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Interspecific Hybrids among Japanese, Formosan, European and American Brown Frogs

By

Toshijiro KAWAMURA, Midori NISHIOKA and Hiroaki UEDA

Laboratory for Amphibian Biology, Faculty of Science, Hiroshima University, Hiroshima, Japan

(With 37 Text-figures)

CONTENTS

INTRODUCTION

Interspecific hybrids of brown frogs have been reported by PFLÜGER (1883), PFLÜGER and SMITH (1883) and BORN (1883, 1886) for the first time. These investigators obtained viable hybrids from crosses between female *Rana arvalis* and male *Rana fusca* (=*temporaria*). The hybrids produced by BORN grew well and were expected to attain sexual maturity, although they died in fact during hibernation of the second year. DÜRKEN (1935, 1938) has thoroughly studied the same kind of hybrids. Nine hybrids obtained by him were four years old in 1932 and all sterile males. Although four of them were continuously reared until they became seven years old, they were still sterile. According to him, natural hybridization did not seem to occur in the vicinity of Breslau, where the two species were sympatric. KAWAMURA (1943) has reported on the hybrids be-

tween female *Rana japonica* and male *Rana chensinensis*. These hybrids all became sterile males just as those produced by Dürken between female *Rana arvalis* and male *Rana fusca* (=*temporaria*). The two brown frog species, *Rana japonica* and *Rana chensinensis* are allopatric in Japan. Thereafter, KAWAMURA (1950) has elucidated that all the hybrids between female *Rana japonica* and male *Rana ornativentris* also become sterile males. These two species are sympatric in a wide area of Japan. The reciprocal hybrids between them have never been obtained due to gametic isolation, just as found between female *Rana temporaria* and male *Rana arvalis*. KAWAMURA and KOBAYASHI (1959) have reported that reciprocal hybrids between *Rana chensinensis* and *Rana ornativentris* become sterile males.

Interspecific hybrids between Japanese and European brown frogs have been produced by KAWAMURA and KOBAYASHI (1960). Hybrids between females of Japanese species and males of European species, such as *Rana japonica*♀×*Rana arvalis*♂, *Rana japonica*♀×*Rana temporaria*♂, *Rana ornativentris*♀×*Rana temporaria*♂ and *Rana chensinensis*♀×*Rana arvalis*♂, and those between females of European species and males of Japanese species, such as *Rana arvalis*♀×*Rana japonica*♂ and *Rana arvalis*♀×*Rana ornativentris*♂, all became males. Four of these six kinds of hybrids except *Rana ornativentris*♀×*Rana temporaria*♂ and *Rana chensinensis*♀×*Rana arvalis*♂ were confirmed to be sterile, and it is very probable that the remaining two kinds of hybrids were also sterile. The finding that the hybrids between a female *Rana chensinensis* and a male *Rana temporaria* are inviable at the tadpole stage has been reconfirmed by KAWAMURA and NISHIOKA (1962) from further crossing experiments carried out in 1962 (Table 3). They have also elucidated that no cleavage occurs in the reciprocal combination.

On the basis of these results of crossing experiments and differences in karyotype, KAWAMURA (1962) placed the Hokkaido population which had so far been called *Rana temporaria temporaria* in a valid species and provisionally named this population *Rana chensinensis* until the existence of isolating mechanisms between Japanese and the continental *Rana chensinensis* is clarified by crossing experiments. The position of *Rana ornativentris* as a valid species was also given by KAWAMURA (1962) on the basis of the above-stated results of crossing experiments. The position of *Rana tsushimensis* as a valid species was given by KAWAMURA (1962) on the basis of the results of crossing experiments performed in 1962 by KAWAMURA and NISHIOKA (1963). While this population had so far been called *Rana temporaria tsushimensis*, it was found to be completely isolated from *Rana temporaria*, *Rana chensinensis*, *Rana ornativentris* and *Rana japonica* by gametic isolation or hybrid inviability. In a picture book of Japanese amphibians and reptiles, NAKAMURA and UENO (1963) have reported that a new brown frog population is found sympatrically with *Rana tsushimensis* in Tsushima which is an island situated between Kyushu and Korea. They considered this population to be a subspecies of *Rana ornativentris*. However, the present authors have observed that this population scarcely differs in external characters from *Rana dybowskii* distributed in Korea together with *Rana amurensis coreana* (SHANNON, 1956). Thus, it is an

interesting problem to examine the existence of any isolating mechanism between the Tsushima and Korean populations of *Rana dybowskii*.

DAITO (1967) who studied in our laboratory on the isolating mechanisms of *Rana dybowskii* distributed in Tsushima from some other species has briefly reported that this population is completely isolated from *Rana tsushimensis, Rana chensinensis, Rana japonica* and *Rana tagoi* by hybrid inviability and also completely isolated from *Rana ornativentris* by gametic isolation or hybrid inviability. KURAMOTO (1974) has made 22 kinds of crosses among *Rana longicrus* from Formosa, *Rana okinavana* from Okinawa and four other Japanese brown frog species. It was found that almost normally metamorphosed hybrids were produced from six kinds of crosses, that is, reciprocal *Rana longicrus* × *Rana japonica*, reciprocal *Rana okinavana* × *Rana tsushimensis*, *longicrus* ♀ × *okinavana* ♂ and *japonica* ♀ × *okinavana* ♂, while the hybrids produced from 14 other combinations were inviable at the embryonic or larval stage. No fertilization occurred between female *Rana ornativentris* and male *longicrus* or *okinavana*. As the metamorphosed frogs were all preserved shortly after metamorphosis in order to examine the sex, it was unknown whether they became sterile or fertile. From these results of crossing experiments and the similarity of external characters, KURAMOTO considered that *Rana longicrus* and *Rana okinavana* are closely related to *Rana japonica* and *Rana tsushimensis*, respectively.

The present authors have made 99 kinds of crosses among 14 brown frog species and one local population collected from Japan, Korea, Formosa, Europe and North America in 20 years from 1962 to 1981 in order to elucidate the phylogenetic relations of brown frogs distributed in the northern hemisphere. It has been found that all the 14 species are completely isolated from one another by gametic isolation, hybrid inviability or hybrid sterility, while Tsushima population of *Rana dybowskii* is not reproductively isolated from Korean population of this species. A part of the results of crossing experiments between Japanese and Korean brown frog species has been preliminarily reported by the present authors (1972). An outline of the results of crossings between Far Eastern and European brown frogs has been previously reported by KAWAMURA and NISHIOKA (1973, 1977).

MATERIALS AND METHODS

The following brown frogs belonging to 14 species and a population were used in hybridization experiments carried out during the period from 1962 to 1981.

1. *Rana japonica* GÜNTHER from the surburbs of Hiroshima.
   a. A total of 56 females:
      Seven in 1962, three in 1963, eight in 1964, 10 in 1967, four in 1968, four in 1970, two in 1972, four in 1975, four in 1976, three in 1977, three in 1978 and four in 1981.
   b. A total of 56 males:
      Seven in 1962, three in 1963, eight in 1964, two in 1966, 10 in 1967,

one in 1968, 15 in 1970, two in 1975, two in 1976, two in 1977, one in 1978 and three in 1981.

2. *Rana ornativentris* WERNER from mountainous areas of Hiroshima Prefecture.
   a. A total of 31 females:
      Six in 1962, three in 1963, three in 1964, one in 1965, three in 1968, four in 1970, one in 1972, two in 1975, two in 1976, four in 1977 and two in 1981.
   b. A total of 40 males:
      Three in 1962, three in 1963, one in 1964, one in 1965, two in 1966, eight in 1967, one in 1968, 11 in 1970, two in 1975, two in 1976, two in 1977, one in 1978, three in 1981.
3. *Rana chensinensis* DAVID from Hokkaido.
   a. A total of 21 females:
      Six in 1962, five in 1963, two in 1970, two in 1975, one in 1976 and five in 1981.
   b. A total of 27 males:
      Six in 1962, five in 1963, one in 1966, six in 1970, two in 1975, one in 1976, two in 1977, one in 1978 and three in 1981.
4. *Rana tsushimensis* STEJNEGER from Tsushima Island.
   a. A total of 41 females:
      Two in 1963, five in 1966, eight in 1967, two in 1968, five in 1970, two in 1972, seven in 1975, two in 1976, three in 1977, one in 1978 and four in 1981.
   b. A total of 47 males:
      Three in 1963, eight in 1964, two in 1966, 10 in 1967, one in 1968, eight in 1970, seven in 1975, two in 1976, two in 1977, one in 1978 and three in 1981.
5. *Rana dybowskii* GÜNTHER (*Rana ornativentris* subsp. by NAKAMURA and UENO, 1963) from Tsushima Island.
   a. A total of 22 females:
      One in 1966, three in 1968, six in 1970, one in 1972, two in 1975, one in 1976, three in 1978 and five in 1981.
   b. A total of 17 males:
      One in 1966, one in 1968, six in 1970, two in 1975, one in 1976, two in 1977, one in 1978 and three in 1981.
6. *Rana dybowskii* GÜNTHER (*Rana temporaria dybowskii* GÜNTHER by SHANNON, 1956) from Korea.
   a. Two males in 1968. Collected from the suburbs of Seoul, Korea, by Professor G. Goo in 1967.
   b. Eight females and eight males in 1970. Collected from Juwangsan, Kyongsang Pukto, Korea by Professor H. K. KIM in 1969.
7. *Rana amurensis coreana* OKADA from Korea.
   Five females and five males in 1970. Collected from Suwon, Kyonggi-Do, Korea by Professor H. K. KIM in 1969.

8. *Rana longicrus* STEJNEGER from Formosa.
   Five females and four males in 1981. Collected from Taipei, Formosa by Mr. P.-S. LIN.
9. *Rana temporaria* L. from Europe.
   a. Two females and two males in 1962. Collected from Luxembourg by Mr. R. THORN.
   b. Two females and two males in 1963. Collected from Saxony, Germany by Mr. R. THORN.
   c. One female and one male in 1964. The same as one of the two pairs used in 1963.
   d. One female and one male in 1965. Collected from Tessin, southern Switzerland by Mr. R. THORN.
   e. Two males in 1975. Offspring of a pair collected from Lescum, Basses-Pyrenees, France by Mr. R. THORN in 1970.
   f. Two males in 1976. The same as those used in 1975.
10. *Rana arvalis* NILSSON from Europe.
   a. Five females and two males in 1962. Collected from Luxembourg by Mr. R. THORN.
   b. One female and one male in 1963. Collected from Saxony, Germany by Mr. R. THORN.
   c. One female and one male in 1966. Collected from Potsdam, eastern Germany by Mr. R. THORN.
   d. Two females and two males in 1976. Collected from Luxembourg by Mr. R. THORN.
   e. Four females and two males in 1977. Offspring of those used in 1976.
11. *Rana macrocnemis* BOULENGER from Europe.
   One male in 1968. Collected from the environs of Bursa, Turkey by Mr. R. THORN in 1968.
12. *Rana dalmatina* BONAPARTE from Europe.
   a. One male in 1975. Collected from a forest area between Reims and Châlons-sur-Marne, east of Paris, France by Mr. R. THORN in 1974.
   b. One male in 1978. Collected from Praglia Abano Terme, Prov. Padua, Italy by Mr. R. THORN in 1977.
13. *Rana okinavana* BOETTGER from Okinawa Island.
   a. Two males in 1977. b. One male in 1978.
   c. One male in 1981.
14. *Rana latouchii* BOULENGER from Formosa.
   One female and two males in 1981. Collected from Taipei, Formasa by Mr. P.-S. LIN in 1981.
15. *Rana sylvatica* LE CONTE from North America.
   One male in 1972. Collected from Vermont, U. S. A. by Dr. G. W. NACE in 1972.

Matings were all made by the artificial fertilization method. Ovulation was

accelerated by injecting *Rana catesbeiana* pituitaries into the body cavity of females. Sperm suspension was made by crushing a testis removed from each male in a small quantity of distilled water. Fertilized eggs were developed in a small glass dish at 17~24°C until the stage shortly after hatching. Tadpoles were usually reared in concrete tanks placed outdoors by feeding on boiled spinach. Before 1975, metamorphosed frogs were principally fed on domestic flies, but from this year and later they were exclusively fed on nymphs or adults of the two-spotted cricket, *Gryllus bimaculatus* DE GEER (NISHIOKA and MATSUURA, 1977).

The inner structure of gonads was observed in serial sections which were cut at 12 μ after the gonads were fixed in NAVASHIN's fluid for 24 hours and embedded in paraffin. The sections were stained with HEIDENHAIN's iron hematoxylin.

The following abbreviations are used for designation of each kind of brown frogs.

amur. .....*Rana amurensis coreana* OKADA
arv. .....*Rana arvalis* NILSSON
chen. .....*Rana chensinensis* DAVID
dalm. .....*Rana dalmatina* BONAPARTE
dyb. K....*Rana dybowskii* GÜNTHER from Korea
dyb. T....*Rana dybowskii* GÜNTHER from Tsushima
jap. .....*Rana japonica* GÜNTHER
lato. .....*Rana latouchii* BOULENGER
long. .....*Rana longicrus* STEJNEGER
macro. ...*Rana macrocnemis* BOULENGER
oki. .....*Rana okinavana* BOETTGER
ornat. .....*Rana ornativentris* WERNER
syl. .....*Rana sylvatica* LE CONTE
temp. .....*Rana temporaria* L.
tsu. .....*Rana tsushimensis* STEJNEGER

OBSERVATION

I. Developmental capacity of hybrids

1. Crosses between female *Rana japonica* and males of 13 species

a. Control matings of *Rana japonica*

In 11 breeding seasons of the years 1962~1981, matings were made between 54 females and 43 males (Table 1). It was found that 84.6~99.7% of the respective total number of eggs in each breeding season, 6430 (92.8%) of 6936 eggs in total, cleaved normally. While 358 eggs died of various abnormalities during the embryonic stage, 75.9~97.8%, 87.5% on the average, hatched normally, and 72.9~97.3%, 85.9% on the average, became normally feeding tadpoles. Eventually, 58.3~91.6%, 5449 (78.6%) in total, of the respective number of eggs normally attained completion of metamorphosis. This number of normally metamorphosed frogs corresponds to 84.7% of the normally cleaved eggs.

TABLE 1

Developmental capacity of hybrids between female *Rana japonica* and male brown frogs of 13 species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1962	*jap.* (7)	*jap.* (7)	713	603(84.6%)	584(81.9%)	582(81.6%)	541(75.9%)	520(72.9%)	493(69.1%)
	jap. (1)	*ornat.* (1)	76	45(59.2%)	43(56.6%)	43(56.6%)	43(56.6%)	40(52.6%)	35(46.1%)
	jap. (7)	*chen.* (7)	973	303(31.1%)	299(30.7%)	299(30.7%)	280(28.8%)	32(3.3%)	20(2.1%)
		temp. (2)	1837	914(49.8%)	434(23.6%)	434(23.6%)	341(18.6%)	195(10.6%)	132(7.2%)
		arv. (2)	897	164(18.3%)	158(17.6%)	158(17.6%)	144(16.1%)	63(7.0%)	36(4.0%)
1963	*jap.* (3)	*jap.* (3)	365	314(86.0%)	314(86.0%)	307(84.1%)	307(84.1%)	307(84.1%)	303(83.0%)
		tsu. (3)	1105	1032(93.4%)	1031(93.3%)	1008(91.2%)	1008(91.2%)	106(9.6%)	0
1964	*jap.* (8)	*jap.* (8)	1236	1113(90.1%)	1102(89.2%)	1096(88.7%)	1094(88.5%)	1082(87.5%)	1047(84.7%)
		tsu. (8)	2732	2621(95.9%)	2601(95.2%)	2581(94.5%)	2581(94.5%)	2470(90.4%)	13(0.5%)
1967	*jap.* (10)	*jap.* (10)	1063	974(91.6%)	945(88.9%)	927(87.2%)	902(84.9%)	864(81.3%)	813(76.5%)
		tsu. (10)	1176	1087(92.4%)	1055(89.7%)	1036(88.1%)	1006(85.5%)	916(77.9%)	6(0.5%)
1968	*jap.* (4)	*jap.* (1)	454	445(98.0%)	443(97.6%)	439(96.7%)	437(96.3%)	437(96.3%)	373(82.2%)
		dyb. K (2)	817	787(96.3%)	778(95.2%)	772(94.5%)	619(75.8%)	512(62.7%)	0
		macr. (1)	540	0	0	0	0	0	0
1970	*jap.* (4)	*jap.* (4)	652	631(96.8%)	605(92.8%)	605(92.8%)	605(92.8%)	593(91.0%)	539(82.7%)
		dyb. K (4)	683	399(58.4%)	380(55.6%)	367(53.7%)	349(51.1%)	121(17.7%)	0
		amur. (4)	939	244(26.0%)	150(16.0%)	95(10.1%)	72(7.7%)	47(5.0%)	0
1972	*jap.* (2)	*syl.* (1)	217	163(75.1%)	0	0	0	0	0
1975	*jap.* (4)	*jap.* (2)	446	413(92.6%)	398(89.2%)	390(87.4%)	390(87.4%)	375(84.1%)	260(58.3%)
		chen. (2)	607	495(81.6%)	490(80.7%)	489(80.6%)	483(79.6%)	460(75.8%)	391(64.4%)
		tsu. (2)	521	473(90.8%)	469(90.0%)	450(86.4%)	411(78.9%)	327(62.8%)	0
		dyb. T (2)	619	570(92.1%)	552(89.2%)	552(89.2%)	536(86.6%)	511(82.6%)	0
		temp. (2)	630	588(93.3%)	521(82.7%)	504(80.0%)	404(64.1%)	358(56.8%)	301(47.8%)
1976	*jap.* (4)	*jap.* (2)	503	483(96.0%)	481(95.6%)	469(93.2%)	459(91.3%)	451(89.7%)	384(76.3%)
		ornat. (1)	272	263(96.7%)	262(96.3%)	257(94.5%)	257(94.5%)	255(93.8%)	227(83.5%)
		chen. (1)	378	344(91.0%)	341(90.2%)	340(90.0%)	336(88.9%)	328(86.8%)	291(77.0%)
		tsu. (2)	277	149(53.8%)	149(53.8%)	145(52.4%)	145(52.4%)	144(52.0%)	3(1.1%)
		dyb. T (1)	644	6(0.9%)	6(0.9%)	6(0.9%)	6(0.9%)	1(0.2%)	0
		temp. (2)	589	346(58.7%)	341(57.9%)	284(48.2%)	282(47.9%)	268(45.5%)	247(41.9%)
		arv. (1)	1372	392(28.6%)	364(26.5%)	363(26.5%)	363(26.5%)	317(23.1%)	276(20.1%)
1977	*jap.* (3)	*jap.* (2)	467	450(96.4%)	425(91.0%)	425(91.0%)	410(87.8%)	408(87.4%)	363(77.7%)
		oki. (2)	507	2(0.4%)	2(0.4%)	2(0.4%)	2(0.4%)	2(0.4%)	2(0.4%)
		arv. (2)	515	22(4.3%)	19(3.7%)	19(3.7%)	19(3.7%)	18(3.5%)	17(3.3%)
1978	*jap.* (3)	*jap.* (1)	444	417(93.9%)	404(91.0%)	403(90.8%)	347(78.2%)	345(77.7%)	331(74.6%)
		ornat. (1)	176	175(99.4%)	173(98.3%)	172(97.7%)	157(89.2%)	147(83.5%)	126(71.6%)
		chen. (1)	179	167(93.3%)	159(88.8%)	158(88.3%)	153(85.5%)	150(83.8%)	142(79.3%)
		oki. (1)	275	6(2.2%)	6(2.2%)	6(2.2%)	5(1.8%)	5(1.8%)	2(0.7%)
	jap. (1)	*dyb.* T (1)	80	38(47.5%)	35(43.8%)	35(43.8%)	29(36.3%)	25(31.3%)	0
	jap. (3)	*dalm.* (1)	444	0	0	0	0	0	0
1981	*jap.* (4)	*jap.* (3)	593	591(99.7%)	590(99.5%)	584(98.5%)	580(97.8%)	577(97.3%)	543(91.6%)
		long. (3)	593	545(91.9%)	515(86.8%)	502(84.7%)	470(79.3%)	438(73.9%)	415(70.0%)
		lato. (1)	762	0	0	0	0	0	0
Total	*jap.* (54)	*jap.* (43)	5936	6430(92.8%)	6291(90.7%)	6227(89.8%)	6072(87.5%)	5959(85.9%)	5449(78.6%)
	jap. (8)	*ornat.* (3)	524	483(92.2%)	478(91.2%)	472(90.1%)	457(87.2%)	442(84.4%)	388(74.1)%
	jap. (18)	*chen.* (11)	2137	1309(61.3%)	1289(60.3%)	1286(60.2%)	1252(58.6%)	970(45.4%)	844(39.5%)
	jap. (6)	*oki.* (3)	782	8(1.0%)	8(1.0%)	8(1.0%)	7(0.9%)	7(0.9%)	4(0.5%)
	jap. (29)	*tsu.* (25)	5811	5362(92.3%)	5305(91.3%)	5220(89.8%)	5151(88.6%)	3963(68.2%)	22(0.4%)
	jap. (9)	*dyb.* T (4)	1343	614(45.7%)	593(44.2%)	593(44.2%)	571(42.5%)	537(40.0%)	0
	jap. (8)	*dyb.* K (6)	1500	1186(79.1%)	1158(77.2%)	1139(75.9%)	968(64.5%)	633(42.2%)	0
	jap. (4)	*amur.* (4)	939	244(26.0%)	150(16.0%)	95(10.1%)	72(7.7%)	47(5.0%)	0
	jap. (4)	*long.* (3)	593	545(91.9%)	515(86.8%)	502(84.7%)	470(79.3%)	438(73.9%)	415(70.0%)
	jap. (4)	*lato.* (1)	762	0	0	0	0	0	0
	jap. (15)	*temp.* (6)	3056	1848(60.5%)	1296(42.4%)	1222(40.0%)	1027(33.6%)	821(26.9%)	680(22.3%)
	jap. (14)	*arv.* (5)	2784	578(20.8%)	541(19.4%)	540(19.4%)	526(18.9%)	398(14.3%)	329(11.8%)
	jap. (3)	*dalm.* (1)	444	0	0	0	0	0	0
	jap. (4)	*macr.* (1)	540	0	0	0	0	0	0
	jap. (2)	*syl.* (1)	217	163(75.1%)	0	0	0	0	0

