the 50 oocytes were connected with each

other by one to three chiasmata or terminal fusions alone. In the remaining 30 and 27 oocytes, they remained as univalents. The mean numbers of chiasmata were 0.52 and 0.52 in bivalents Nos. 12 and 13, respectively. In each of bivalents Nos. 12 and 13, there was a statistical difference between the mean chiasma numbers of the (B)BF and (F)FB hybrids (Table 11).

There was a considerable difference in number of chiasmata in bivalents Nos. 1~13 between the (B)BF and (F)FB hybrid. The chiasmata of bivalents Nos. 1~13 in the 50 oocytes from the (B)BF hybrids ranged in number from 0 to 30 with average of 17.2, while those of the 13 bivalents in the 50 oocytes from the (F)FB hybrids ranged in number from 0 to 29 with average of 9.1. There was a statistical difference at the 5% level between these mean chiasma numbers of the reciprocal hybrids. The five large bivalents in each of the (B)BF and (F)FB hybrids were 1.44~2.32 and 0.48~1.10 in mean chiasma number, respectively, while the eight small bivalents in each of the (B)BF and (F)FB hybrids were 0.92~1.18 and 0.44~0.84 in mean chiasma number, respectively. In contrast to the oocytes of *R. brevipoda* and *R. p. fukienensis*, there were 294 univalents in 37 of the 50 oocytes from the (B)BF hybrids and 726 univalents in 48 of the 50 oocytes from the (F)FB hybrids (Tables 6, 11).

6. Reciprocal intersubspecific hybrids between *Rana plancyi chosenica* and *R. p. fukienensis*

The lampbrush chromosomes were observed in 50 oocytes of eight female (C)CF hybrids between a female *R. p. chosenica* and a male *R. p. fukienensis* and in 50 oocytes of seven female (F)FC hybrids between a female *R. p. fukienensis* and a male *R. p. chosenica*. The oocytes of the (C)CF and (F)FC hybrids were 1.3~1.6 mm, 1.41 mm on the average, and 1.2~1.5 mm, 1.33 mm on the average, in diameter, respectively. The lampbrush chromosomes found in these oocytes were nearly at the same stage as those of the parental subspecies. In reciprocal (C)CF and (F)FC hybrids, it was found that one of the two homologous chromosomes was completely of the same appearance as that of the paternal species, while the other was completely of the same appearance as that of the maternal species. The landmarks located on *R. p. chosenica* chromosomes did not fuse with those located on *R. p. fukienensis* chromosomes. Most of the homologous lampbrush chromosomes in the reciprocal hybrids formed bivalents connected with each other by chiasmata and occasionally by one or two terminal fusions in addition (Table 6). A few bivalents were formed by terminal fusions alone.

In bivalent No. 1, the two homologous chromosomes in 48 of the 50 oocytes of (C)CF hybrids and all the 50 oocytes of (F)FC hybrids were connected with each other by one to seven chiasmata, while those in the remaining two oocytes did not form a bivalent. The mean numbers of chiasmata were 4.22 and 4.34 in the (C)CF and (F)FC hybrids, respectively. These mean numbers did not statistically differ from each other (Table 12).

In bivalent No. 2, the two homologous chromosomes in 46 of the 50 oocytes of (C)CF hybrids and all the 50 oocytes of (F)FC hybrids were connected with each

TABLE 12

Numbers of univalents, bivalents and chiasmata in each of the 13 pairs of homologous chromosomes in 50 oocytes from reciprocal hybrids between *R. p. chosenica* and *R. p. fukienensis*