b. Crosses with male *Rana ornativentris*

Eight female *Rana japonica* were mated with three male *Rana ornativentris* in

1962, 1976 and 1978 (Table 1). The results showed that 59.2~99.4% of the respective total number of eggs in each year, 483 (92.2%) of 524 eggs in total, cleaved normally. While some eggs died of various abnormalities during development, 56.6~94.5%, 457 (87.2%) in total, hatched normally, and 46.1~83.5%, 388 (74.1%) in total, metamorphosed normally. This number of normally metamorphosed frogs corresponds to 80.3% of the normally cleaved eggs.

c. Crosses with male *Rana chensinensis*

Eighteen female *Rana japonica* were mated with 11 male *Rana chensinensis* in 1962, 1975, 1976 and 1978 (Table 1). It was found that of 973 eggs obtained from seven female *Rana japonica* in 1962, 303 (31.1%) cleaved normally, 280 (28.8%) hatched normally and only 32 (3.3%) became normally feeding tadpoles. Eventually, 20 (2.1%) eggs attained completion of metamorphosis during this year. In contrast, 81.6~93.3% of the respective number of eggs obtained from three or four females cleaved normally, 79.6~88.9% hatched normally, 75.8~86.8% became normally feeding tadpoles, and 64.4~79.3% metamorphosed normally in 1975, 1976 and 1978. In total, 61.3% of 2137 eggs obtained from the 18 females in the four years cleaved normally, 58.6% hatched normally, 45.4% became normally feeding tadpoles and 39.5% attained completion of metamorphosis.

d. Crosses with male *Rana okinavana*

In 1977 and 1978, six female *Rana japonica* were mated with three male *Rana okinavana* (Table 1). Of 782 eggs obtained from the six females, only eight (1.0%) cleaved normally, seven hatched normally and four metamorphosed normally. All the four frogs gradually died before sexual maturity.

The percentage of normally cleaved eggs was too low as compared with that obtained by KURAMOTU (1974). As this low percentage was considered to be attributable to captivity of the males in a colder condition for about three months, the present authors repeated this kind of cross late in 1981 by using a male *Rana okinavana* shortly after collection. It was found that 287 (91.4%) of 314 eggs obtained from two female *Rana japonica* cleaved normally and 247 (78.7%) hatched normally by inseminating with sperm of this male, while 222 (91.7%) of 242 control eggs cleaved normally and 181 (74.8%) hatched normally.

e. Crosses with male *Rana tsushimensis*

A total of 29 female *Rana japonica* were mated with 25 male *Rana tsushimensis* in 1963, 1964, 1967, 1975 and 1976 (Table 1). It was found that 53.8~95.9% of the respective total number of eggs in each year, 92.3% of 5811 eggs in total, cleaved normally and 52.4~94.5%, 88.6% on the average, hatched normally. However, hybrid embryos slightly retarded in development from the gastrula stage as compared with the controls. Although 3963 (68.2%) attained the feeding tadpole stage, most of them were emaciated and gradually died, as they could not eat owing to ill-development of their teeth. Only 43 of the feeding

tadpoles attained the metamorphosing stage and 22 barely completed metamorphosis. These metamorphosed frogs were dwarf and feeble; all of them died without taking food.

f. Crosses with male *Rana dybowskii* from Tsushima or Korea

Nine female *Rana japonica* were mated with four male *Rana dybowskii* from Tsushima in 1975, 1976 and 1978 (Table 1). The results showed that 570 (92.1%) of 619 eggs obtained from four females in 1975 cleaved normally, while only six (0.9%) of 644 eggs obtained from four females in 1976 did so. In 1978, 38 (47.5%) of 80 eggs obtained from a female cleaved normally. In total, 614 (45.7%) of 1343 eggs obtained from the nine females in the three years cleaved normally. The normally cleaved eggs developed almost normally during the embryonic stage. While a few embryos became abnormal about the hatching stage, 571 (42.5%) embryos hatched normally (Fig. 1a). Although 537 (40.0%) became feeding tadpoles, they were gradualy delayed in development, became thin and died without attaining metamorphosis.

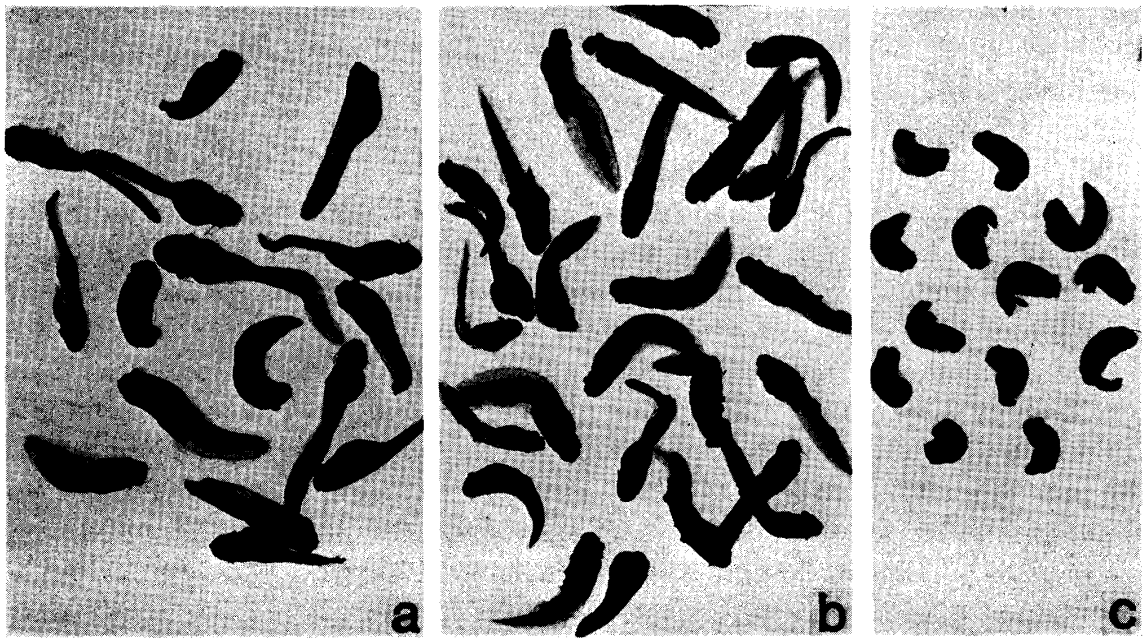


Fig. 1. Abnormalities at the embryonic and tadpole stages in the hybrids between female *Rana japonica* and male *Rana dybowskii* or *Rana amurensis coreana*. ×2.5

a. Hybrids, *Rana japonica* ♀ × *Rana dybowskii* from Tsushima ♂
b. Hybrids, *Rana japonica* ♀ × *Rana dybowskii* from Korea ♂
c. Hybrids, *Rana japonica* ♀ × *Rana amurensis coreana* ♂

Eight female *Rana japonica* were mated with six male *Rana dybowskii* from Korea in 1968 and 1970 (Table 1). While 787 (96.3%) of 817 eggs obtained from four females in 1968 cleaved normally, 399 (58.4%) of 683 eggs obtained from four females in 1970 did so. Thus, 79.1% of 1500 eggs in total obtained from the eight females in the two years cleaved normally. These normally cleaved eggs were

very similar in developmental capacity to those inseminated with sperm of the males from Tsushima (Fig. 1b). Although 64.5% hatched normally and 42.2% became feeding tadpoles, all the tadpoles gradually became emaciated and died before metamorphosis.

g. Crosses with male *Rana amurensis coreana*

Four female *Rana japonica* were mated with four male *Rana amurensis coreana* in 1970 (Table 1). Of 939 eggs obtained from these females, 244 (26.0%) cleaved normally. Most of the normally cleaved eggs died of various abnormalities during the embryonic stage (Fig. 1c). Eventually, only 72 (7.7%) hatched normally and 47 (5.0%) became feeding tadpoles. All of these tadpoles gradually became thin and died before metamorphosis.

h. Crosses with male *Rana longicrus*

Four female *Rana japonica* were mated with three male *Rana longicrus* in 1981 (Table 1). Of 593 eggs obtained from these females, 545 (91.9%) cleaved normally. Most of the normally cleaved eggs developed normally; 470 (79.3%) hatched normally, 438 (73.9%) became feeding tadpoles, and 415 (70.0%) attained completion of metamorphosis.

i. Crosses with a male *Rana latouchii*

No normally cleaved eggs were obtained from four female *Rana japonica* by mating with a male *Rana latouchii* in 1981 (Table 1).

j. Crosses with male *Rana temporaria*

Fifteen female *Rana japonica* were mated with six male *Rana temporaria* in 1962, 1975 and 1976 (Table 1). While 93.3% of 630 eggs obtained from four females in 1975 cleaved normally, 49.8% and 58.7% of the respective total number of eggs obtained from seven or four females did so in 1962 and 1976, respectively. In these two years, almost all of the remaining eggs cleaved abnormally owing to polyspermy. Many of the normally cleaved eggs became abnormal and died during the embryonic stage. In total, 33.6% of 3056 eggs obtained from the 15 females hatched normally, 26.9% became feeding tadpoles and 22.3% attained completion of metamorphosis.

k. Crosses with male *Rana arvalis*

Fourteen female *Rana japonica* were mated with five male *Rana arvalis* in 1962, 1976 and 1977 (Table 1). In each of these years, 4.3~28.6%, 20.8% on the average, of the respective total number of eggs obtained from three, four or seven females cleaved normally. While a small number of the normally cleaved eggs died of various abnormalities during the embryonic stage, 526 (18.9%) embryos hatched normally. Thereafter, 398 (14.3%) became feeding tadpoles and 329 (11.8%) could metamorphose normally.

1. Crosses with a male *Rana dalmatina*

No normally cleaved eggs were obtained from three female *Rana japonica* by mating with a male *Rana dalmatina* in 1978 (Table 1).

m. Crosses with a male *Rana macrocnemis*

No normally cleaved eggs were obtained from four female *Rana japonica* by mating with a male *Rana macrocnemis* in 1968 (Table 1).

n. Crosses with a male *Rana sylvatica*

Two female *Rana japonica* were mated with a male *Rana sylvatica* in 1972. Although 163 (75.1%) of 217 eggs cleaved normally and 141 became late blastulae, all of them died before beginning of gastrulation.

2. Crosses between female *Rana ornativentris* and males of 13 species

a. Control matings of *Rana ornativentris*

In 10 breeding seasons of the years 1962~1981, matings were made between 30 females and 20 males (Table 2). The results showed that 76.9~97.5% of the respective total number of eggs in each breeding season, 2980 (89.7%) of 3322 eggs in total, cleaved normally. After a small number of the normally cleaved eggs died of various abnormalities during the embryonic stage, 82.3% hatched normally. Thereafter, 79.6% became feeding tadpoles and 74.3% attained completion of metamorphosis.

b. Crosses with male *Rana japonica*

No normally cleaved eggs were obtained from two females by mating with two male *Rana japonica* in 1962 (Table 2).

c. Crosses with male *Rana chensinensis*

Eight female *Rana ornativentris* were mated with eight male *Rana chensinensis* in 1962 and 1975 (Table 2). While 424 (31.5%) of 1348 eggs obtained from six females cleaved normally by inseminating with sperm of six male *Rana chensinensis* in 1962, only two (0.8%) of 265 eggs obtained from two females did so by inseminating with sperm of two male *Rana chensinensis* in 1975. Although the normally cleaved eggs mostly developed normally during the embryonic stage, that is, 23.1% of the total number of eggs hatched normally, only 12.2% became feeding tadpoles and 1.6% attained completion of metamorphosis.

d. Crosses with male *Rana okinavana*

No normally cleaved eggs were obtained from four female *Rana ornativentris* by mating with two male *Rana okinavana* in 1977 (Table 2).

e. Crosses with male *Rana tsushimensis*

No normally cleaved eggs were obtained from three female *Rana ornativentris* by mating with two male *Rana tsushimensis* in 1963 (Table 2).

TABLE 2

Developmental capacity of hybrids between female *Rana ornativentris* and male brown frogs of 13 species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1962	*ornat.* (2)	*ornat.* (2)	364	343(94.2%)	342(94.0%)	342(94.0%)	339(93.1%)	337(92.6%)	316(86.8%)
		jap. (2)	210	0	0	0	0	0	0
	ornat. (6)	*chen.* (6)	1348	424(31.5%)	415(30.8%)	413(30.6%)	371(27.5%)	194(14.4%)	23(1.7%)
	ornat. (3)	*temp.* (2)	239	164(68.6%)	154(64.4%)	139(58.2%)	22(9.2%)	20(8.4%)	13(5.4%)
	ornat. (2)	*arv.* (2)	292	0	0	0	0	0	0
1963	*ornat.* (3)	*ornat.* (3)	314	306(97.5%)	306(97.5%)	306(97.5%)	306(97.5%)	306(97.5%)	303(96.5%)
		tsu. (2)	530	0	0	0	0	0	0
1964	*ornat.* (3)	*ornat.* (1)	160	150(93.8%)	147(91.9%)	147(91.9%)	144(90.0%)	137(85.6%)	126(78.8%)
		temp. (1)	286	163(57.0%)	155(54.2%)	142(49.7%)	29(10.1%)	17(5.9%)	4(1.4%)
1965	*ornat.* (1)	*ornat.* (1)	153	151(98.7%)	150(98.0%)	150(98.0%)	147(96.1%)	146(95.4%)	144(94.1%)
		temp. (1)	789	455(57.7%)	441(55.9%)	436(55.3%)	421(53.4%)	380(48.2%)	21(2.7%)
1968	*ornat.* (3)	*ornat.* (1)	255	196(76.9%)	196(76.9%)	195(76.5%)	188(73.7%)	181(71.0%)	172(67.5%)
		dyb. K (2)	454	14(3.1%)	10(2.2%)	10(2.2%)	10(2.2%)	5(1.1%)	1(0.2%)
		macro. (1)	161	0	0	0	0	0	0
1970	*ornat.* (4)	*ornat.* (3)	827	745(90.1%)	728(88.0%)	715(86.5%)	713(86.2%)	690(83.4%)	606(73.7%)
		dyb. T (3)	265	13(4.9%)	8(3.1%)	8(3.1%)	8(3.1%)	8(3.1%)	0
		dyb. K (2)	285	0	0	0	0	0	0
		amur. (2)	196	11(5.6%)	0	0	0	0	0
1972	*ornat.* (1)	*syl.* (1)	462	0	0	0	0	0	0
1975	*ornat.* (2)	*ornat.* (2)	260	246(94.6%)	246(94.6%)	240(92.3%)	218(83.9%)	213(81.9%)	213(81.9%)
		chen. (2)	265	2(0.8%)	2(0.8%)	2(0.8%)	2(0.8%)	2(0.8%)	2(0.8%)
		dyb. T (2)	270	3(1.1%)	3(1.1%)	3(1.1%)	3(1.1%)	3(1.1%)	0
		temp. (2)	290	254(87.6%)	217(74.8%)	209(72.1%)	184(63.5%)	53(18.3%)	48(16.6%)
		dalm. (1)	235	0	0	0	0	0	0
1976	*ornat.* (2)	*ornat.* (2)	234	218(93.2%)	192(82.1%)	184(78.6%)	171(73.1%)	166(70.9%)	161(68.8%)
		dyb. T (1)	122	0	0	0	0	0	0
		temp. (1)	233	83(35.6%)	82(35.2%)	41(17.6%)	39(16.7%)	11(4.7%)	3(1.3%)
1977	*ornat.* (4)	*ornat.* (2)	406	324(79.8%)	312(76.9%)	301(74.1%)	295(72.7%)	280(69.0%)	274(67.5%)
		oki. (2)	491	0	0	0	0	0	0
		arv. (2)	519	0	0	0	0	0	0
1981	*ornat.* (2)	*ornat.* (3)	349	301(80.3%)	222(63.6%)	219(62.8%)	213(61.0%)	189(54.2%)	154(44.1%)
		long. (3)	296	0	0	0	0	0	0
		lato. (1)	276	0	0	0	0	0	0
Total	*ornat.* (30)	*ornat.* (20)	3322	2980(89.7%)	2841(85.5%)	2799(84.3%)	2734(82.3%)	2645(79.6%)	2469(74.3%)
	ornat. (2)	*jap.* (2)	212	0	0	0	0	0	0
	ornat. (8)	*chen.* (8)	1613	426(26.4%)	417(25.9%)	415(25.7%)	373(23.1%)	196(12.2%)	25(1.6%)
	ornat. (4)	*oki.* (2)	491	0	0	0	0	0	0
	ornat. (3)	*tsu.* (2)	530	0	0	0	0	0	0
	ornat. (8)	*dyb.* T (6)	657	16(2.4%)	11(1.7%)	11(1.7%)	11(1.7%)	11(1.7%)	0
	ornat. (7)	*dyb.* K (4)	739	14(1.9%)	10(1.4%)	10(1.4%)	10(1.4%)	5(0.7%)	1(0.1%)
	ornat. (4)	*amur.* (2)	196	11(5.6%)	0	0	0	0	0
	ornat. (2)	*long.* (3)	296	0	0	0	0	0	0
	ornat. (2)	*lato.* (1)	276	0	0	0	0	0	0
	ornat. (11)	*temp.* (7)	1837	1119(60.9%)	1049(57.1%)	967(52.6%)	695(37.8%)	481(26.2%)	89(4.8%)
	ornat. (6)	*arv.* (4)	811	0	0	0	0	0	0
	ornat. (2)	*dalm.* (1)	235	0	0	0	0	0	0
	ornat. (3)	*macro.* (1)	161	0	0	0	0	0	0
	ornat. (1)	*syl.* (1)	462	0	0	0	0	0	0

f. Crosses with male *Rana dybowskii* from Tsushima or Korea

Eight female *Rana ornativentris* were mated with six male *Rana dybowskii* from Tsushima in 1970, 1975 and 1976 (Table 2). While no normally cleaved eggs were obtained from five of these females, eight of 138 eggs from one of the other three females and five of 53 eggs from another female cleaved normally in 1970, and three of 130 eggs from one female did so in 1975. It was found that 16 (2.4%) of 657 eggs in total obtained from the eight females cleaved normally. Of these normally cleaved eggs, the five which had been derived from one female in 1970

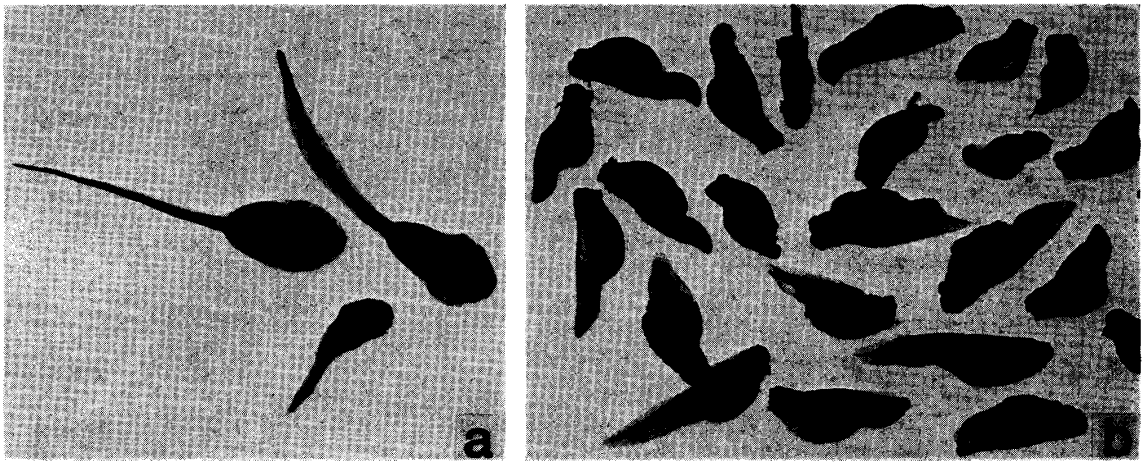


Fig. 2. Abnormalities at the embryonic and tadpole stages in the hybrids between female *Rana ornativentris* and male *Rana dybowskii* from Tsushima or *Rana temporaria*. ×2.5

a. Hybrids, *Rana ornativentris* ♀ × *Rana dybowskii* from Tsushima ♂

b. Hybrids, *Rana ornativentris* ♀ × *Rana temporaria* ♂

could not develop beyond the blastula stage. The other 11 eggs hatched normally and became feeding tadpoles. However, all of them died of underdevelopment without attaining metamorphosis (Fig. 2a).

Seven female *Rana ornativentris* were mated with four male *Rana dybowskii* collected from Korea in 1968 and 1970 (Table 2). The results were very similar to those obtained from matings with male *Rana dybowskii* from Tsushima. While no normally cleaved eggs were produced from four females by mating with two males in 1970, five of 84 eggs obtained from one of the two females used in 1968 and nine of 191 eggs obtained from the other female cleaved normally. Thus, it was found that only 14 (1.9%) of 739 eggs in total obtained from the seven females cleaved normally. Of these normally cleaved eggs, five and five derived from the two females hatched normally, four and one became feeding tadpoles and eventually one of the former four tadpoles completed metamorphosis. The others died of underdevelopment or edema.

g. Crosses with male *Rana amurensis coreana*

Four female *Rana ornativentris* were mated with two male *Rana amurensis coreana* in 1970 (Table 2). While no normally cleaved eggs were produced from two females, eight of 75 eggs obtained from another female and three of 83 eggs from the remaining female cleaved normally. However, all these normally cleaved eggs became abnormal and died at the blastula stage.

h. Crosses with male *Rana longicrus*

No normally cleaved eggs were obtained from two female *Rana ornativentris* by mating with three male *Rana longicrus* in 1981 (Table 2).

i. Crosses with a male *Rana latouchii*

No normally cleaved eggs were obtained from two female *Rana ornativentris* by

mating with a male *Rana latouchii* in 1981 (Table 2).

j. Crosses with male *Rana temporaria*

Eleven female *Rana ornativentris* were mated with seven male *Rana temporaria* in 1962, 1964, 1965, 1975 and 1976 (Table 2). It was found that 35.6~87.6% of the respective total number of eggs in each of the five years, 1119 (60.9%) of 1837 eggs in total, cleaved normally, while 494 other eggs cleaved irregularly owing to polyspermy. Most of the normally cleaved eggs developed normally during the embryonic stage, although they were slightly delayed in development as compared with the controls. A small number of embryos became abnormal in tail shape with the tail being short, curved or dorso-ventrally wide (Fig. 2b). After many embryos died of underdevelopment or edema, 695 (37.8%) hatched normally. Of these normally hatched tadpoles, 214 died of ill-development without taking food. Although the others began to eat and grow, 132 of them died before too long from loss of appetite. Of the other tadpoles, 260 were abnormal in body shape; they had a excessively large head and a short tail. These abnormal tadpoles were all feeble and died before the metamorphosing stage. The remaining 89 (4.8%) tadpoles could attain completion of metamorphosis.

k. Crosses with male *Rana arvalis*

No normally cleaved eggs were obtained from six female *Rana ornativentris* by mating with four male *Rana arvalis* in 1962 and 1977 (Table 2).

l. Crosses with a male *Rana dalmatina*

No normally cleaved eggs were obtained from two female *Rana ornativentris* by mating with a male *Rana dalmatina* in 1975 (Table 2).

m. Crosses with a male *Rana macrocnemis*

No normally cleaved eggs were obtained from three female *Rana ornativentris* by mating with a male *Rana macrocnemis* in 1968 (Table 2).

n. Cross with a male *Rana sylvatica*

No normally cleaved eggs were obtained from a female *Rana ornativentris* by mating with a male *Rana sylvatica* in 1972.

3. Crosses between female *Rana chensinensis* and males of nine species

a. Control matings of *Rana chensinensis*

In six breeding seasons of the years 1962~1981, matings were made between 21 females and 19 males (Table 3). The results showed that 61.3~98.1% of the respective total number of eggs in each year, 2185 (83.0%) of 2633 eggs in total, cleaved normally. After a comparatively large number of the normally cleaved eggs died of various abnormalities during the embryonic stage, 38.3~97.4%, 60.6% on the average, hatched normally. After 36.1~95.5%, 57.3% on the average, became feeding tadpoles, 30.1~93.5%, 52.9% on the average, attained

TABLE 3

Developmental capacity of hybrids between female *Rana chensinensis* and male brown frogs of nine species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1962	*chen.* (6)	*chen.* (6)	870	619(71.2%)	591(67.9%)	580(66.7%)	536(61.6%)	522(60.0%)	512(58.9%)
		jap. (3)	618	246(39.8%)	176(28.5%)	176(28.5%)	71(11.5%)	63(10.2%)	29(4.7%)
		ornat. (3)	471	363(77.1%)	154(32.7%)	140(29.7%)	80(17.0%)	72(15.3%)	26(5.5%)
		temp. (2)	466	318(68.2%)	214(45.9%)	203(43.6%)	60(12.9%)	13(2.8%)	0
		arv. (2)	240	92(38.3%)	86(35.8%)	86(35.8%)	84(35.0%)	51(21.3%)	20(8.3%)
1963	*chen.* (5)	*chen.* (5)	462	453(98.1%)	452(97.8%)	452(97.8%)	450(97.4%)	441(95.5%)	432(93.5%)
		tsu. (2)	1570	764(48.7%)	726(46.2%)	723(46.1%)	720(45.9%)	156(9.9%)	0
1970	*chen.* (2)	*chen.* (2)	164	150(91.5%)	115(70.1%)	115(70.1%)	109(66.5%)	78(47.6%)	70(42.7%)
		jap. (2)	101	49(48.5%)	20(19.8%)	15(14.9%)	12(11.9%)	8(7.9%)	1(1.0%)
		ornat. (2)	101	97(96.0%)	48(47.5%)	46(45.5%)	37(36.6%)	32(31.7%)	27(26.7%)
		tsu. (2)	86	40(46.5%)	28(32.6%)	28(32.6%)	24(27.9%)	0	0
		dyb. T (2)	382	376(98.4%)	171(44.8%)	153(40.1%)	90(23.6%)	24(6.3%)	4(1.0%)
	chen. (1)	*dyb.* K (1)	112	106(94.6%)	52(46.4%)	52(46.4%)	19(17.0%)	0	0
		amur. (1)	83	0	0	0	0	0	0
1975	*chen.* (2)	*chen.* (2)	269	165(61.3%)	144(53.5%)	104(38.7%)	103(38.3%)	97(36.1%)	81(30.1%)
		jap. (2)	161	122(75.8%)	98(60.9%)	39(24.2%)	26(16.2%)	12(7.5%)	2(1.2%)
		ornat. (2)	165	111(67.3%)	82(49.7%)	43(26.1%)	32(19.4%)	3(1.8%)	0
		tsu. (2)	101	48(47.5%)	40(39.6%)	26(25.7%)	19(18.8%)	14(13.9%)	0
		dyb. T (2)	337	301(89.3%)	265(78.6%)	121(35.9%)	118(35.0%)	76(22.6%)	0
		temp. (2)	130	78(60.0%)	57(43.9%)	30(23.1%)	28(21.5%)	15(11.5%)	2(1.5%)
1976	*chen.* (1)	*chen.* (1)	214	190(88.8%)	106(49.5%)	101(47.2%)	101(47.2%)	97(45.3%)	95(44.4%)
		dyb. T (1)	162	7(4.3%)	3(1.6%)	2(1.2%)	1(0.6%)	0	0
		arv. (1)	133	12(9.0%)	10(7.5%)	2(1.5%)	1(0.8%)	1(0.8%)	1(0.8%)
1981	*chen.* (5)	*chen.* (3)	654	608(93.0%)	353(94.0%)	311(47.6%)	296(45.3%)	273(41.7%)	201(30.7%)
	chen. (1)	*ornat.* (1)	78	71(91.0%)	16(20.5%)	14(18.0%)	12(15.4%)	11(14.1%)	11(14.1%)
	chen. (3)	*dyb.* T (3)	266	255(95.1%)	126(47.4%)	102(38.4%)	6(2.3%)	2(0.8%)	1(0.4%)
	chen. (5)	*long.* (3)	378	73(19.3%)	0	0	0	0	0
		lato. (1)	420	0	0	0	0	0	0
Total	*chen.* (21)	*chen.* (19)	2633	2185(83.0%)	1761(66.9%)	1663(63.2%)	1595(60.6%)	1508(57.3%)	1391(52.9%)
	chen. (10)	*jap.* (7)	880	417(47.4%)	294(33.4%)	230(26.1%)	109(12.4%)	83(9.4%)	32(3.6%)
	chen. (11)	*ornat.* (8)	815	642(78.8%)	300(36.8%)	243(29.8%)	161(19.8%)	118(14.5%)	64(7.9%)
	chen. (9)	*tsu.* (6)	1757	852(48.5%)	794(45.2%)	777(44.2%)	763(43.4%)	170(9.7%)	0
	chen. (8)	*dyb.* T (8)	1147	939(81.9%)	565(49.3%)	378(33.0%)	215(18.7%)	102(8.9%)	5(0.4%)
	chen. (1)	*dyb.* K (1)	112	106(94.6%)	52(46.4%)	52(46.4%)	19(17.0%)	0	0
	chen. (1)	*amur.* (1)	83	0	0	0	0	0	0
	chen. (5)	*long.* (3)	378	73(19.3%)	0	0	0	0	0
	chen. (5)	*lato.* (1)	420	0	0	0	0	0	0
	chen. (8)	*temp.* (4)	596	396(66.4%)	271(45.5%)	233(39.1%)	88(14.8%)	28(4.7%)	2(0.3%)
	chen. (7)	*arv.* (3)	373	104(27.9%)	96(25.7%)	88(23.6%)	85(22.8%)	52(13.9%)	21(5.6%)

completion of metamorphosis.

b. Crosses with male *Rana japonica*

Ten female *Rana chensinensis* were mated with seven male *Rana japonica* in 1962, 1970 and 1975 (Table 3). It was found that 39.8~75.8% of the respective total number of eggs in each year, 417 (47.4%) of 880 in total, cleaved normally. During the embryonic stage, about three-fourths of the normally cleaved eggs became abnormal and died (Fig. 3a), while 11.5~16.2%, 12.4% on the average, hatched normally. Eventually, 83 (9.4%) became feeding tadpoles and 32 (3.6%) attained completion of metamorphosis.

c. Crosses with male *Rana ornativentris*

Eleven female *Rana chensinensis* were mated with eight male *Rana ornativentris*

in 1962, 1970, 1975 and 1981 (Table 3). Of the respective total number of eggs in each year, 67.3~96.0%, 642 (78.8%) of 815 eggs in total, cleaved normally. However, more than half of the normally cleaved eggs became abnormal neurulae and died owing to incomplete invagination at the gastrula stage, while 20.5~49.7%, 300 (36.8%) in total, became normal neurulae. After most of the normal neurulae gradually became abnormal embryos and died (Fig. 3b), 15.4~36.6%, 19.8% on the average, hatched normally. Thereafter, 1.8~31.7%, 14.5% on the average, became feeding tadpoles, and 0~26.7%, only 64 (7.9%) in total, attained completion of metamorphosis.

d. Crosses with male *Rana tsushimensis*

Nine female *Rana chensinensis* were mated with six male *Rana tsushimemsis* in 1963, 1970 and 1975 (Table 3). In each year, 46.5~48.7% of the respective total number of eggs, 852 (48.5%) of 1757 eggs in total, cleaved normally, and 18.8~45.9%, 43.4% on the average, hatched normally. Although 0~13.9%,

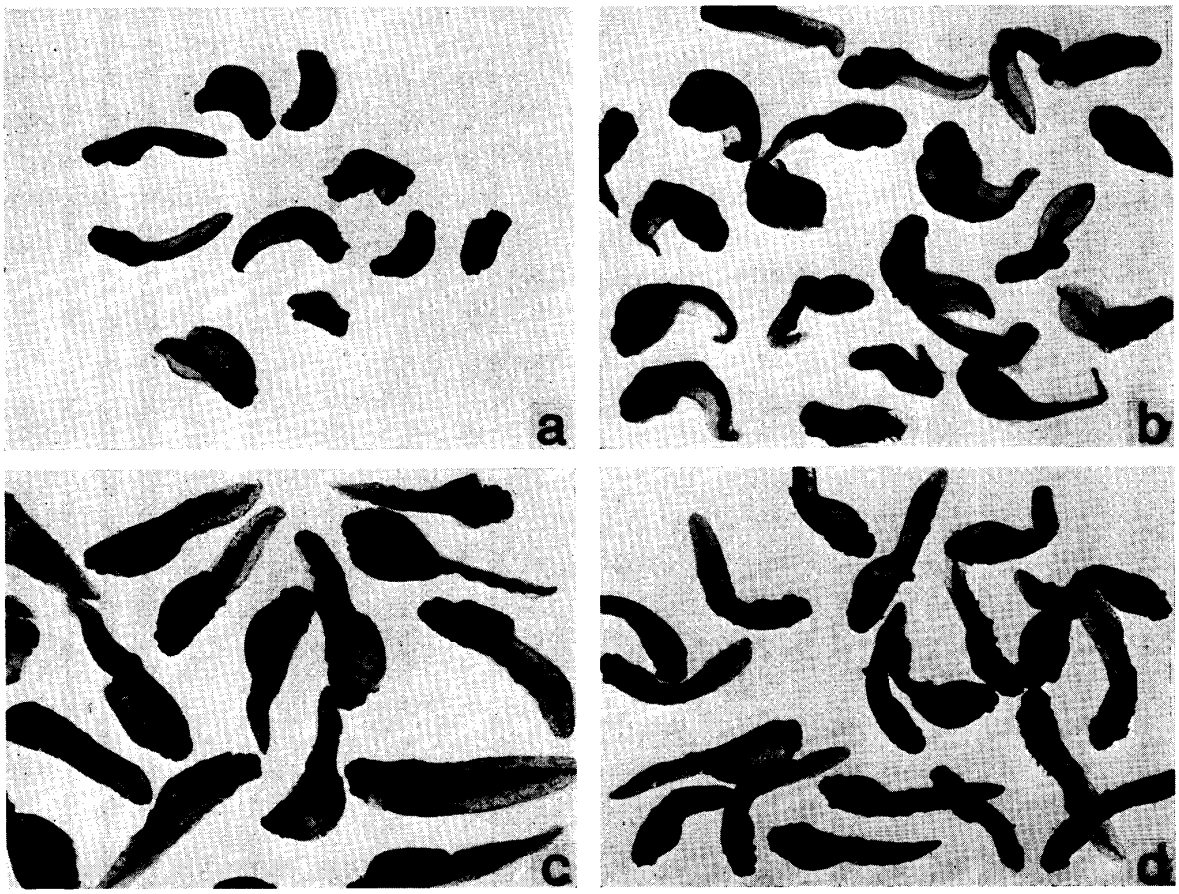


Fig. 3. Abnormalities at the embryonic and tadpole stages in the hybrids between female *Rana chensinensis* and males of three species. ×2.5

a. Hybrids, *Rana chensinensis* ♀ × *Rana japonica* ♂
b. Hybrids, *Rana chensinensis* ♀ × *Rana ornativentris* ♂
c. Hybrids, *Rana chensinensis* ♀ × *Rana dybowskii* from Tsushima ♂
d. Hybrids, *Rana chensinensis* ♀ × *Rana dybowskii* from Korea ♂

9.7% on the average, became feeding tadpoles, all of them became gradually emaciated and died without attaining metamorphosis.

e. Crosses with male *Rana dybowskii* from Tsushima or Korea

Eight female *Rana chensinensis* were mated with eight male *Rana dybowskii* from Tsushima in 1970, 1975, 1976 and 1981 (Table 3). While only seven (4.3%) of 162 eggs obtained from a female cleaved normally in 1976, 89.3~98.4% of the respective total number of eggs did so in each of the other three years. About two-fifths of the normally cleaved eggs were incomplete in gastrulation and died of abnormalities at the gastrula or neurula stage. After the remaining embryos became normal neurulae, about one-third of them became abnormal at the tail-bud stage. At the hatching stage, 163 (14.2%) embryos became abnormal, that is, the gills were underdeveloped, the tail was curved, and the body was emaciated or edematous (Fig. 3c). The other 215 (18.7%) hatched normally, but about half of them died without taking food (Fig. 3c). Although 102 (8.9%) tadpoles barely began to eat, all of them gradually died, except five (0.4%). The latter completed metamorphosis and became dwarf frogs. These frogs died without taking food.