Kind	Chromosome no.	No. of univalents	No. of bivalents								Total no. of chiasmata	Mean no. of chiasmata
			Total	No. of chiasmata								
				0	1	2	3	4	5	6	7	
(C)CF	1	4	48		1	3	9	10	14	10	1	211	4.22
	2	8	46	1	7	12	15	8	3			123	2.46
	3	4	48		2	9	21	11	5			152	3.04
	4		50		3	8	20	11	7	1		164	3.28
	5	4	48		8	13	18	8	1			125	2.50
	6	2	49		12	21	15	1				103	2.06
	7	10	45		11	25	8	1				89	1.78
	8		50		10	28	12					102	2.04
	9	8	46	1	19	22	4					75	1.50
	10	4	48	1	11	33	3					86	1.72
	11	2	49		12	35	2					88	1.76
	12	8	46		15	27	4					81	1.62
	13	12	44	1	25	18						61	1.22
	Total	66	617									1460	29.2 (12~40)
(F)FC	1		50			3	11	13	14	7	2	217	4.34
	2		50		4	14	20	9	3			143	2.86
	3		50			5	23	16	6			173	3.46
	4		50		1	4	15	25	5			179	3.58
	5		50		3	14	21	11	1			143	2.86
	6	2	49		3	32	13	1				110	2.20
	7		50		9	27	14					105	2.10
	8		50		7	29	12	2				109	2.18
	9	4	48	1	14	27	6					86	1.72
	10	2	49	1	6	31	11					101	2.02
	11	2	49	1	12	35	1					85	1.70
	12		50	1	18	28	3					83	1.66
	13	8	46	2	22	22						66	1.32
	Total	18	641									1600	32.0 (18~42)

The parentheses show the range of chiasma numbers in the 13 pairs of homologous chromosomes.

other by one to five chiasmata or a terminal fusion alone. In the remaining four oocytes, they remained as univalents. The mean numbers of chiasmata were 2.46 and 2.86 in the (C)CF and (F)FC hybrids, respectively. There was no statistical difference between these mean numbers (Table 12).

In bivalent No. 3, the two homologous chromosomes in 48 of the 50 oocytes of (C)CF hybrids and all the 50 oocytes of (F)FC hybrids were connected with each

other by one to five chiasmata. In the remaining two oocytes, they remained as univalents. The mean numbers of chiasmata were 3.04 and 3.46 in the (C)CF and (F)FC hybrids, respectively. These mean numbers statistically differed from each other (Table 12).

In bivalents Nos. 4 and 5, the two homologous chromosomes in all and 48 of the 50 oocytes of (C)CF hybrids were connected with each other by one to six chiasmata, while those in the other two oocytes remained as univalents. The mean numbers of chiasmata were 3.28 and 2.50 in bivalents Nos. 4 and 5, respectively. In (F)FC hybrids, the two homologous chromosomes in all the 50 oocytes of each of bivalents Nos. 4 and 5 were connected with each other by one to five chiasmata. The mean numbers of chiasmata were 3.58 and 2.86 in bivalents Nos. 4 and 5, respectively. There was no statistical difference between the mean chiasma numbers of the (C)CF and (F)FC hybrids (Table 12).

In bivalents Nos. 6 and 7, the two homologous chromosomes in 49 and 45 of the 50 oocytes of (C)CF hybrids were connected with each other by one to four chiasmata, while those in the other one and five oocytes remained as univalents. The mean numbers of chiasmata were 2.06 and 1.78 in bivalents Nos. 6 and 7, respectively. On the other hand, in 49 and all of the 50 oocytes of (F)FC hybrids, the two homologous chromosomes were connected with each other by one to four chiasmata, while those in the other oocyte remained as univalents. The mean numbers of chiasmata were 2.20 and 2.10 in bivalents Nos. 6 and 7, respectively. There was no statistical difference between the mean chiasma numbers of the (C)CF and (F)FC hybrids (Table 12).

In bivalent No. 8, the two homologous chromosomes in all the 50 oocytes of (C)CF hybrids and the 50 oocytes of (F)FC hybrids were connected with each other by one to four chiasmata. The mean numbers of chiasmata were 2.04 and 2.18 in the (C)CF and (F)FC hybrids, respectively. There was no statistical difference between these mean numbers (Table 12).

In bivalent No. 9, the two homologous chromosomes in 46 of the 50 oocytes of (C)CF hybrids and 48 of the 50 oocytes of (F)FC hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining four and two oocytes, they remained as univalents. The mean numbers of chiasmata were 1.50 and 1.72 in the (C)CF and (F)FC hybrids, respectively. There was no statistical difference between these mean numbers (Table 12).

In bivalent No. 10, the two homologous chromosomes in 48 of the 50 oocytes of (C)CF hybrids and 49 of the 50 oocytes of (F)FC hybrids were connected with each other by one to three chiasmata or terminal fusions alone. In the remaining two and one oocytes, they remained as univalents. The mean numbers of chiasmata were 1.72 and 2.02 in the (C)CF and (F)FC hybrids, respectively. There was a statistical difference between these mean numbers (Table 12).