A female *Rana chensinensis* was mated with a male *Rana dybowskii* collected from Korea in 1970 (Table 3). Although 106 (94.6%) of 112 eggs cleaved normally, 36 died at the blastula stage and 18 others died of incomplete invagination at the gastrula stage. Of the remaining 52 which became normal tail-bud embryos, 33 were abnormal at the hatching stage. The other 19 embryos hatched normally, but died without taking food (Fig. 3d).

f. A cross with a male *Rana amurensis coreana*

No normally cleaved eggs were obtained from a female *Rana chensinensis* by mating with a male *Rana amurensis coreana* in 1970 (Table 3).

g. Crosses with male *Rana longicrus*

Five female *Rana chensinensis* were mated with three male *Rana longicrus* in 1981. Although 73 (19.3%) of 378 eggs cleaved normally, all of them died at the blastula stage without commencing invagination (Table 3).

h. Crosses with a male *Rana latouchii*

No normally cleaved eggs were obtained from five female *Rana chensinensis* by mating with a male *Rana latouchii* in 1981 (Table 3).

i. Crosses with male *Rana temporaria*

Eight female *Rana chensinensis* were mated with four male *Rana temporaria* in 1962 and 1975 (Table 3). Of 596 eggs obtained from the females, 396 (66.4%) cleaved normally, while 196 others cleaved abnormally owing to polyspermy, as observed in the crosses between *Rana ornativentris* and *Rana temporaria*. The normally cleaved eggs began to retard in development as compared with the controls

at the early embryonic stage. Most of them became abnormal and died during the embryonic stage. Their general characteristic was that their tail was short and dorso-ventrally wide. While 88 (14.8%) hatched normally, 145 others were microcephalic, edematous and abnormal in tail shape. Chromosomes were examined in 20 of these abnormal embryos. The results showed that they were chromosomal mosaics.

Of the normally hatched tadpoles, 60 died without taking food. Although the other 28 began to eat, only five attained the metamorphosing stage and the remainders gradually became edematous and died. Three of the five metamorphosing tadpoles had a large head and a short tail and died before extrusion of the fore-legs. The other two barely completed metamorphosis.

j. Crosses with male *Rana arvalis*

Seven female *Rana chensinensis* were mated with three male *Rana arvalis* in 1962 and 1976 (Table 3). In 1962, 92 (38.3%) of 240 eggs obtained from six females cleaved normally, while only 12 (9.0%) of 133 eggs from one female did so in 1976. In total, 104 (27.9%) of 373 eggs cleaved normally. Most of them developed normally during the embryonic stage and 85 (22.8%) hatched normally. While many of the normally hatched tadpoles died of edema or underdevelopment without taking food, 52 (13.9%) became feeding tadpoles and 21 (5.6%) completed metamorphosis.

4. Crosses between female *Rana tsushimensis* and males of 13 species

a. Control matings of *Rana tsushimensis*

In 10 breeding seasons of the years 1963~1981, mating experiments were made between 39 females and 29 males (Table 4). It was found that 70.0~98.0% of the respective total number of eggs in each year, 3651 (90.9%) of 4016 eggs in total, cleaved normally. After about 15% died of various abnormalities during the embryonic stage, 48.9~92.2%, 75.7% on the average, hatched normally. Thereafter, 45.1~92.2%, 72.3% on the average, became feeding tadpoles, and 41.6~90.0%, 67.3% on the average, attained completion of metamorphosis (Fig. 4a).

b. Crosses with male *Rana japonica*

A total of 22 female *Rana tsushimensis* were mated with 14 male *Rana japonica* in 1963, 1966, 1967 and 1975 (Table 4). It was found that 84.7~92.9% of the respective total number of eggs in each year, 2185 (89.8%) of 2432 eggs in total, cleaved normally. While many of the normally cleaved eggs obtained in 1963, 1966 and 1967 and all of those obtained in 1975 died of various abnormalities during the tadpole stage, 55.5~77.3% hatched normally in 1963, 1966 and 1967. In total of the four years, 1237 (50.9%) eggs hatched normally. While most of the normally hatched tadpoles began to eat, they gradually lost their appetite and became emaciated. All the tadpoles died without attaining metamorphosis except three obtained in 1967. The latter barely completed meta-

TABLE 4

Developmental capacity of hybrids between female *Rana tsushimensis* and male brown frogs of 13 species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1963	*tsu.* (2)	*tsu.* (2)	141	135(95.7%)	133(94.3%)	130(92.2%)	130(92.2%)	130(92.2%)	127(90.0%)
		jap. (2)	221	192(86.9%)	123(55.7%)	123(55.7%)	123(55.7%)	85(38.5%)	0
		ornat. (2)	186	175(94.1%)	60(32.3%)	57(30.7%)	55(29.6%)	32(17.2%)	0
		chen. (2)	186	169(90.9%)	143(76.9%)	141(75.8%)	140(75.3%)	102(54.8%)	0
		temp. (2)	198	94(47.5%)	24(12.1%)	20(10.1%)	20(10.1%)	16(8.1%)	0
1966	*tsu.* (5)	*tsu.* (2)	213	201(94.4%)	197(92.5%)	192(90.1%)	186(87.3%)	180(84.5%)	172(80.8%)
		jap. (2)	454	413(91.0%)	304(67.0%)	295(65.0%)	252(55.5%)	141(31.1%)	0
		ornat. (2)	325	286(88.0%)	218(67.1%)	177(54.5%)	134(41.2%)	76(23.4%)	0
		arv. (1)	452	243(53.8%)	224(49.6%)	212(46.9%)	202(44.7%)	174(38.5%)	0
1967	*tsu.* (8)	*tsu.* (4)	677	639(94.4%)	620(91.6%)	607(89.7%)	599(88.5%)	568(83.9%)	532(78.6%)
		jap. (8)	1115	1036(92.9%)	994(89.2%)	955(85.7%)	862(77.3%)	814(73.0%)	3(0.3%)
		ornat. (8)	1019	1002(98.3%)	736(72.2%)	715(70.2%)	612(60.1%)	507(49.8%)	0
1968	*tsu.* (2)	*tsu.* (1)	255	250(98.0%)	239(93.7%)	230(90.2%)	188(73.7%)	176(69.0%)	172(67.5%)
		dyb. K (1)	601	591(98.3%)	294(48.9%)	0	0	0	0
		macro. (1)	386	32(8.3%)	32(8.3%)	32(8.3%)	32(8.3%)	32(8.3%)	0
1970	*tsu.* (5)	*tsu.* (5)	967	909(94.0%)	827(85.5%)	827(85.5%)	815(84.3%)	810(83.8%)	696(72.0%)
		dyb. K (5)	1241	1079(87.0%)	666(53.7%)	589(47.5%)	80(6.5%)	2(0.2%)	0
		amur. (5)	1314	1016(77.3%)	0	0	0	0	0
1972	*tsu.* (2)	*syl.* (1)	194	149(76.8%)	0	0	0	0	0
1975	*tsu.* (7)	*tsu.* (7)	646	535(82.8%)	493(76.3%)	418(64.7%)	408(63.2%)	362(56.0%)	355(55.0%)
		jap. (2)	642	544(84.7%)	435(67.8%)	273(42.5%)	0	0	0
		ornat. (2)	694	540(77.8%)	389(56.1%)	336(48.4%)	0	0	0
		chen. (2)	636	519(81.6%)	419(65.9%)	389(61.2%)	285(44.8%)	253(39.8%)	0
	tsu. (2)	*dyb.* T (1)	187	140(74.9%)	49(26.2%)	4(2.1%)	0	0	0
	tsu. (7)	*temp.* (2)	882	542(61.5%)	307(34.8%)	240(27.2%)	240(27.2%)	77(8.7%)	0
1976	*tsu.* (2)	*tsu.* (2)	286	271(94.8%)	262(91.6%)	215(75.2%)	201(70.3%)	192(67.1%)	182(63.6%)
		ornat. (2)	245	207(84.5%)	201(82.0%)	144(58.8%)	91(37.1%)	29(11.8%)	0
		chen. (1)	381	329(86.4%)	329(86.4%)	244(64.0%)	188(49.3%)	82(21.5%)	0
		dyb. T (1)	267	77(28.8%)	72(27.0%)	56(21.0%)	10(3.8%)	3(1.1%)	0
		temp. (1)	80	25(31.3%)	25(31.3%)	3(3.8%)	3(3.8%)	2(2.5%)	0
		arv. (2)	444	365(82.2%)	346(77.9%)	236(53.2%)	172(38.7%)	80(18.0%)	0
1977	*tsu.* (3)	*tsu.* (2)	232	163(70.0%)	129(55.4%)	123(52.8%)	114(48.9%)	105(45.1%)	97(41.6%)
		oki. (2)	362	194(53.6%)	175(48.3%)	163(45.0%)	156(43.1%)	154(42.5%)	108(29.8%)
		arv. (2)	514	297(57.8%)	187(36.4%)	181(35.2%)	160(31.1%)	155(30.2%)	0
1978	*tsu.* (1)	*tsu.* (1)	142	131(92.3%)	70(49.3%)	70(49.3%)	70(49.3%)	67(47.2%)	67(47.2%)
		oki. (1)	150	29(19.3%)	29(19.3%)	25(16.7%)	23(15.3%)	20(13.3%)	13(8.7%)
		dalm. (1)	127	6(4.7%)	0	0	0	0	0
1981	*tsu.* (4)	*tsu.* (3)	456	417(91.4%)	358(78.5%)	352(77.2%)	328(71.9%)	313(68.6%)	303(66.5%)
		long. (3)	504	432(85.7%)	410(81.3%)	56(11.1%)	3(0.6%)	3(0.6%)	0
		lato. (1)	356	69(19.4%)	0	0	0	0	0
Total	*tsu.* (39)	*tsu.* (29)	4016	3651(90.9%)	3323(82.7%)	3164(78.8%)	3039(75.7%)	2903(72.3%)	2703(67.3%)
	tsu. (22)	*jap.* (14)	2432	2185(89.8%)	1856(76.3%)	1646(67.7%)	1237(50.9%)	1040(42.8%)	3(0.1%)
	tsu. (24)	*ornat.* (16)	2469	2210(89.5%)	1604(65.0%)	1429(57.9%)	854(34.6%)	644(26.1%)	0
	tsu. (11)	*chen.* (5)	1203	1017(84.5%)	891(74.1%)	774(64.3%)	613(51.0%)	437(36.3%)	0
	tsu. (4)	*oki.* (3)	512	223(43.6%)	204(39.8%)	188(36.7%)	179(35.0%)	174(34.0%)	121(23.6%)
	tsu. (4)	*dyb.* T (2)	454	217(47.8%)	121(26.7%)	60(13.2%)	10(2.2%)	3(0.7%)	0
	tsu. (7)	*dyb.* K (6)	1842	1670(90.7%)	960(52.1%)	589(32.0%)	80(4.3%)	2(0.2%)	0
	tsu. (5)	*amur.* (5)	1314	1016(77.3%)	0	0	0	0	0
	tsu. (4)	*long.* (3)	504	432(85.7%)	410(81.3%)	56(11.1%)	3(0.6%)	3(0.6%)	0
	tsu. (4)	*lato.* (1)	356	69(19.4%)	0	0	0	0	0
	tsu. (11)	*temp.* (5)	1160	661(57.0%)	356(30.7%)	263(22.7%)	263(22.7%)	95(8.2%)	0
	tsu. (10)	*arv.* (5)	1414	905(64.0%)	757(53.5%)	629(44.5%)	534(37.8%)	409(28.9%)	0
	tsu. (1)	*dalm.* (1)	127	6(4.7%)	0	0	0	0	0
	tsu. (2)	*macro.* (1)	386	32(8.3%)	32(8.3%)	32(8.3%)	32(8.3%)	32(8.3%)	0
	tsu. (2)	*syl.* (1)	194	149(76.8%)	0	0	0	0	0

morphosis.

c. Crosses with male *Rana ornativentris*

A total of 24 female *Rana tsushimensis* were mated with 16 male *Rana ornativentris* in 1963, 1966, 1967, 1975 and 1976 (Table 4). Of the respective total number of eggs in each year, 77.8~98.3%, 2210 (89.5%) of 2469 eggs in total, cleaved normally. However, many of the normally cleaved eggs in 1963, 1966, 1967 and 1976 and all of those in 1975 died of various abnormalities during the embryonic stage. Although 29.6~60.1% of eggs in 1963, 1966, 1967 and 1976 hatched normally, and 11.8~49.8% became feeding tadpoles, all the tadpoles became abnormal and died without attaining the metamorphosing stage.

d. Crosses with male *Rana chensinensis*

Eleven female *Rana tsushimensis* were mated with five male *Rana chensinensis* in 1963, 1975 and 1976 (Table 4). The results showed that 81.6~90.9% of the respective total number of eggs in each year, 1017 (84.5%) of 1203 eggs in total, cleaved normally. After many of the normally cleaved eggs died of various abnormalities during the embryonic stage, 44.8~75.3% hatched normally. Although 21.5~54.8% became feeding tadpoles, all of them lost their appetite and died of emaciation without attaining metamorphosis.

e. Crosses with male *Rana okinavana*

Four female *Rana tsushimensis* were mated with three male *Rana okinavana* in 1977 and 1978 (Table 4). In these two years, 53.6% and 19.3% of the respective total number of eggs obtained from three or one female, 223 (43.6%) of 512 eggs in total, cleaved normally. After many of the normally cleaved eggs died of various abnormalities during the embryonic stage, 43.1% and 15.3% hatched normally, and thereafter 29.8% and 8.7% attained completion of metamorphosis in 1977 and 1978, respectively. In total, 121 of the normally cleaved eggs became normally metamorphosed frogs.

The percentages of normally cleaved eggs were considerably lower than those obtained by KURAMOTO (1974). As these lower percentages were considered to be attributable to captivity of the males in a colder condition for about three months, the present authors repeated this kind of cross late in 1981 by using a male *Rana okinavana* shortly after collection. The result showed that 712 (97.1%) of 733 eggs obtained from three female *Rana tsushimensis* cleaved normally and 518 (70.7%) hatched normally by inseminating with sperm of this male, while 463 (99.1%) of 467 control eggs cleaved normally and 346 (74.1%) hatched normally.

f. Crosses with male *Rana dybowskii* from Tsushima and Korea

Four female *Rana tsushimensis* were mated with two male *Rana dybowskii* from Tsushima in 1975 and 1976 (Table 4). Of the respective total number of eggs obtained from two females in each year, 74.9% and 28.8%, 217 (47,8%) of 454 eggs in total, cleaved normally.

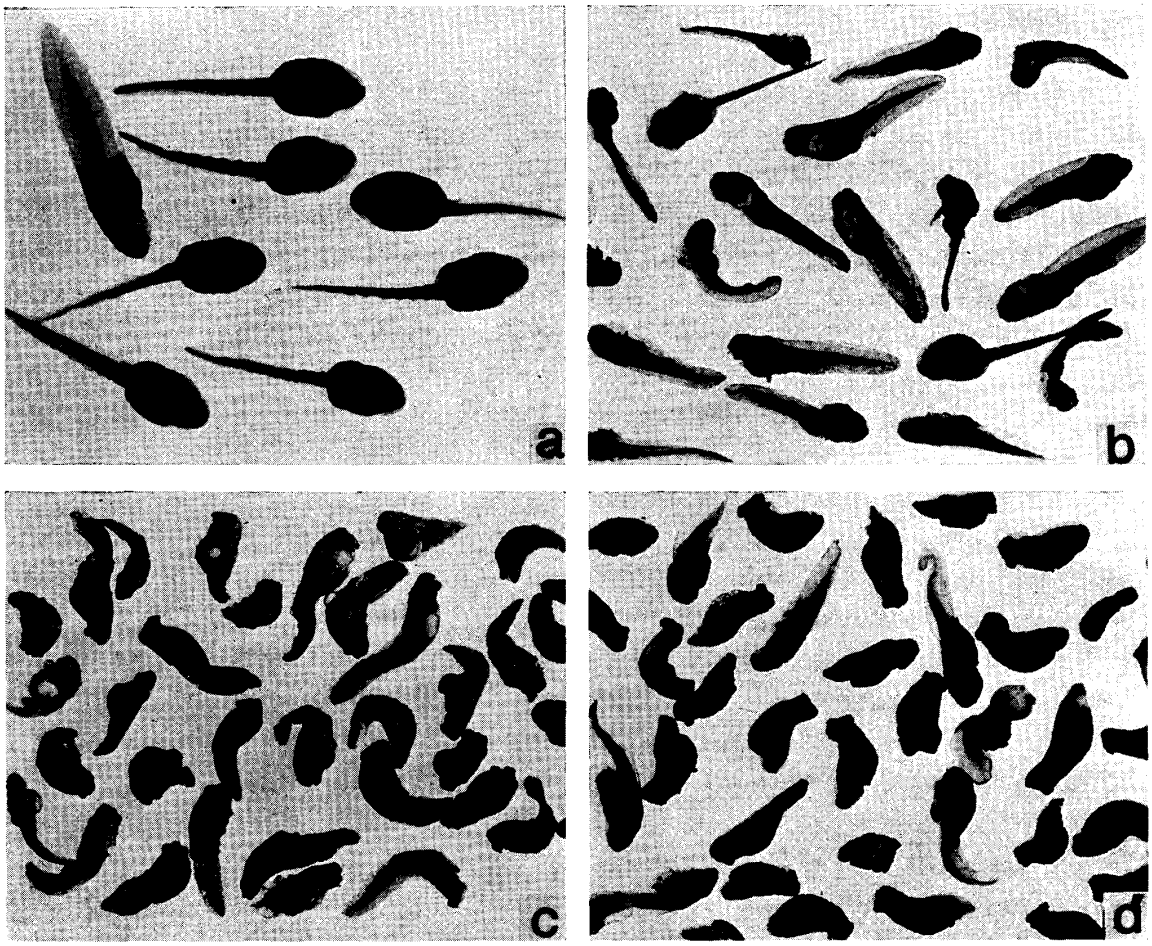


Fig. 4. Abnormalities at the embryonic and tadpole stages in the hybrids between female *Rana tsushimensis* and males of three species. ×2.5

a. Controls, *Rana tsushimensis* ♀ × *Rana tsushimensis* ♂
b. Hybrids, *Rana tsushimensis* ♀ × *Rana dybowskii* from Korea ♂
c. Hybrids, *Rana tsushimensis* ♀ × *Rana longicrus* ♂
d. Hybrids, *Rana tsushimensis* ♀ × *Rana temporaria* ♂

The normally cleaved eggs obtained in 1975 mostly became abnormal neurulae and tail-bud embryos owing to incomplete invagination at the gastrula stage. No eggs hatched normally in this year. In contrast, most of the normally cleaved eggs became normal tail-bud embryos in 1976, although only 10 (3.8%) hatched normally and only three (1.1%) began to eat. No tadpoles could attain metamorphosis.

Seven female *Rana tsushimensis* were mated with six male *Rana dybowskii* from Korea in 1968 and 1970 (Table 4). In 1968, 98.3% of 601 eggs obtained from two females cleaved normally and 48.9% became normal neurulae. However, all of them died of abnormalities at the tail-bud stage. In 1970, 87.0% of 1241 eggs obtained from five females cleaved normally, and 47.5% became normal tail-bud embryos, while the others died of abnormalities. An overwhelming majority of the normal tail-bud embryos died of various abnormalities about the hatching stage (Fig. 4b). Although 80 (6.5%) embryos barely hatched nor-

mally, all of them died without taking food except two which could not attain the metamorphosing stage.

g. Crosses with male *Rana amurensis coreana*

Five female *Rana tsushimensis* were mated with five male *Rana amurensis coreana* in 1970 (Table 4). Of 1314 eggs obtained from the five females, 1016 (77.3%) cleaved normally. All the normally cleaved eggs ceased their development at the late blastula or early gastrula stage.

h. Crosses with male *Rana longicrus*

Four female *Rana tsushimensis* were mated with three male *Rana longicurus* in 1981 (Table 4). Of 504 eggs of these females, 432 (85.7%) cleaved normally, and 410 (81.3%) became normal neurulae. However, most of the latter became haploid-shaped embryos at the tail-bud stage and died sooner or later. Although the other 56 were normal at the tail-bud stage, 53 of them became abnormal at the hatching stage and died before too long (Fig. 4c). Only three embryos exceptionally hatched normally and became feeding tadpoles. These tadpoles died without attaining metamorphosis.

i. Crosses with a male *Rana latouchii*

Four female *Rana tsushimensis* were mated with a male *Rana latouchii* in 1981 (Table 4). Of 356 eggs obtained from the four females, 69 (19.4%) cleaved normally. All the normally cleaved eggs became abnormal owing to incomplete invagination at the gastrula stage. They died of abnormalities at the neurula stage.

j. Crosses with male *Rana temporaria*

Eleven female *Rana tsushimensis* were mated with five male *Rana temporaria* in 1963, 1975 and 1976 (Table 4). In each of these years, 31.3~61.5% of the respective total number of eggs obtained from two or seven females, 661 (57.0%) of 1160 eggs in total, cleaved normally. After more than half of the normally cleaved eggs died of various abnormalities during the embryonic stage (Fig. 4d), 263 (22.7%) hatched normally. Most of the hatched tadpoles died without taking food, while 95 (8.2%) became feeding tadpoles which gradually lost their appetite and died without attaining metamorphosis.

k. Crosses with male *Rana arvalis*

Ten female *Rana tsushimensis* were mated with five male *Rana arvalis* in 1966, 1976 and 1977 (Table 4). In each of these years, 53.8~82.2% of the respective total number of eggs obtained from 2~5 females, 905 (64.0%) of 1414 eggs in total, cleaved normally. While some of the normally cleaved eggs died of various abnormalities, 31.1~44.7%, 37.8% on the average, hatched normally, and 18.0~38.5%, 28.9% on the average, became feeding tadpoles. However, all these tadpoles gradually lost their appetite, became emaciated and died without

attaining metamorphosis.

1. A cross with a male *Rana dalmatina*

A female *Rana tsushimensis* was mated with a male *Rana dalmatina* in 1978. Although six (4.7%) of 127 eggs obtained from the female cleaved normally, all of the normally cleaved eggs ceased development at the blastula stage (Table 4).

m. Crosses with a male *Rana macrocnemis*

Two female *Rana tsushimensis* were mated with a male *Rana macrocnemis* in 1968 (Table 4). Only 32 (8.3%) of 386 eggs obtained from the two females cleaved normally. The normally cleaved eggs all developed normally during the embryonic stage, hatched normally and became feeding tadpoles. However, all these tadpoles gradually lost their appetite, became emaciated and died without attaining metamorphosis.

n. Crosses with a male *Rana sylvatica*

Two female *Rana tsushimensis* were mated with a male *Rana sylvatica* in 1972 (Table 4). Although 149 (76.8%) of 194 eggs cleaved normally and 130 became late blastulae, all of them died before beginning of gastrulation.

5. Crosses between female *Rana dybowskii* from Tsushima and males of 13 species

a. Control matings of *Rana dybowskii* from Tsushima

A total of 21 female *Rana dybowskii* collected from Tsushima were mated with 14 male *Rana dybowskii* from Tsushima in 1968, 1970, 1975, 1976, 1978 and 1981 (Table 5). In each of these years, 71.0~99.1% of the respective number of eggs obtained from 1~6 females, 1990 (90.3%) of 2203 eggs in total, cleaved normally. The normally cleaved eggs mostly developed normally during the embryonic stage, while a small number of them died of various abnormalities. Of 1633 embryos (74.1%) which hatched normally, 1544 (70.1%) became normally feeding tadpoles and 1441 (65.4%) attained completion of metamorphosis.

b. Crosses with male *Rana dybowskii* from Korea

Six female *Rana dybowskii* collected from Tsushima were mated with four male *Rana dybowskii* from Korea in 1968 and 1970 (Table 5). Of 1312 eggs, 1298 (98.9%) cleaved normally. The normally cleaved eggs were nearly the same as the controls in developmental capacity. Most of them developed normally during the embryonic stage as those produced from the control matings. After 1239 (94.4%) eggs became normal tail-bud embryos, 1122 (85.5%) hatched normally and 1086 (82.8%) became normally feeding tadpoles. Eventually, 841 (64.1%) attained completion of metamorphosis.

c. Crosses with male *Rana japonica*

Eleven female *Rana dybowskii* collected from Tsushima were mated with nine

TABLE 5

Developmental capacity of hybrids between female *Rana dybowskii* from Tsushima and male brown frogs of 13 species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1966	*dyb.* T (1)	arv. (1)	157	8(5.1%)	2(1.3%)	2(1.3%)	2(1.3%)	0	0
1968	*dyb.* T (3)	*dyb.* T (1)	348	345(99.1%)	325(93.4%)	324(93.1%)	277(79.6%)	270(77.6%)	231(66.4%)
		dyb. K (1)	1038	1028(99.0%)	998(96.2%)	993(95.7%)	883(85.1%)	858(82.7%)	664(64.0%)
		macro. (1)	271	0	0	0	0	0	0
1970	*dyb.* T (6)	*dyb.* T (6)	457	399(87.3%)	384(84.0%)	374(81.8%)	374(81.8%)	354(77.5%)	341(74.6%)
		jap. (6)	838	513(61.2%)	321(38.3%)	292(34.8%)	247(29.5%)	201(24.0%)	25(3.0%)
		ornat. (6)	718	525(73.1%)	453(63.1%)	440(61.3%)	369(51.4%)	351(48.9%)	284(39.6%)
		chen. (6)	1485	245(16.5%)	131(8.8%)	108(7.3%)	100(6.7%)	99(6.7%)	75(5.1%)
	dyb. T (3)	*tsu.* (3)	265	144(54.3%)	120(45.3%)	43(16.2%)	43(16.2%)	43(16.2%)	0
		dyb. K (3)	274	270(98.5%)	259(94.5%)	246(89.8%)	239(87.2%)	228(83.2%)	177(64.6%)
		amur. (3)	333	31(9.3%)	0	0	0	0	0
1972	*dyb.* T (1)	*syl.* (1)	172	0	0	0	0	0	0
1975	*dyb.* T (2)	*dyb.* T (2)	295	249(84.4%)	233(79.0%)	225(76.3%)	223(75.6%)	208(70.5%)	199(67.5%)
		jap. (2)	185	164(88.7%)	142(76.8%)	138(74.6%)	117(63.2%)	102(55.1%)	102(55.1%)
		ornat. (2)	212	104(49.1%)	95(44.8%)	91(42.9%)	90(42.5%)	74(34.9%)	56(26.4%)
		chen. (2)	222	69(31.1%)	62(27.9%)	58(26.1%)	55(24.8%)	39(17.6%)	31(14.0%)
		tsu. (2)	196	125(63.8%)	112(57.1%)	103(52.6%)	82(41.8%)	34(17.4%)	0
		temp. (2)	498	415(83.3%)	280(56.2%)	260(52.2%)	236(47.4%)	163(32.7%)	46(9.2%)
1976	*dyb.* T (1)	*dyb.* T (1)	69	49(71.0%)	42(60.9%)	37(53.6%)	32(46.4%)	32(46.4%)	29(42.0%)
		ornat. (1)	81	19(23.5%)	14(17.3%)	11(13.6%)	11(13.6%)	11(13.6%)	10(12.4%)
		arv. (1)	181	55(30.4%)	0	0	0	0	0
1978	*dyb.* T (3)	*dyb.* T (1)	301	242(80.4%)	237(78.7%)	235(78.1%)	227(75.4%)	221(73.4%)	215(71.4%)
		jap. (1)	210	198(94.3%)	193(91.9%)	183(87.1%)	176(83.8%)	164(78.1%)	68(32.4%)
		ornat. (1)	132	116(87.9%)	110(83.3%)	108(81.8%)	104(78.8%)	97(73.5%)	89(67.4%)
		oki. (1)	241	0	0	0	0	0	0
		chen. (1)	390	58(14.9%)	57(14.6%)	57(14.6%)	57(14.6%)	57(14.6%)	53(13.6%)
		dalm. (1)	215	18(8.4%)	3(1.4%)	0	0	0	0
1981	*dyb.* T (5)	*dyb.* T (3)	733	706(96.3%)	553(75.4%)	531(72.4%)	500(68.2%)	459(62.6%)	426(58.1%)
		long. (3)	861	66(7.7%)	0	0	0	0	0
		lato. (1)	750	0	0	0	0	0	0
Total	*dyb.* T(21)	*dyb.*T(14)	2203	1990(90.3%)	1774(80.5%)	1726(78.3%)	1633(74.1%)	1544(70.1%)	1441(65.4%)
	dyb. T (6)	*dyb.* K (4)	1312	1298(98.9%)	1257(95.8%)	1239(94.4%)	1122(85.5%)	1086(82.8%)	841(64.1%)
	dyb. T(11)	*jap.* (9)	1233	875(71.0%)	656(53.2%)	613(49.7%)	540(43.8%)	467(37.9%)	195(15.8%)
	dyb. T(12)	*ornat.* (10)	1143	764(66.8%)	672(58.8%)	650(56.9%)	574(50.2%)	533(46.6%)	439(38.4%)
	dyb. T(11)	*chen.* (9)	2097	372(17.7%)	250(11.9%)	223(10.6%)	212(10.1%)	195(9.3%)	159(7.6%)
	dyb. T (3)	*oki.* (1)	241	0	0	0	0	0	0
	dyb. T (5)	*tsu.* (5)	461	269(58.4%)	232(50.3%)	146(31.7%)	125(27.1%)	77(16.7%)	0
	dyb. T (3)	*amur.* (3)	333	31(9.3%)	0	0	0	0	0
	dyb. T (5)	*long.* (3)	861	66(7.7%)	0	0	0	0	0
	dyb. T (5)	*lato.* (1)	750	0	0	0	0	0	0
	dyb. T (2)	*temp.* (2)	498	415(83.3%)	280(56.2%)	260(52.2%)	236(47.4%)	163(32.7%)	46(9.2%)
	dyb. T (2)	*arv.* (2)	338	63(18.6%)	2(0.6%)	2(0.6%)	2(0.6%)	0	0
	dyb. T (3)	*dalm.* (1)	215	18(8.4%)	3(1.4%)	0	0	0	0
	dyb. T (3)	*macro.* (1)	271	0	0	0	0	0	0
	dyb. T (1)	*syl.* (1)	172	0	0	0	0	0	0

male *Rana japonica* in 1970, 1975 and 1978 (Table 5). In each of these years, 61.2~94.3% of the respective total number of eggs obtained from 2~6 females, 875 (71.0%) of 1233 eggs in total, cleaved normally. Although the normally cleaved eggs were prone to delay in development during the embryonic stage, 540 (43.8%) hatched normally and 467 (37.9%) began to eat. However, most of the later gradually lost their appetite and became emaciated. Eventually, 195 (15.8%) tadpoles, that is, 22.3% of the normally cleaved eggs attained completion of metamorphosis.

d. Crosses with male *Rana ornativentris*

Twelve female *Rana dybowskii* collected from Tsushima were mated with 10 male *Rana ornativentris* in 1970, 1975, 1976 and 1978 (Table 5). While 19 (23.5%) of 81 eggs obtained from a female cleaved normally in 1976, 49.1~87.9% of the respective total number of eggs obtained from 2~6 females cleaved normally in each of the other three years. In 1976, 11 (13.6%) eggs hatched normally, and 10 (12.4%) attained completion of metamorphosis, while in the other three years, 42.5~78.8% of eggs hatched normally, and 26.4~67.4% attained completion of metamorphosis. In total, 764 (66.8%) of 1143 eggs cleaved normally, 574 (50.2%) hatched normally and 439 (38.4%) metamorphosed normally.

e. Crosses with male *Rana chensinensis*

Eleven female *Rana dybowskii* collected from Tsushima were mated with nine male *Rana chensinensis* in 1970, 1975 and 1978 (Table 5). In each of these years, 14.9~31.1% of the respective total number of eggs obtained from 2~6 females, 372 (17.7%) of 2097 in total, cleaved normally. About half of the normally cleaved eggs showed incomplete invagination at the gastrula stage and died before too long in 1970, while almost all or most of the normally cleaved eggs developed normally during the embryonic stage in the other two years. Eventually, 6.7~24.8% of eggs, 212 (10.1%) in total, hatched normally, and 5.1~14.0%, 159 (7.6%) in total, attained completion of metamorphosis, while many tadpoles died of underdevelopment or edema before metamorphosis.

f. Crosses with a male *Rana okinavana*

No normally cleaved eggs were obtained from three females by mating with a male *Rana okinavana* in 1978 (Table 5).

g. Crosses with male *Rana tsushimensis*

Five female *Rana dybowskii* collected from Tsushima were mated with five male *Rana tsushimensis* in 1970 and 1975 (Table 5). It was found that 54.3% of 265 eggs in 1970 and 63.8% of 196 eggs in 1975, 58.4% on the average, cleaved normally. After more than half of the normally cleaved eggs died of various abnormalities during the embryonic stage, 125 (27.1%) hatched normally. Although 77 (16.7%) began to eat, all of them died without attaining metamorphosis.

h. Crosses with male *Rana amurensis coreana*

Three female *Rana dybowskii* collected from Tsushima were mated with three male *Rana amurensis coreana* in 1970 (Table 5). Although 31 (9.3%) of 333 eggs obtained from these females cleaved normally, all of them ceased development by the early or mid-gastrula stage.

i. Crosses with male *Rana longicrus*

Five female *Rana dybowskii* collected from Tsushima were mated with three male *Rana longicrus* in 1981 (Table 5). Of 861 eggs obtained from the five females, 66 (7.7%) cleaved normally, but all of them ceased development at the late blastula or the earliest gastrula stage.

j. Crosses with a male *Rana latouchii*

No normally cleaved eggs were produced from five females by mating with a male *Rana latouchii* in 1981 (Table 5).

k. Crosses with male *Rana temporaria*

Two female *Rana dybowskii* collected from Tsushima were mated with two male *Rana temporaria* in 1975 (Table 5). Of 498 eggs obtained from the two females, 415 (83.3%) cleaved normally. Many of the normally cleaved eggs were prone to delay in development at the gastrula stage and died without completing gastrulation or of various abnormalities at the neurula, tail-bud and hatching stages. Although 236 (47.4%) embryos hatched normally and 163 (32.7%) became feeding tadpoles, only 46 (9.2%) attained completion of metamorphosis. Some of the normally hatched embryos died without taking food. Most of the feeding tadpoles gradually lost their appetite and died of emaciation without attaining the metamorphosing stage. Some of the inviable embryos and tadpoles had an abnormal tail which was short and dorso-laterally wide.

l. Crosses with male *Rana arvalis*

Two female *Rana dybowskii* collected from Tsushima were mated with two male *Rana arvalis* in 1966 and 1976 (Table 5). In 1966, only eight (5.1%) of 157 eggs obtained from a female cleaved normally. Six of them showed incomplete invagination at the gastrula stage and died of abnormalities at the neurula stage. Although the other two barely hatched normally, they died without taking food. In 1976, 55 (30.4%) of 181 eggs obtained from a female cleaved normally. However, all of them became abnormal at the gastrula stage and died at the neurula stage.

m. Crosses with male *Rana dalmatina*

Three female *Rana dybowskii* collected from Tsushima were mated with a male *Rana dalmatina* in 1978 (Table 5). Although 18 (8.4%) of 215 eggs obtained from these females cleaved normally, 12 ceased to develop at the early or mid-gastrula stage. Three others died as abnormal early neurulae with an unclosed yolk plug. The remaining three died of edema at the late neurula stage.

n. Crosses with a male *Rana macrocnemis*

No normally cleaved eggs were produced from three females by mating with a male *Rana macrocnemis* in 1968 (Table 5).

o. Cross with a male *Rana sylvatica*

No normally cleaved eggs were obtained from a female *Rana dybowskii* by mating with a male *Rana sylvatica* in 1972.

6. Crosses between female *Rana dybowskii* from Korea and males of five species

a. Control matings with male *Rana dybowskii* from Korea

Eight female *Rana dybowskii* collected from Korea were mated with eight male *Rana dybowskii* from Korea in 1970 (Table 6). It was found that 1352 (91.7%) of 1475 eggs obtained from the eight females cleaved normally. While some of the normally cleaved eggs died of various abnormalities during the embryonic stage, 1125 (76.3%) hatched normally. After hatching, 992 (67.3%) tadpoles began to eat and 934 (63.3%) attained completion of metamorphosis.

TABLE 6

Developmental capacity of hybrids between female *Rana dybowskii* from Korea and male brown frogs of five species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1970	*dyb.* K (8)	*dyb.* K (8)	1475	1352(91.7%)	1220(82.7%)	1185(80.3%)	1125(76.3%)	992(67.3%)	934(63.3%)
		dyb. T (4)	1740	1703(97.9%)	1446(83.1%)	1395(80.2%)	1346(77.4%)	1259(72.4%)	1140(65.5%)
		jap. (8)	1245	1185(95.2%)	899(72.2%)	855(68.7%)	777(62.4%)	563(45.2%)	63(5.1%)
		ornat. (8)	1101	859(78.0%)	801(72.8%)	796(72.3%)	751(68.2%)	717(65.1%)	669(60.8%)
		chen. (4)	1829	1473(80.5%)	946(51.7%)	842(46.0%)	786(43.0%)	625(34.2%)	468(25.6%)
		tsu. (8)	1239	889(71.8%)	716(57.8%)	685(55.3%)	629(50.8%)	475(38.3%)	20(1.6%)
		amur. (4)	345	200(58.0%)	0	0	0	0	0

b. Crosses with male *Rana dybowskii* from Tsushima

Eight female *Rana dybowskii* collected from Korea were mated with four male *Rana dybowskii* from Tsushima in 1970 (Table 6). The results showed that 1703 (97.9%) of 1740 eggs obtained from the eight females cleaved normally. These normally cleaved eggs were nearly the same as the controls in developmental capacity. Most of them developed normally during the embryonic stage, and 1346 (77.4%) hatched normally. After hatching, 1259 (72.4%) became feeding tadpoles and 1140 (65.5%) attained completion of metamorphosis.

c. Crosses with male *Rana japonica*

Eight female *Rana dybowskii* collected from Korea were mated with eight male *Rana japonica* in 1970 (Table 6). Of 1245 eggs obtained from the eight females, 1185 (95.2%) cleaved normally. The normally cleaved eggs were prone to delay in development at the gastrula stage. While some of them ceased development during gastrulation and some others became abnormal at the neurula stage, 899 (72.2%) became nearly normal neurulae. At the tail-bud stage, 44 embryos died of edema, microcephaly, blisters or some other abnormalities, while 855 (68.7%) embryos were nearly normal. Of 777 (62.4%) tadpoles which hatched normally, 214 died without taking food. Although the other 563 (45.2%) tadpoles began to eat, only 63 (5.1%) barely attained completion of metamorpho-

sis. The others gradually lost their appetite and died of emaciation during the tadpole stage.

d. Crosses with male *Rana ornativentris*

Eight female *Rana dybowskii* collected from Korea were mated with eight male *Rana ornativentris* in 1970 (Table 6). Of 1101 eggs obtained from these females, 859 (78.0%) cleaved normally. The normally cleaved eggs were nearly the same as the controls in developmental capacity; 751 (68.2%) hatched normally and 669 (60.8%) attained completion of metamorphosis.

e. Crosses with male *Rana chensinensis*

Eight female *Rana dybowskii* collected from Korea were mated with four male *Rana chensinensis* in 1970 (Table 6). Of 1829 eggs obtained from the eight females, 1473 (80.5%) cleaved normally. The normally cleaved eggs were prone to delay in development at the gastrula stage. Many eggs ceased development during gastrulation or died of various abnormalities at the late embryonic stage. Although 786 (43.0%) eggs hatched normally, many of them died of emaciation sooner or later after hatching, and eventually 468 (25.6%) tadpoles completed metamorphosis.

f. Crosses with male *Rana tsushimensis*

Eight female *Rana dybowskii* collected from Korea were mated with eight male *Rana tsushimensis* in 1970 (Table 6). It was found that 889 (71.8%) of 1239 eggs obtained from the eight females cleaved normally and 629 (50.8%) hatched normally. Although 475 (38.3%) tadpoles barely began to eat after hatching, most of them lost appetite and died of emaciation. Only 20 (1.6%) tadpoles completed metamorphosis and became dwarf frogs. The latter died before too long without taking food except one which attained sexual maturity.

g. Crosses with male *Rana amurensis coreana*

Eight female *Rana dybowskii* collected from Korea were mated with four male *Rana amurensis coreana* in 1970 (Table 6). Of 345 eggs obtained from these females, 200 (58.0%) cleaved normally. The normally cleaved eggs derived from five of the eight females generally ceased development at the late blastula or early or mid-gastrula stage and died before too long, while those derived from the other three females generally ceased development at the early or mid-gastrula stage and died. However, four of the normally cleaved eggs derived from two of the latter females lived much longer than the others in spite of their abnormal body structure. They grew into abnormal neurulae with an unclosed yolk plug. Thereafter, they became abnormal tail-bud embryos and then hatched as abnormal tadpoles. While three of them died before too long, the remainder grew into a feeding tadpole and died of emaciation at the age of 50 days.