In bivalent No. 11, the two homologous chromosomes in 49 of the 50 oocytes of (C)CF hybrids and 49 of the 50 oocytes of (F)FC hybrids were connected with each other by one to three chiasmata or a terminal fusion alone. In the other oocytes, they remained as univalents. The mean numbers of chiasmata were 1.76

and 1.70 in the (C)CF and (F)FC hybrids, respectively. The mean chiasma numbers did not statistically differ between the reciprocal hybrids (Table 12).

In bivalent No. 12, the two homologous chromosomes in 46 of the 50 oocytes of (C)CF hybrids and all the 50 oocytes of (F)FC hybrids were connected with each other by one to three chiasmata or a terminal fusion alone. Those in the other four oocytes remained as univalents. The mean numbers of chiasmata were 1.62 and 1.66 in the (C)CF and (F)FC hybrids, respectively. There was no statistical difference between these mean numbers (Table 12).

In bivalent No. 13, the two homologous chromosomes in 44 of the 50 oocytes of (C)CF hybrids and 46 of the 50 oocytes of (F)FC hybrids were connected with each other by one or two chiasmata or terminal fusions alone. Those in the remaining six and four oocytes were not connected with each other and remained as univalents. The mean numbers of chiasmata were 1.22 and 1.32 in the (C)CF and (F)FC hybrids, respectively. There was no statistical difference between these mean numbers (Table 12).

The chiasmata of bivalents Nos. 1~13 in the 50 oocytes from the (C)CF hybrids ranged in number from 12 to 40 with average of 29.2, while those of the 13 bivalents in the 50 oocytes from the (F)FC hybrids ranged in number from 18 to 42 with average of 32.0. There was a statistical difference at the 5% level between these mean chiasma numbers of the reciprocal hybrids. The five large bivalents in each of the (C)CF and (F)FC hybrids were 2.46~4.22 and 2.86~4.34 in mean chiasma number, respectively, while the eight small bivalents in each of the (C)CF and (F)FC hybrids were 1.22~2.06 and 1.32~2.20 in mean chiasma number, respectively. In contrast to the oocytes of *R. p. chosenica* and *R. p. fukienensis,* there were 66 univalents in 14 of the 50 oocytes from the (C)CF hybrids and 18 univalents in six of the 50 oocytes from the (F)FC hybrids (Tables 6, 12).

DISCUSSION

1. Landmarks of lampbrush chromosomes

The maps of lampbrush chromosomes of three subspecies of *Triturus cristatus, T. c. cristatus, T. c. carnifex* and *T. c. karelinii,* drawn by CALLAN and LLOYD (1960) were somewhat similar to one another in general aspects, although the lampbrush chromosomes of these three subspecies were evidently distinguished from one another in the kind, position and number of landmarks. They remarkably differed in the pattern of landmarks from those of five other species of *Triturus, T. marmoratus* (NARDI, RAGGHIANTI and MANCINO, 1972), *T. alpestris apuanus* (RAGGHIANTI, NARDI and MANCINO, 1972), *T. vulgaris meridionalis* (BARSACCHI, BUSSOTTI and MANCINO, 1970), *T. helveticus helveticus* (MANCINO and BARSACCHI, 1966) and *T. italicus* (MANCINO and BARSACCHI, 1969). The maps of lampbrush chromosomes of these six species were quite different from one another, although the map of *T. marmoratus* was somewhat similar to those of *Triturus cristatus* subspecies. There were remarkable similarities in landmarks between the lampbrush chromosomes of

Pleurodeles waltl and *P. poireti*, while the lampbrush chromosomes of *P. waltl* were distinguished from those of *P. poireti* by many characteristics (LACROIX, 1968).