7. Crosses between female *Rana amurensis coreana* and males of five species

a. Control matings with male *Rana amurensis coreana*

Five female *Rana amurensis coreana* were mated with five male *Rana amurensis coreana* in 1970 (Table 7). It was found that 189 (83.3%) of 227 eggs obtained from these females cleaved normally. While a small number of the normally cleaved eggs became abnormal and died during the embryonic stage, 179 (78.9%) hatched normally and 167 (73.6%) attained completion of metamorphosis.

TABLE 7

Developmental capacity of hybrids between female *Rana amurensis coreana* and male brown frogs of five species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1970	*amur.* (5)	*amur.* (5)	227	189(83.3%)	182(80.2%)	181(79.7%)	179(78.9%)	175(77.1%)	167(73.6%)
		jap. (5)	236	228(96.6%)	217(92.0%)	213(90.3%)	212(89.8%)	127(53.8%)	0
		ornat. (5)	296	274(92.6%)	264(89.2%)	257(86.8%)	221(74.7%)	19(6.4%)	0
		chen. (5)	255	231(90.6%)	196(76.9%)	196(76.9%)	196(76.9%)	60(23.5%)	0
		tsu. (5)	260	230(88.5%)	222(85.4%)	221(85.0%)	216(83.1%)	89(34.2%)	0
		dyb. T (5)	228	219(96.1%)	194(85.1%)	193(84.7%)	183(80.3%)	0	0
		dyb. K (5)	211	205(97.2%)	162(76.8%)	159(75.4%)	140(66.4%)	44(20.9%)	0

b. Crosses with male *Rana japonica*

Five female *Rana amurensis coreana* were mated with five male *Rana japonica* in 1970 (Table 7). Of 236 eggs obtained from females, 228 (96.6%) cleaved normally and 212 (89.8%) hatched normally. Although 127 (53.8%) began to eat (Fig. 5a), all of them gradually lost appetite and died of emaciation without attaining metamorphosis.

c. Crosses with male *Rana ornativentris*

Five female *Rana amurensis coreana* were mated with five male *Rana ornativentris* in 1970 (Table 7). Of 296 eggs obtained from these females, 274 (92.6%) cleaved normally and 221 (74.7%) hatched normally. While only 19 of the hatched tadpoles began to eat, all of the others died of abnormalities before too long (Fig. 5b). The feeding tadpoles lost appetite sooner or later and became emaciated. All of them died at the tadpole stage.

d. Crosses with male *Rana chensinensis*

Five female *Rana amurensis coreana* were mated with five male *Rana chensinensis* in 1970 (Table 7). Of 255 eggs obtained from these females, 231 (90.6%) cleaved normally and 196 (76.9%) hatched normally. Most of the hatched tadpoles became abnormal before long and died, while 60 (23.5%) became feeding tadpoles. All these tadpoles lost appetite and died of emaciation without attaining metamorphosis.

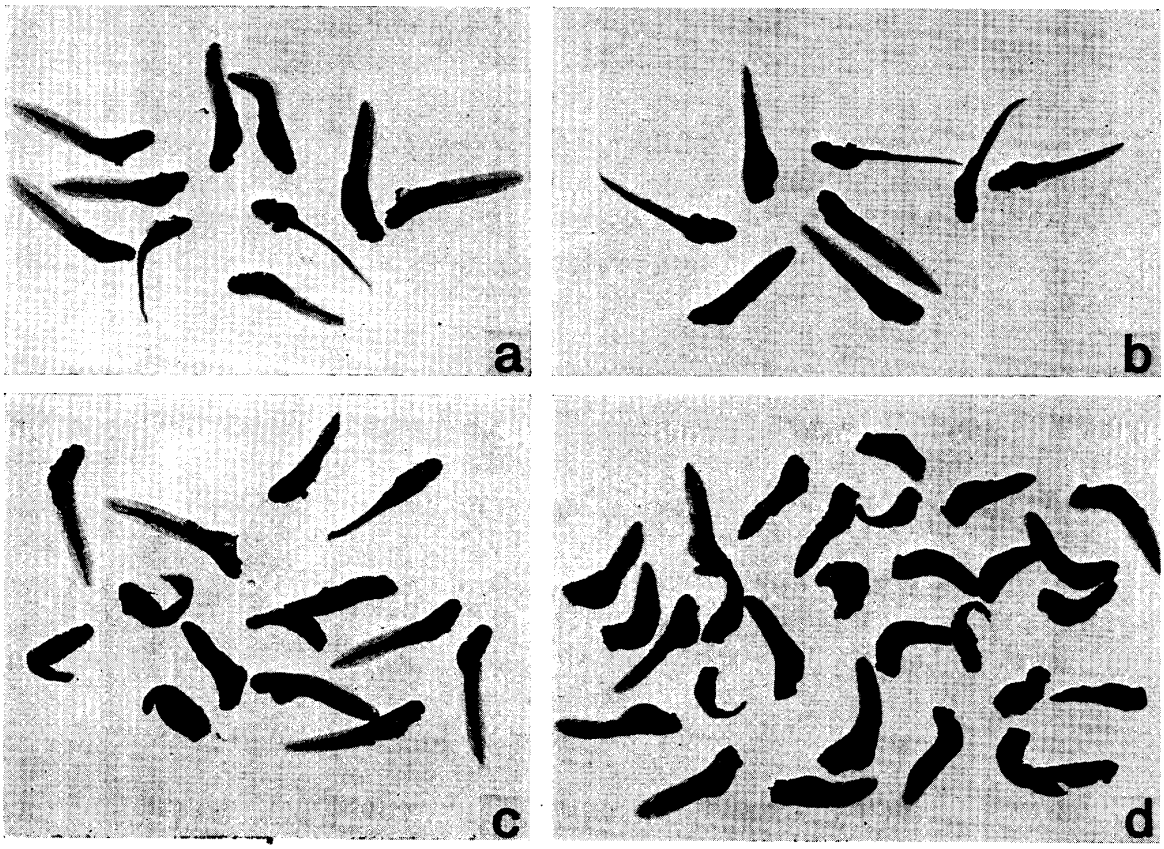


Fig. 5. Abnormalities at the embryonic and tadpole stages in the hybrids between female *Rana amurensis coreana* and males of four species. ×2.5

a. Hybrids, *Rana amurensis coreana* ♀ × *Rana japonica* ♂
b. Hybrids, *Rana amurensis coreana* ♀ × *Rana ornativentris* ♂
c. Hybrids, *Rana amurensis coreana* ♀ × *Rana tsushimensis* ♂
d. Hybrids, *Rana amurensis coreana* ♀ × *Rana dybowskii* from Tsushima ♂

e. Crosses with male *Rana tsushimensis*

Five female *Rana amurensis coreana* were mated with five male *Rana tsushimensis* in 1970 (Table 7). Of 260 eggs obtained from these females, 230 (88.5%) cleaved normally and 216 (83.1%) hatched normally. Although 89 (34.2%) became feeding tadpoles, all of them died of abnormalities before metamorphosis. All the other tadpoles which hatched normally died of abnormalities shortly after hatching (Fig. 5c).

f. Crosses with male *Rana dybowskii* from Tsushima

Five female *Rana amurensis coreana* were mated in 1970 with five male *Rana dybowskii* collected from Tsushima (Table 7). Of 228 eggs obtained from these females, 219 (96.1%) cleaved normally and 183 (80.3%) hatched normally. However, all the hatching embryos and hatched tadpoles died of abnormalities without taking food (Fig. 5d).

g. Crosses with male *Rana dybowskii* from Korea

Five female *Rana amurensis coreana* were mated in 1970 with five male *Rana*

dybowskii collected from Korea (Table 7). Of 211 eggs obtained from these females, 205 (97.2%) cleaved normally. Some of the normally cleaved eggs died of abnormalities at the gastrula or neurula stage, while 159 (75.4%) became normal tail-bud embryos. Thereafter, 140 (66.4%) embryos hatched normally. They mostly died of abnormalities shortly after hatching. Eventually, only 44 (20.9%) became feeding tadpoles, although they gradually lost appetite and died of emaciation without attaining metamorphosis.

8. Crosses between female *Rana longicrus* and males of six species

a. Control matings with male *Rana longicrus*

Five female *Rana longicrus* were mated with three male *Rana longicrus* in 1981 (Table 8). It was found that 460 (92.7%) of 496 eggs obtained from these females cleaved normally. While less than one-tenth of the normally cleaved eggs died of various abnormalities during the embryonic stage, 422 (85.1%) hatched normally. Thereafter, 416 (83.9%) became feeding tadpoles (Fig. 6a) and 389 (78.4%) attained completion of metamorphosis.

TABLE 8

Developmental capacity of hybrids between female *Rana longicrus* and male brown frogs of six species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1981	*long.* (5)	*long.* (3)	496	460(92.7%)	437(88.1%)	425(85.7%)	422(85.1%)	416(83.9%)	389(78.4%)
		jap. (3)	662	585(88.4%)	561(84.7%)	518(78.3%)	512(77.3%)	500(75.5%)	342(51.7%)
		ornat. (3)	524	447(85.3%)	420(80.2%)	399(76.2%)	397(75.8%)	395(75.4%)	5(1.0%)
		chen. (3)	452	329(72.8%)	325(71.9%)	313(69.2%)	309(68.4%)	302(66.8%)	0
		tsu. (3)	456	332(72.8%)	325(71.3%)	317(69.5%)	317(69.5%)	312(68.4%)	0
		dyb. T (3)	550	473(86.0%)	451(82.0%)	435(79.1%)	426(77.5%)	419(76.2%)	0
		lato. (1)	513	8(1.6%)	4(0.8%)	4(0.8%)	3(0.6%)	2(0.4%)	0

b. Crosses with male *Rana japonica*

Five female *Rana longicrus* were mated with three male *Rana japonica* in 1981 (Table 8). Of 662 eggs obtained from these females, 585 (88.4%) cleaved normally. The normally cleaved eggs were not remarkably inferior to the controls in developmental capacity; 512 (77.3%) hatched normally and 500 (75.5%) became feeding tadpoles. At the tadpole stage, the hybrids were somewhat inferior to the controls in viability. After a comparatively large number of tadpoles gradually died of emaciation, 342 (51.7%) tadpoles completed metamorphosis.

c. Crosses with male *Rana ornativentris*

Five female *Rana longicrus* were mated with three male *Rana ornativentris* in 1981 (Table 8). Of 524 eggs obtained from these females, 447 (85.3%) cleaved normally. The normally cleaved eggs were not remarkably inferior to the controls in developmental capacity during the embryonic stage. Of 397 (75.8%) tadpoles which hatched normally, 395 (75.4%) began to eat (Fig. 6b). How-

ever, nearly all the tadpoles gradually lost appetite and died of emaciation. Eventually, only five (1.0%) tadpoles completed metamorphosis.

d. Crosses with male *Rana chensinensis*

Five female *Rana longicrus* were mated with three male *Rana chensinensis* in 1981 (Table 8). Of 452 eggs obtained from these females, 329 (72.8%) cleaved normally. The normally cleaved eggs were not inferior to the controls in developmental capacity during the embryonic stage; 309 (68.4%) hatched normally and 302 (66.8%) began to eat (Fig. 6c). However, all the tadpoles gradually

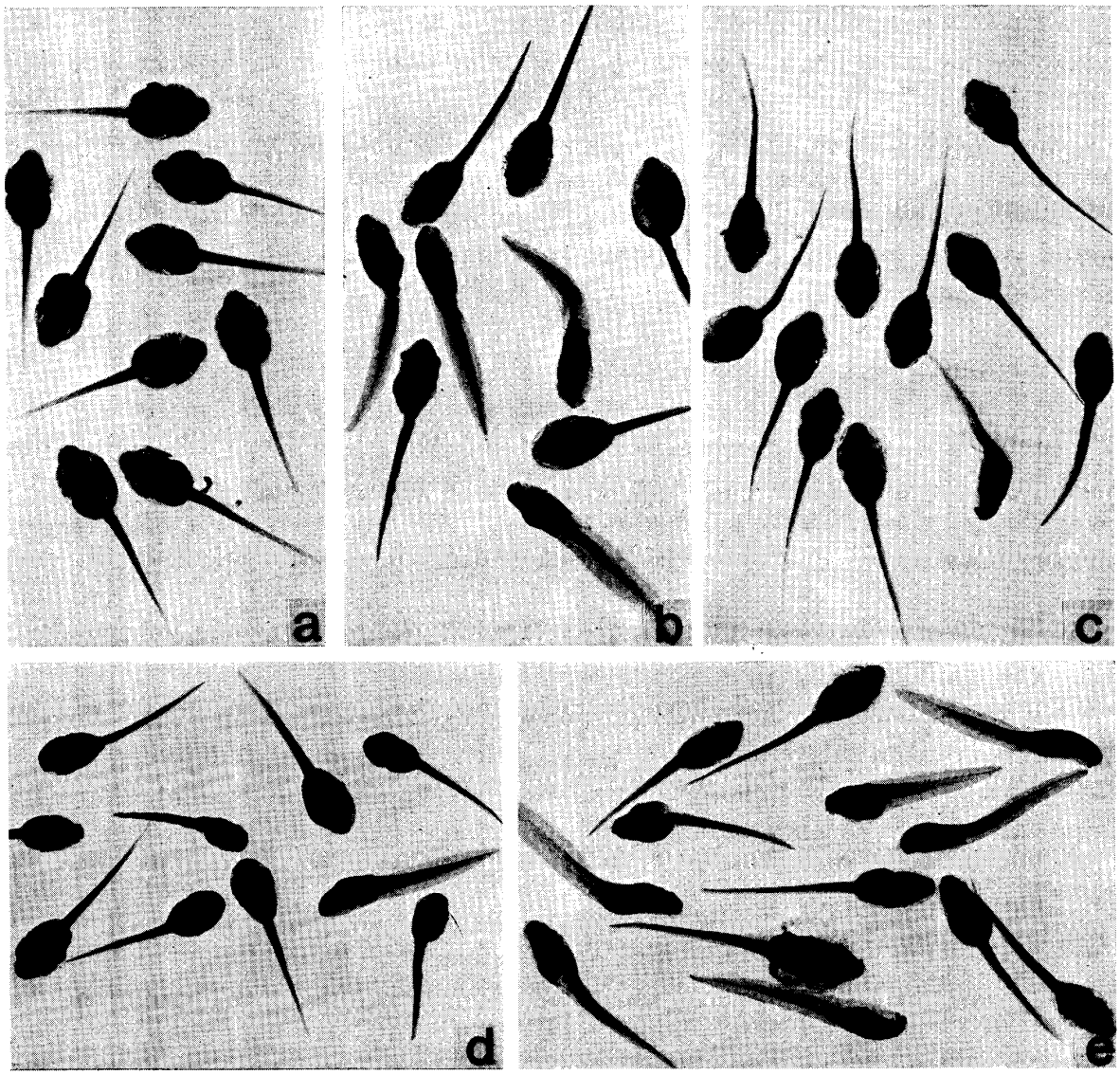


Fig. 6. Abnormalities at the tadpole stage in the hybrids between female *Rana longicrus* and males of four species. ×2.5

a. Controls, *Rana longicrus* ♀ × *Rana longicrus* ♂
b. Hybrids, *Rana longicrus* ♀ × *Rana ornativentris* ♂
c. Hybrids, *Rana longicrus* ♀ × *Rana chensinensis* ♂
d. Hybrids, *Rana longicrus* ♀ × *Rana tsushimensis* ♂
e. Hybrids, *Rana longicrus* ♀ × *Rana dybowskii* from Tsushima ♂

lost appetite and died of emaciation before the metamorphosing stage.

e. Crosses with male *Rana tsushimensis*

Five female *Rana longicrus* were mated with three male *Rana tsushimensis* in 1981 (Table 8). Of 456 eggs obtained from these females, 332 (72.8%) cleaved normally. The normally cleaved eggs were not inferior to the controls in developmental capacity during the embryonic stage; 317 (69.5%) hatched normally and 312 (68.4%) began to eat (Fig. 6d). However, all the tadpoles gradually lost appetite and died of emaciation before the metamorphosing stage.

f. Crosses with male *Rana dybowskii* from Tsushima

Five female *Rana longicrus* were mated in 1981 with three male *Rana dybowskii* collected from Tsushima (Table 8). Of 550 eggs obtained from these females, 473 (86.0%) cleaved normally. The normally cleaved eggs were not inferior to the controls in developmental capacity during the embryonic stage; 426 (77.5%) tadpoles hatched normally and 419 (76.2%) began to eat (Fig. 6e). However, all the tadpoles gradually lost appetite and died of emaciation before the metamorphosing stage.

g. Crosses with a male *Rana latouchii*

Five female *Rana longicrus* were mated with a male *Rana latouchii* in 1981 (Table 8). Only eight (1.6%) of 513 eggs obtained from these females cleaved normally. While five of the normally cleaved eggs died of abnormalities during the embryonic stage, three (0.6%) hatched normally. Although two of the latter began to eat, all of them died of emaciation without attaining metamorphosis.

9. Crosses between a female *Rana latouchii* and males of five species

a. Control matings with a male *Rana latouchii*

A female *Rana latouchii* was mated with a male *Rana latouchii* in 1981. Of 518 eggs obtained from this female, 469 (90.5%) cleaved normally and 38 did abnormally. Of the normally cleaved eggs, 448 (86.5%) became normal gastrulae. Almost all of them developed normally and 426 hatched.

b. Cross with a male *Rana japonica*

The female *Rana latouchii* was mated with a male *Rana japonica* in 1981. Although 90 (92.8%) of 97 eggs cleaved normally and 82 became late blastulae, all of them died before beginning of gastrulation.

c. Cross with a male *Rana ornativentris*

The female *Rana latouchii* was mated with a male *Rana ornativentris* in 1981. Of 76 eggs, 20 (26.3%) cleaved normally and 29 did abnormally. Although 19 of the normally cleaved eggs became late blastulae, all of them died before beginning of gastrulation.

d. Cross with a male *Rana chensinensis*

The female *Rana latouchii* was mated with a male *Rana chensinensis* in 1981. Of 77 eggs, 13 (16.9%) cleaved normally and 32 did abnormally. Although the normally cleaved eggs became late blastulae, none of them attained beginning of gastrulation.

e. Cross with a male *Rana tsushimensis*

The female *Rana latouchii* was mated with a male *Rana tsushimensis* in 1981. Of 96 eggs, 25 (26.0%) cleaved normally and 30 did abnormally. Although 24 of them became late blastulae, all of them died before beginning of gastrulation.

f. Cross with a male *Rana dybowskii* from Tsushima

The female *Rana latouchii* was mated with a male *Rana dybowskii* from Tsushima in 1981. Of 88 eggs, 13 (14.8%) cleaved normally and 42 did abnormally. Although all the normally cleaved eggs became late blastulae, none of them attained beginning of gastrulation.

10. Crosses between female *Rana temporaria* and males of five species

a. Control matings with male *Rana temporaria*

Four female *Rana temporaria* were mated with four male *Rana temporaria* in 1963, 1964 and 1965 (Table 9). The results showed that 375 (70.6%) of 531 eggs obtained from these four females cleaved normally. The normally cleaved eggs mostly developed normally; 295 (55.6%) hatched normally, 293 (55.2%) became feeding tadpoles and 278 (52.4%) attained completion of metamorphosis.

TABLE 9

Developmental capacity of hybrids between female *Rana temporaria* and male brown frogs of five species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1963	*temp.* (2)	*temp.* (2)	336	224(66.7%)	200(59.5%)	200(59.5%)	178(53.0%)	177(52.7%)	169(50.3%)
		jap. (2)	268	0	0	0	0	0	0
		ornat. (2)	282	0	0	0	0	0	0
		chen. (2)	476	0	0	0	0	0	0
		tsu. (2)	262	0	0	0	0	0	0
		arv. (1)	196	0	0	0	0	0	0
1964	*temp.* (1)	*temp.* (1)	93	75(80.6%)	63(67.7%)	63(67.7%)	52(55.9%)	52(55.9%)	50(53.8%)
		jap. (1)	184	0	0	0	0	0	0
		ornat. (1)	141	0	0	0	0	0	0
		chen. (1)	238	0	0	0	0	0	0
1965	*temp.* (1)	*temp.* (1)	102	76(74.5%)	69(67.6%)	65(63.7%)	65(63.7%)	64(62.7%)	59(57.8%)
Total	*temp.* (4)	*temp.* (4)	531	375(70.6%)	332(62.5%)	328(61.8%)	295(55.6%)	293(55.2%)	278(52.4%)
		jap. (3)	452	0	0	0	0	0	0
		ornat. (3)	423	0	0	0	0	0	0
		chen. (3)	714	0	0	0	0	0	0
	temp. (2)	*tsu.* (2)	262	0	0	0	0	0	0
		arv. (1)	196	0	0	0	0	0	0

b. Crosses with male *Rana japonica*

No normally cleaved eggs were produced from four female *Rana temporaria* by mating with three male *Rana japonica* in 1963 and 1964 (Table 9).

c. Crosses with male *Rana ornativentris*

No normally cleaved eggs were produced from four female *Rana temporaria* by mating with three male *Rana ornativentris* in 1963 and 1964 (Table 9).

d. Crosses with male *Rana chensinensis*

No normally cleaved eggs were produced from four female *Rana temporaria* by mating with three male *Rana chensinensis* in 1963 and 1964 (Table 9).

e. Crosses with male *Rana tsushimensis*

No normally cleaved eggs were produced from two female *Rana temporaria* by mating with two male *Rana tsushimensis* in 1963 (Table 9).

f. Crosses with male *Rana arvalis*

No normally cleaved eggs were produced from two female *Rana temporaria* by mating with a male *Rana arvalis* in 1963 (Table 9).

11. Crosses between female *Rana arvalis* and males of seven species

a. Control matings with male *Rana arvalis*

A total of 13 female *Rana arvalis* were mated with seven male *Rana arvalis* in 1962, 1963, 1966, 1976 and 1977 (Table 10). While 64.6~94.4% of the respective number of eggs obtained from 1~5 females, 650 (73.4%) of 886 eggs in total, cleaved normally in 1962, 1963, 1966 and 1976, only 88 (33.0%) of 267 eggs obtained from four females did so in 1977. Thus, the eggs used in 1977 were considered to be in an unfavorable condition. In total of the five years, 738 (64.0%) of 1153 eggs from the 13 females cleaved normally.

The normally cleaved eggs mostly developed normally during the embryonic stage in 1962, 1963, 1966 and 1976, while slightly more than half of the normally cleaved eggs did so in 1977. Eventually, 44.9% of eggs hatched normally, 42.9% began to eat and 39.2% attained completion of metamorphosis in the five years.

b. Crosses with male *Rana japonica*

Eleven female *Rana arvalis* were mated with six male *Rana japonica* in 1962, 1976 and 1977 (Table 10). While 82.9% and 71.5% of the respective total number of eggs obtained from five or two females cleaved normally in 1962 and 1976, respectively, only 98 (27.5%) of 356 eggs did so in 1977. In 1962 and 1976, the normally cleaved eggs were extremely inferior to the controls in developmental capacity; only 9.7% and 12.2% hatched normally, 3.4% and 8.9% began to eat, and 3.1% and 2.4% attained completion of metamorphosis in 1962 and 1976, respectively. The other embryos and tadpoles died of underdevelopment, edema or various abnormalities. In 1977, the normally cleaved

TABLE 10

Developmental capacity of hybrids between female *Rana arvalis* and male brown frogs of seven species

Year	Parents (No.)		No. of eggs	No. of normal cleavages	No. of normal neurulae	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1962	*arv.* (5)	*arv.* (2)	441	285(64.6%)	204(46.3%)	197(44.7%)	174(39.5%)	160(36.3%)	154(34.9%)
		jap. (3)	1515	1256(82.9%)	951(62.8%)	929(61.3%)	147(9.7%)	52(3.4%)	47(3.1%)
		ornat. (2)	971	681(70.1%)	399(41.1%)	396(40.8%)	308(31.7%)	96(9.7%)	84(8.7%)
		chen. (3)	572	0	0	0		0	0
		temp. (2)	1214	6(0.5%)	6(0.5%)	6(0.5%)	5(0.4%)	5(0.4%)	3(0.3%)
1963	*arv.* (1)	*arv.* (1)	160	151(94.4%)	131(81.9%)	130(81.3%)	125(78.1%)	122(76.3%)	112(70.0%)
		tsu. (1)	55	35(63.6%)	27(49.1%)	0	0	0	0
1966	*arv.* (1)	*arv.* (1)	69	52(75.4%)	43(62.3%)	43(62.3%)	40(58.0%)	40(58.0%)	32(46.4%)
		chen. (1)	176	27(15.3%)	20(11.4%)	16(9.1%)	12(6.8%)	9(5.1%)	5(2.8%)
		tsu. (1)	107	21(19.6%)	20(11.4%)	19(17.8%)	17(15.9%)	8(7.5%)	0
		dyb. T (1)	139	11(7.9%)	9(6.5%)	9(6.5%)	5(3.6%)	4(2.9%)	3(2.2%)
1976	*arv.* (2)	*arv.* (1)	216	162(75.0%)	157(72.7%)	148(68.5%)	133(61.6%)	128(59.3%)	118(54.6%)
		jap. (1)	123	88(71.5%)	64(52.0%)	31(25.2%)	15(12.2%)	11(8.9%)	3(2.4%)
		ornat. (1)	130	76(58.5%)	48(36.9%)	36(27.7%)	22(16.9%)	16(12.3%)	6(4.6%)
		chen. (1)	144	64(44.4%)	35(24.3%)	27(18.8%)	22(15.3%)	19(13.2%)	8(5.6%)
		tsu. (1)	210	113(53.8%)	59(28.1%)	36(17.1%)	18(8.6%)	10(4.8%)	0
		dyb. T (1)	192	3(1.6%)	3(1.6%)	2(1.0%)	2(1.0%)	2(1.0%)	1(0.5%)
		temp. (1)	159	0	0	0	0	0	0
1977	*arv.* (4)	*arv.* (2)	267	88(33.0%)	72(27.0%)	71(26.6%)	46(17.2%)	45(16.9%)	36(13.5%)
		jap. (2)	356	98(27.5%)	68(19.1%)	59(16.6%)	54(15.2%)	53(14.9%)	41(11.5%)
		ornat. (2)	346	96(27.8%)	74(21.4%)	57(16.5%)	49(14.2%)	34(9.8%)	32(9.3%)
		chen. (2)	211	83(39.3%)	52(24.6%)	48(22.8%)	27(12.8%)	25(11.9%)	7(3.3%)
		tsu. (2)	274	88(32.1%)	74(27.0%)	67(24.5%)	44(16.1%)	40(14.6%)	3(1.1%)
		dyb. T (2)	178	49(27.5%)	40(22.5%)	33(18.5%)	29(16.3%)	24(13.5%)	3(1.7%)
		oki. (2)	625	62(9.9%)	55(8.8%)	43(6.9%)	27(4.3%)	26(4.2%)	22(3.5%)
Total	*arv.* (13)	*arv.* (7)	1153	738(64.0%)	607(52.7%)	589(51.1%)	518(44.9%)	495(42.9%)	452(39.2%)
	arv. (11)	*jap.* (6)	1994	1442(72.3%)	1083(54.3%)	1019(51.1%)	216(10.8%)	116(5.8%)	91(4.6%)
	arv. (11)	*ornat.* (5)	1447	853(59.0%)	521(36.0%)	489(33.8%)	379(26.2%)	146(10.1%)	122(8.4%)
	arv. (12)	*chen.* (7)	1103	174(15.8%)	107(9.7%)	91(8.3%)	61(5.5%)	53(4.8%)	20(1.8%)
	arv. (4)	*oki.* (2)	625	62(9.9%)	55(8.8%)	43(6.9%)	27(4.3%)	26(4.2%)	22(3.5%)
	arv. (8)	*tsu.* (5)	646	257(39.8%)	153(23.7%)	122(18.9%)	79(12.2%)	58(9.0%)	3(0.5%)
	arv. (7)	*dyb.* T (4)	509	63(12.4%)	52(10.2%)	44(8.6%)	36(7.1%)	30(5.9%)	7(1.4%)
	arv. (7)	*temp.* (3)	1373	6(0.4%)	6(0.4%)	6(0.4%)	5(0.4%)	5(0.4%)	3(0.2%)

eggs did not remarkably differ from the controls in developmental capacity during the embryonic stage; 54 (15.2%) eggs hatched normally. Thereafter, 53 (14.9%) tadpoles began to eat and 41 (11.5%) attained completion of metamorphosis. In total of the three years, 1442 (72.3%) of 1994 eggs obtained from the 11 females cleaved normally, 216 (10.8%) hatched normally, and 91 (4.6%) metamorphosed normally.

c. Crosses with male *Rana ornativentris*

Eleven female *Rana arvalis* were mated with five male *Rana ornativentris* in 1962, 1976 and 1977 (Table 10). While 70.1% and 58.5% of the respective total number of eggs obtained from five or two females cleaved normally in 1962 and 1976, respectively, 96 (27.8%) of 346 eggs obtained from four females did so in 1977. In total of the three years, 853 (59.0%) of 1447 eggs obtained from the 11 females cleaved normally. The normally cleaved eggs did not remarkably differ from the hybrids between female *Rana arvalis* and male *Rana japonica* in developmental capacity; 379 (26.2%) hatched normally and 122 (8.4%) attained

completion of metamorphosis. An overwhelming majority of the normally cleaved eggs died of various abnormalities during the embryonic or tadpole stage.

d. Crosses with male *Rana chensinensis*

Twelve female *Rana arvalis* were mated with seven male *Rana chensinensis* in 1962, 1966, 1976 and 1977 (Table 10). No normally cleaved eggs were produced from five females by mating with three male *Rana chensinensis* in 1962. In contrast, 15.3~44.4% of the respective number of eggs obtained from 1~4 females, 174 (32.8%) of 531 eggs in total, cleaved normally in 1966, 1976 and 1977. In these years, the normally cleaved eggs mostly died of various abnormalities during the embryonic stage, while 6.8~15.3%, 61 (11.5%) in total, hatched normally. Although most of the latter began to eat, only 2.8~5.6%, 20 (3.8%) in total, attained completion of metamorphosis. The other tadpoles gradually lost appetite and died of emaciation without attaining metamorphosis. In total of the four years, 174 (15.8%) of 1103 eggs cleaved normally, 61 (5.5%) hatched normally and 20 (1.8%) metamorphosed normally.

e. Crosses with male *Rana okinavana*

Four female *Rana arvalis* were mated with two male *Rana okinavana* in 1977 (Table 10). It was found that only 62 (9.9%) of 625 eggs obtained these females cleaved normally. The normally cleaved eggs mostly died of various abnormalities during the embryonic stage, while 27 (4.3%) hatched normally. Although 26 tadpoles began to eat, four gradually lost appetite and died of emaciation. Eventually, 22 (3.5%) tadpoles completed metamorphosis.

f. Crosses with male *Rana tsushimensis*

Eight female *Rana arvalis* were mated with five male *Rana tsushimensis* in 1963, 1966, 1976 and 1977 (Table 10). The results showed that 19.6~63.6% of the respective number of eggs obtained from 1~4 females cleaved normally in the four years and that the normally cleaved eggs mostly died of various abnormalities during the embryonic stage. In 1963, no normal tail-bud embryos were produced, although 35 (63.6%) of 55 eggs cleaved normally and 27 (49.1%) became normal neurulae. In 1966 and 1976, 21 (19.6%) of 107 and 113 (53.8%) of 210 eggs cleaved normally, and 17 (15.9%) and 18 (8.6%) hatched normally, respectively. Although some of these hatched tadpoles began to eat, they lost appetite sooner or later and died of emaciation before the metamorphosing stage. In 1977, 88 (32.1%) of 274 eggs obtained from four females cleaved normally, and 44 (16.1%) hatched normally. Only three (1.1%) of the latter completed metamorphosis, although 40 (14.6%) tadpoles began to eat.

In total of the four years, 257 (39.8%) of 646 eggs obtained from the eight females cleaved normally, 79 (12.2%) hatched normally and only three (0.5%) metamorphosed normally.

g. Crosses with male *Rana dybowskii* from Tsushima

Seven female *Rana arvalis* were mated in 1966, 1976 and 1977 with four male *Rana dybowskii* collected from Tsushima (Table 10). In 1966 and 1976, only 11 (7.9%) of 139 and 3 (1.6%) of 192 eggs obtained from one or two females cleaved normally in 1966 and 1976, respectively. Thereafter, five (3.6%) and two (1.0%) hatched normally, and three (2.2%) and one (0.5%) attained completion of metamorphosis in 1966 and 1976, respectively. In 1977, 49 (27.5%) of 178 eggs obtained from four females cleaved normally, and 29 (16.3%) hatched normally. Although 24 tadpoles began to eat in this year, only three (1.7%) of them completed metamorphosis.

In total of the three years, 63 (12.4%) of 509 eggs obtained from the seven females cleaved normally, 36 (7.1%) hatched normally, and seven (1.4%) metamorphosed normally.

h. Crosses with male *Rana temporaria*

Seven female *Rana arvalis* were mated with three male *Rana temporaria* in 1962 and 1976 (Table 10). In 1962, only six (0.5%) of 1214 eggs obtained from five females cleaved normally, while no normally cleaved eggs were produced from two females by mating with a male *Rana temporaria* in 1976. Five of the six normally cleaved eggs produced in 1962 hatched normally and became feeding tadpoles. Three of them completed metamorphosis, while the others died of emaciation before metamorphosis. In total of the two years, six (0.4%) cleaved normally, five (0.4%) hatched normally, and three (0.2%) metamorphosed normally.

II. Sex of hybrids

1. Hybrids between female *Rana japonica* and males of seven species

a. Control *Rana japonica*

Of 5086 normally metamorphosed frogs produced from control matings in 1962, 1963, 1964, 1967, 1968, 1970, 1975, 1976, 1978 and 1981, the sex of 4119 was examined at the juvenile or mature stage (Table 11). At the juvenile stage, 1813 of 3720 frogs were females with normal ovaries, 40 others were hermaphrodites with gonads transforming from ovaries into testes, and the remaining 1867 were males with normal testes. Of 399 mature frogs, 192 were females and the other 207 were males. When the juvenile hermaphrodites were counted as males, 2005 frogs were females and 2114 (51.3%) were males in total of juvenile and mature ones.

b. *Rana japonica*♀ × *Rana ornativentris*♂

The sex of 361 of 388 normally metamorphosed frogs produced from crosses between female *Rana japonica* and male *Rana ornativentris* in 1962, 1976 and 1978 was examined at the juvenile or mature stage (Table 11). Of 343 juvenile

hybrids, 341 were males and the remaining two were hermaphrodites. At the mature stage, 18 were all males. When the two juvenile hermaphrodites were counted as males, the 361 hybrids in total were all males.