A comparative study on the karyotypes of *Rana nigromaculata*, (N)NN, *R. brevipoda*, (B)BB, *R. plancyi chosenica*, (C)CC, and *R. p. fukienensis*, (F)FF, has been made by NISHIOKA, OKUMOTO and RYUZAKI (1987). The karyotypes of these species and subspecies were compared with one another by counting the numbers of chromosome pairs which significantly differ in relative length and centromere position. Of these numbers, a smaller one was considered to indicate a closer similarity between the karyotypes of two species or subspecies. The measurements showed that the smallest numbers were found between (B)BB or (N)NN and (C)CC and that the second smallest number was between (B)BB and (N)NN and between (C)CC and (F)FF. The largest numbers were found between (B)BB or (N)NN and (F)FF. These results seemed to indicate that the karyotype of (C)CC differs from that of (F)FF at the same degree as found between the karyotypes of (B)BB and (N)NN, regardless of the taxonomic positions of these species and subspecies.

It was noteworthy that the lampbrush chromosomes of the three species and one subspecies were not always parallel to the mitotic chromosomes of these species and subspecies in morphological comparison. Lampbrush chromosomes were characteristic in having four kinds of landmarks, compound-type giant loop, simple-type giant loop, sphere and oval-like structure in addition to the short segment including a centromere. While there were most numerous common landmarks in lampbrush chromosomes between (N)NN and (B)BB and between (B)BB and (F)FF, the number of mitotic chromosome pairs which significantly differ in either relative chromosome length or centromere position was remarkably numerous between these species or subspecies. However, it was difficult to compare the number of common landmarks in (C)CC with those in the other species or subspecies, as (C)CC was peculiar in extreme scarcity of landmarks, as compared with the other subspecies and species. It is noteworthy that (C)CC remarkably differs from conspecific (F)FF like other species, (N)NN and (B)BB, in the number of landmarks. From this point of view, (C)CC seems systematically to differ from (F)FF at nearly the same degree as (N)NN and (B)BB.

2. Lampbrush chromosomes of hybrids

Lacroix (1968) has observed 12 bivalents in the oocytes of female hybrids between *Pleurodeles waltl* and *P. poireti*, as found in those of the parental species. In contrast to these hybrids, MANCINO, RAGGHIANTI and BUCCI-INNOCENTI (1979) have confirmed that 24 unpaired lampbrush chromosomes were contained in the overwhelming majority of the oocytes from each female of reciprocal hybrids between *Triturus cristatus carnifex* and *T. vulgaris meridionalis*. On the other hand, MÜLLER (1977) have counted the numbers of bivalents and chiasmata found in oocytes of 27 interspecific and five intersubspecific hybrids among six *Xenopus* species, *X. borealis*, *X. clivii*, *X. fraseri*, *X. gilli*, *X. mulleri* and *X. laevis*, and three subspecies of *X. laevis*, *X. l. laevis*, *X. l. petersi* and *X. l. victorianus*. He has

confirmed that the closer the two crossed species are systematically, the higher the expected number of bivalents. In 24 interspecific hybrids, the bivalents were 0.07~13.4 in mean number per oocyte, and the chiasmata were 1.0~22.8 in mean number per oocyte. In contrast, oocytes of intersubspecific hybrids always formed the maximum number of 18 bivalents. The chiasma frequencies per bivalent in intersubspecific hybrids were not inferior than those in the parental subspecies.

In the present study, *Rana nigromaculata*, (N)NN, *R. brevipoda*, (B)BB, *R. plancyi chosenica*, (C)CC, and *R. p. fukienensis*, (F)FF, had 13 bivalents in each of 50 oocytes and were 38.5, 38.7, 42.5 and 38.2, respectively, in the mean number of chiasmata of the 13 bivalents. The number of oocytes having 13 bivalents among 50 oocytes as well as the mean number of chiasmata found in the 13 pairs of homologous lampbrush chromosomes in 50 oocytes from each of the 12 hybrids among (N)NN, (B)BB, (C)CC and (F)FF seems directly to show the kind of hybrid sterility in these hybrids (KAWAMURA and NISHIOKA, 1975, 1977, 1979). In reciprocal hybrids between *Rana nigromaculata* and *R. brevipoda*, (N)NB and (B)BN, the oocytes having 13 bivalents were 47 and 48 in number, respectively, and the mean numbers of chiasmata found in the 13 pairs of homologous lampbrush chromosomes were 27.6 and 28.9, respectively. In reciprocal hybrids between *R. nigromaculata* and *R. p. chosenica*, (N)NC and (C)CN, the oocytes having 13 bivalents were 47 and 47 in number, respectively, and the mean numbers of chiasmata were 30.6

TABLE 13

Means and ranges of chiasma numbers in the 13 pairs of homologous chromosomes in 50 oocytes from each of the four parental species and subspecies and the 12 hybrids among them

Kinds	Number of oocytes having 13 bivalents	Mean number of chiasmata	Range of chiasma numbers
(N)NN	50	38.5	30~46
(B)BB	50	38.7	31~53
(C)CC	50	42.5	35~52
(F)FF	50	38.2	33~44
(N)NB	47	27.6	22~36
(B)BN	48	28.9	20~40
(N)NC	47	30.6	21~41
(C)CN	47	32.0	22~39
(N)NF	36	25.9	18~35
(F)FN	31	24.0	11~33
(B)BC	32	27.8	14~35
(C)CB	0	0.9	0~14
(B)BF	13	17.2	0~30
(F)FB	2	9.1	0~29
(C)CF	36	29.2	12~40
(F)FC	44	32.0	18~42

and 32.0, respectively. In reciprocal hybrids between *R. nigromaculata* and *R. p. fukienensis,* (N)NF and (F)FN, the oocytes having 13 bivalents were 36 and 31 in number, respectively, and the mean numbers of chiasmata were 25.9 and 24.0, respectively. In isolating mechanisms, all the males of each of these hybrids were almost completely sterile by hybrid sterility, while the females were fertile. In reciprocal hybrids between *R. p. chosenica* and *R. p. fukienensis,* (C)CF and (F)FC, the oocytes having 13 bivalents were 36 and 44 in number, respectively, and the mean numbers of chiasmata were 29.2 and 32.0, respectively. In isolating mechanisms, the males of these hybrids were incompletely sterile, while the females were fertile (KAWAMURA and NISHIOKA, 1979) (Table 13).

In reciprocal hybrids between *R. brevipoda* and *R. p. chosenica,* (B)BC and (C)CB, the oocytes having 13 bivalents were 32 and 0 in number, respectively, and the mean numbers of chiasmata were 27.8 and 0.9, respectively. In reciprocal hybrids between *R. brevipoda* and *R. p. fukienensis,* (B)BF and (F)FB, the oocytes having 13 bivalents were 13 and 2 in number, respectively, and the mean numbers of chiasmata were 17.2 and 9.1, respectively. In isolating mechanisms, both males and females of hybrids (B)BC and (C)CB and hybrids (B)BF and (F)FB were incompletely sterile (KAWAMURA and NISHIOKA, 1979). In these two kinds of reciprocal hybrids, the lampbrush chromosomes of hybrids (C)CB and (F)FB remarkably differed from those of hybrids (B)BC and (B)BF, respectively, in number of oocytes having 13 bivalents and mean number of chiasmata, in contrast to the lampbrush chromosomes of the other four kinds of reciprocal hybrids.

When compared with the parental species and subspecies, all the 12 kinds of hybrids among them were fewer in the number of oocytes having 13 bivalents as well as in the mean number of chiasmata found in the 13 pairs of homologous lampbrush chromosomes (Table 13). These fewer numbers in bivalents and chiasmata are attributable as a matter of course to the difference between the lampbrush chromosomes of the two parental species or subspecies. In contrast, the difference between reciprocal hybrids in the number of oocytes having 13 bivalents and the mean number of chiasmata found in the 13 pairs of homologous lampbrush chromosomes seems to be attributable to a difference in cytoplasm between the two parental species or subspecies. While the cytoplasm of (N)NN does not differ much from that of (B)BB, (C)CC or (F)FF, the cytoplasm of (B)BB seems to differ considerably from that of (C)CC or (F)FF. Hybrids (C)CF and (F)FC were 36 and 44 in number of oocytes having 13 bivalents, respectively. The chiasmata found in the 13 pairs of homologous lampbrush chromosomes of (C)CF and (F)FC ranged in number from 12 to 40 and from 18 to 42 with mean of 29.2 and 32.0, respectively. This seems to show that the two parental subspecies do not differ much from each other in the genetic nature of lampbrush chromosomes, although they remarkably differ from each other in number of landmarks.

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