TABLE 11

Sex of hybrids between female *Rana japonica* and males of seven species and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs						Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1962	*jap.*	*jap.*	493	422	209	0	0	0	213	57	27	30	479	236	243 (50.7)
		ornat.	35	30	0	0	2	0	28	5	0	5	35	0	35
		chen.	20	8	0	0	1	0	7	11	0	11	19	0	19
		temp.	132	83	0	0	5	0	78	42	0	42	125	0	125
		arv.	36	23	0	0	3	0	20	13	0	13	36	0	36
1963	*jap.*	*jap.*	303	250	119	0	1	0	130	32	14	18	282	133	149 (52.8)
1964	*jap.*	*jap.*	1047	854	421	0	16	0	417	103	54	49	957	475	482 (50.4)
		tsu.	13	11	0	0	1	0	10	—	—	—	11	0	11
1967	*jap.*	*jap.*	813	262	127	0	4	0	131	44	21	23	306	148	158 (51.6)
		tsu.	6	5	0	0	0	0	5	—	—	—	5	0	5
1968	*jap.*	*jap.*	373	323	156	0	7	0	160	15	7	8	338	163	175 (51.8)
1970	*jap.*	*jap.*	539	493	241	0	2	0	250	23	11	12	516	252	264 (51.2)
1975	*jap.*	*jap.*	260	215	101	0	2	0	112	28	12	16	243	113	130 (53.5)
		chen.	391	351	0	0	0	0	351	18	0	18	369	0	369
		temp.	301	263	0	0	0	0	263	4	0	4	267	0	267
1976	*jap.*	*jap.*	384	259	123	0	0	0	136	45	25	20	304	148	156 (51.3)
		ornat.	227	208	0	0	0	0	208	13	0	13	221	0	221
		chen.	291	174	0	0	0	0	174	92	0	92	266	0	266
		tsu.	3	3	0	0	0	0	3	—	—	—	3	0	3
		temp.	247	133	0	0	0	0	133	114	0	114	247	0	247
		arv.	276	107	0	0	0	0	107	121	0	121	228	0	228
1978	*jap.*	*jap.*	331	219	103	0	6	0	110	7	2	5	226	105	121 (53.5)
		ornat.	126	105	0	0	0	0	105	—	—	—	105	0	105
		chen.	142	114	0	0	0	0	114	—	—	—	114	0	114
		oki.	2	2	0	0	0	0	2	—	—	—	2	0	2
1981	*jap.*	*jap.*	543	423	213	0	2	0	208	45	19	26	468	232	236 (50.4)
		long.	415	295	0	3	3	0	289	93	0	93	388	3	385 (99.2)
Total	*jap.*	*jap.*	5086	3720	1813	0	40	0	1867	399	192	207	4119	2005	2114 (51.3)
		ornat.	388	343	0	0	2	0	341	18	0	18	361	0	361
		chen.	844	647	0	0	1	0	646	121	0	121	768	0	768
		oki.	2	2	0	0	0	0	2	—	—	—	2	0	2
		tsu.	22	19	0	0	1	0	18	—	—	—	19	0	19
		long.	415	295	0	3	3	0	289	93	0	93	388	3	385 (99.2)
		temp.	680	479	0	0	5	0	474	160	0	160	639	0	639
		arv.	312	130	0	0	3	0	127	134	0	134	264	0	264

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries

⚥, Hermaphrodites ♂R, Males with rudimentary testes

♂N, Males with normal testes * Including hermaphrodites

c. *Rana japonica*♀ × *Rana chensinensis*♂

The sex of 768 of 844 normally metamorphosed frogs produced from crosses between female *Rana japonica* and male *Rana chensinensis* in 1962, 1975, 1976 and 1978 was examined at the juvenile or mature stage (Table 11). Of 647 juvenile frogs, 646 were males and the remaining was a hermaphrodite. At the mature stage, 121 frogs were all males. Thus, the 768 hybrids in total were all males when the only hermaphrodite was counted as a male.

d. *Rana japonica*♀ × *Rana okinavana*♂

Of four normally metamorphosed frogs produced from crosses between female *Rana japonica* and male *Rana okinavana* in 1977 and 1978, the sex of two obtained in 1978 was examined immediately after metamorphosis (Table 11). It was found that both were males.

e. *Rana japonica*♀ × *Rana tsushimensis*♂

Of 22 normally metamorphosed frogs produced from crosses between female *Rana japonica* and male *Rana tsushimensis* in 1964, 1967 and 1976, the sex of 19 was examined shortly after metamorphosis (Table 11). It was found that 18 of them were males and the remaining was a hermaphrodite.

f. *Rana japonica*♀ × *Rana longicrus*♂

The sex of 388 of 415 normally metamorphosed frogs produced from crosses between female *Rana japonica* and male *Rana longicrus* in 1981 was examined at the juvenile or mature stage (Table 11). At the juvenile stage, 289 of 295 hybrids were males, three others were hermaphrodites and the remaining three were females with underdeveloped ovaries. At the mature stage, 93 hybrids were all males. When the hermaphrodites were counted as males, 385 (99.2%) of the total 388 hybrids were males. The three females with underdeveloped ovaries were assumed to become males before too long by sex reversal.

g. *Rana japonica*♀ × *Rana temporaria*♂

The sex of 639 of 680 normally metamorphosed frogs produced from crosses between female *Rana japonica* and male *Rana temporaria* in 1962, 1975 and 1976 was examined at the juvenile or mature stage (Table 11). At the juvenile stage, 474 of 479 hybrids were males and the other five were hermaphrodites, while 160 mature frogs were all males. When the hermaphrodites were counted as males, the 639 hybrids in total were all males.

h. *Rana japonica*♀ × *Rana arvalis*♂

The sex of 264 of 312 normally metamorphosed frogs produced from crosses between female *Rana japonica* and male *Rana arvalis* in 1962 and 1976 was examined at the juvenile or mature stage (Table 11). At the juvenile stage, 127 of 130 were males and the other three were hermaphrodites, while 134 mature hybrids were all males. When the hermaphrodites were counted as males, the 264 hybrids in total were all males.

2. Hybrids between female *Rana ornativentris* and males of three species

a. Control *Rana ornativentris*

Of 2041 normally metamorphosed frogs produced from control matings in 1962, 1963, 1964, 1965, 1968, 1970, 1975 and 1976, the sex of 1863 was examined at the juvenile or mature stage (Table 12). At the juvenile stage, 796 of 1679

TABLE 12

Sex of hybrids between female *Rana ornativentris* and males of three species and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs					Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1962	*ornat.*	*ornat.*	316	236	111	0	2	0	123	42	25	17	278	136	142 (51.1)
		chen.	23	18	0	0	5	0	13	5	0	5	23	0	23
		temp.	13	10	0	0	0	0	10	3	0	3	13	0	13
1963	*ornat.*	*ornat.*	303	303	143	0	26	0	134	—	—	—	303	143	160 (52.8)
1964	*ornat.*	*ornat.*	126	80	34	0	13	0	33	31	16	15	111	50	61 (55.0)
		temp.	4	2	0	0	0	0	2	2	0	2	4	0	4
1965	*ornat.*	*ornat.*	144	126	53	0	21	0	52	16	8	8	142	61	81 (57.0)
		temp.	21	7	0	0	0	0	7	14	0	14	21	0	21
1968	*ornat.*	*ornat.*	172	141	72	0	5	0	64	8	3	5	149	75	74 (49.7)
		dyb. K	1	1	0	0	0	0	1	—	—	—	1	0	1
1970	*ornat.*	*ornat.*	606	477	231	0	7	0	239	47	25	22	524	256	268 (51.4)
1975	*ornat.*	*ornat.*	213	159	82	0	0	0	77	40	21	19	199	103	96 (48.2)
		chen.	2	2	0	0	0	0	2	—	—	—	2	0	2
		temp.	48	32	0	0	1	0	31	15	0	15	47	0	47
1976	*ornat.*	*ornat.*	161	157	70	2	11	0	74	—	—	—	157	72	85
		temp.	3	1	0	0	0	0	1	2	0	2	3	0	3
Total	*ornat.*	*ornat.*	2041	1679	796	2	85	0	796	184	98	86	1863	896	967 (51.9)
		chen.	25	20	0	0	5	0	15	5	0	5	25	0	25
		dyb. K	1	1	0	0	0	0	1	—	—	—	1	0	1
		temp.	89	52	0	0	1	0	51	36	0	36	88	0	88

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries
⚥, Hermaphrodites ♂R, Males with rudimentary testes
♂N, Males with normal testes * Including hermaphrodites

frogs were females with normal ovaries, two others were females with underdeveloped ovaries, in addition 85 others were hermaphrodites with gonads transforming from ovaries to testes and the remaining 796 were males with normal testes. At the mature stage, 98 of 184 frogs were females and the other 86 were males. When the hermaphrodites were counted as males, 896 frogs were females and 967 (51.9%) were males in total of the juvenile and mature ones.

b. *Rana ornativentris*♀ × *Rana chensinensis*♂

The sex of 25 normally metamorphosed frogs produced from crosses between female *Rana ornativentris* and male *Rana chensinensis* in 1962 and 1975 was examined at the juvenile or mature stage (Table 12). At the juvenile stage, 15 of 20 hybrids were males and the other five were hermaphrodites, while five mature hybrids were all males. When the hermaphrodites were counted as males, the 25 hybrids in total were all males.

c. *Rana ornativentris*♀ × *Rana dybowskii*♂

One juvenile hybrid produced from a cross between a female *Rana ornativentris* and a male *Rana dybowskii* from Korea in 1968 was a male (Table 12).

d. *Rana ornativentris*♀ × *Rana temporaria*♂

The sex of 88 of 89 normally metamorphosed frogs produced from crosses between female *Rana ornativentris* and male *Rana temporaria* in 1962, 1964, 1965, 1975

and 1976 was examined at the juvenile or mature stage (Table 12). At the juvenile stage, 51 of 52 hybrids were males and the remaining was a hermaphrodite, while 36 mature hybrids were all males. When the hermaphrodite was counted as a male, the 88 hybrids in total were all males.

3. Hybrids between female *Rana chensinensis* and males of four species

a. Control *Rana chensinensis*

Of 1215 normally metamorphosed frogs produced from control matings in 1962, 1963, 1970 and 1981, the sex of 1106 was examined at the juvenile or mature stage (Table 13). At the juvenile stage, 408 were females with normal ovaries, 32 others were hermaphrodites with gonads transforming from ovaries into testes and the remaining 518 were males with normal testes. At the mature stage, 57 of 148 frogs were females and the other 91 were males. When the hermaphrodites were counted as males, 465 frogs were females and 641 (58.0%) were males in total of the juvenile and mature ones.

This abundance of males in the control *Rana chensinensis* was attributable to the existence of triploids. The chromosomes were examined in 100 of 441 feeding tadpoles which had been produced in 1963 from matings between five females and five males. The results indicated that 29 of them were triploids which became all males, while the other 71 were diploids. In contrast with the findings in 1963, there was only one triploid among 20 of 78 feeding tadpoles which had been produced in 1970 from matings between two females and two males.

TABLE 13

Sex of hybrids between female *Rana chensinensis* and males of four species and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs						Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1962	*chen.*	*chen.*	512	359	172	0	3	0	184	100	43	57	459	215	244 (53.2)
		jap.	29	22	0	0	2	0	20	2	0	2	24	0	24
		ornat.	26	18	0	0	1	0	17	5	0	5	23	0	23
		arv.	20	14	0	0	3	0	11	6	0	6	20	0	20
1963	*chen.*	*chen.*	432	396	143	0	29	0	224	25	4	21	421	147	274 (65.1)
1970	*chen.*	*chen.*	70	40	17	0	0	0	23	23	10	13	63	27	36 (57.1)
		ornat.	27	19	0	0	0	0	19	—	—	—	19	0	19
1981	*chen.*	*chen.*	201	163	76	0	0	0	87	—	—	—	163	76	78 (53.4)
		ornat.	11	7	0	0	0	0	7	—	—	—	7	0	7
		dyb. T	1	1	0	0	0	0	1	—	—	—	1	0	1
Total	*chen.*	*chen.*	1215	958	408	0	32	0	518	148	57	91	1106	465	641 (58.0)
		jap.	29	22	0	0	2	0	20	2	0	2	24	0	24
		ornat.	64	44	0	0	1	0	43	5	0	5	49	0	49
		dyb. T	1	1	0	0	0	0	1	—	—	—	1	0	1
		arv.	20	14	0	0	3	0	11	6	0	6	20	0	20

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries
⚥, Hermaphrodites ♂R, Males with rudimentary testes
♂N, Males with normal testes * Including hermaphrodites

b. *Rana chensinensis*♀ × *Rana japonica*♂

The sex of 24 of 29 normally metamorphosed frogs produced from crosses

between female *Rana chensinensis* and male *Rana japonica* in 1962 was examined at the juvenile or mature stage (Table 13). At the juvenile stage, 20 of 22 hybrids were males and the other two were hermaphrodites, while two mature hybrids were males. When the hermaphrodites were counted as males, the 24 hybrids in total were all males.

c. *Rana chensinensis* ♀ × *Rana ornativentris* ♂

Of 64 normally metamorphosed frogs produced from crosses between female *Rana chensinensis* and male *Rana ornativentris* in 1962, 1970 and 1981, the sex of 49 was examined at the juvenile or mature stage (Table 13). At the juvenile stage, 43 of 44 hybrids were males and the remaining was a hermaphrodite, while five mature hybrids were all males. When the hermaphrodite was counted as a male, the 49 hybrids in total were all males.

d. *Rana chensinensis* ♀ × *Rana dybowskii* ♂

One juvenile hybrid produced from a cross between a female *Rana chensinensis* and a male *Rana dybowskii* from Tsushima was a male (Table 13).

e. *Rana chensinensis* ♀ × *Rana arvalis* ♂

The sex of 20 normally metamorphosed frogs produced from crosses between female *Rana chensinensis* and male *Rana arvalis* in 1962 was examined at the juvenile or mature stage (Table 13). At the juvenile stage, 11 of 14 hybrids were males and the other three were hermaphrodites, while six mature hybrids were all males. When the hermaphrodites were counted as males, the 20 hybrids in total were all males.

4. Hybrids between female *Rana tsushimensis* and male *Rana japonica*

a. Control *Rana tsushimensis*

Of 1003 normally metamorphosed frogs produced from control matings in 1963, 1966, 1967 and 1968, the sex of 927 was examined at the juvenile or mature stage (Table 14). At the juvenile stage, 426 of 882 frogs were females with

TABLE 14

Sex of hybrids between female *Rana tsushimensis* and male *Rana japonica* and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs						Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1963	*tsu.*	*tsu.*	127	111	51	0	1	0	59	7	3	4	118	54	64 (54.2)
1966	*tsu.*	*tsu.*	172	164	80	0	3	0	81	6	3	3	170	83	87 (51.2)
1967	*tsu.*	*tsu.*	532	449	214	0	5	0	230	23	12	11	472	226	246 (52.1)
		jap.	3	3	0	0	0	0	3	—	—	—	3	0	3
1968	*tsu.*	*tsu.*	172	158	81	0	3	0	74	9	4	5	167	85	82 (49.1)
Total	*tsu.*	*tsu.*	1003	882	426	0	12	0	444	45	22	23	927	448	479 (51.7)
		jap.	3	3	0	0	0	0	3	—	—	—	3	0	3

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries
⚥, Hermaphrodites ♂R, Males with rudimentary testes
♂N, Males with normal testes * Including hermaphrodites

normal ovaries, 12 others were hermaphrodites with gonads transforming from ovaries into testes and the remaining 444 were males with normal testes. At the mature stage, 22 of 45 frogs were females and the other 23 were males. When the hermaphrodites were counted as males, 448 frogs were females and 479 (51.7%) were males in total of the juvenile and mature ones.

b. *Rana tsushimensis* ♀ × *Rana japonica* ♂

Three juvenile hybrids produced from crosses between female *Rana tsushimensis* and male *Rana japonica* in 1967 were all males (Table 14).

5. Hybrids between female *Rana dybowskii* from Tsushima and males of four species

a. Control *Rana dybowskii* from Tsushima

Of 1441 normally metamorphosed frogs produced from control matings in 1968, 1970, 1975, 1976, 1978 and 1981, the sex of 1221 was examined at the juvenile or mature stage (Table 15). At the juvenile stage, 508 of 1078 frogs were females with normal ovaries, 35 others were hermaphrodites with gonads trans-

TABLE 15

Sex of inter- and intraspecific hybrids between female *Rana dybowskii* from Tsushima and males of five species and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs						Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1968	*dyb.* T	*dyb.* T	231	191	78	0	10	0	103	22	10	12	213	88	125(58.7)
		dyb. K	664	587	253	0	56	0	278	30	14	16	617	267	350(56.7)
1970	*dyb.* T	*dyb.* T	341	260	126	0	4	0	130	46	21	25	306	147	159(52.0)
		jap.	25	16	0	0	3	0	13	7	0	7	23	0	23
		ornat.	284	232	0	0	27	4	201	21	0	21	253	0	253
		chen.	75	64	0	0	19	10	35	0	0	9	73	0	73
		dyb. K	177	119	58	0	2	0	59	53	26	27	172	84	88(51.2)
1975	*dyb.* T	*dyb.* T	199	137	63	0	14	0	60	5	2	3	142	65	77(54.2)
		jap.	102	93	0	0	15	0	78	5	0	5	98	0	98
		ornat.	56	38	0	0	6	0	32	18	0	18	56	0	56
		chen.	31	27	0	0	3	0	24	3	0	3	30	0	30
		temp.	46	31	0	0	0	0	31	4	0	4	35	0	35
1976	*dyb.* T	*dyb.* T	29	20	8	0	0	0	12	—	—	—	20	8	12 (60.0)
		ornat.	10	8	0	0	0	0	8	—	—	—	8	0	8
1978	*dyb.* T	*dyb.* T	215	116	54	0	3	0	59	70	36	34	186	90	96(51.6)
		jap.	68	42	0	0	0	0	42	26	1**	25	68	1**	67
		ornat.	89	52	0	0	0	1	51	29	0	29	81	0	81
		chen.	53	29	0	0	3	2	24	20	0	20	49	0	49
1981	*dyb.* T	*dyb.* T	426	354	179	0	4	0	171	—	—	—	354	179	175(49.4)
Total	*dyb.* T	*dyb.* T	1441	1078	508	0	35	0	535	143	69	74	1221	577	644(52.7)
		dyb. K	841	706	311	0	58	0	337	83	40	43	789	351	438(55.5)
		jap.	195	151	0	0	18	0	133	38	1**	37	189	1**	188(99.5)
		ornat.	439	330	0	0	33	5	292	68	0	68	398	0	398
		chen.	159	120	0	0	25	12	83	23	0	23	143	0	143
		temp.	46	31	0	0	0	0	31	4	0	4	35	0	35

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries

⚥, Hermaphrodites ♂R, Males with rudimentary testes

♂N, Males with normal testes * Including hermaphrodites

** Abnormal female whose gonads have completely degenerated

forming from ovaries into testes and the remaining 535 were males with normal testes. At the mature stage, 69 of 143 frogs were females and the other 74 were males. When the hermaphrodites were counted as males, 577 frogs were females and 644 (52.7%) were males in total of the juvenile and mature ones.

b. *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Korea♂

Of 841 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Tsushima and male *Rana dybowskii* from Korea in 1968 and 1970, the sex of 789 was examined at the juvenile or mature stage (Table 15). At the juvenile stage, 311 of 706 frogs were females, 58 others were hermaphrodites and the remaining 337 were males, while 40 of 83 mature frogs were females and the other 43 were males. When the hermaphrodites were counted as males, 351 of 789 frogs in total were females and 438 (55.5%) were males.

c. *Rana dybowskii* from Tsushima♀ × *Rana japonica*♂

The sex of 189 of 195 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Tsushima and male *Rana japonica* in 1970, 1975 and 1978 was examined at the juvenile or mature stage (Table 15). At the juvenile stage, 133 of 151 hybrids were males and the other 18 were hermaphrodites, while 38 mature hybrids included 37 males and a single female whose gonads had completely degenerated. When the hermaphrodites were counted as males, 188 (99.5%) of the 189 hybrids in total were males.

d. *Rana dybowskii* from Tsushima♀ × *Rana ornativentris*♂

Of 439 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Tsushima and male *Rana ornativentris* in 1970, 1975, 1976 and 1978, the sex of 398 was examined at the juvenile or mature stage (Table 15). At the juvenile stage, 292 of 330 hybrids were males with apparently normal testes, 33 others were hermaphrodites with gonads transforming from ovaries into testes and the remaining five were males with rudimentary testes. At the mature stage, 68 hybrids were all males. When the hermaphrodites were counted as males, the 398 hybrids in total were all males.

e. *Rana dybowskii* from Tsushima♀ × *Rana chensinensis*♂

Of 159 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Tsushima and male *Rana chensinensis* in 1970, 1975 and 1978, the sex of 143 was examined at the juvenile and mature stage (Table 15). At the juvenile stage, 83 of 120 hybrids were males with apparently normal testes, 25 others were hermaphrodites with gonads transforming from ovaries into testes and the remaining 12 were males with rudimentary testes. At the mature stage, 23 hybrids were all males. When the hermaphrodites were counted as males, the 143 hybrids in total were all males.

f. *Rana dybowskii* from Tsushima♀ × *Rana temporaria*♂

Of 46 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Tsushima and male *Rana temporaria* in 1975, the sex of 35 was examined at the juvenile or mature stage (Table 15). It was found that the hybrids including 31 juvenile and four mature ones were all males.

6. Hybrids between female *Rana dybowskii* from Korea and males of four species

a. Control *Rana dybowskii* from Korea

Of 934 normally metamorphosed frogs produced from control matings in 1970, the sex of 794 was examined at the juvenile or mature stage (Table 16). At the juvenile stage, 260 of 535 frogs were females with normal ovaries, one was a hermaphrodite with gonads transforming from ovaries into testes and the remaining 274 were males with normal testes. At the mature stage, 122 of 259 frogs were females and the other 137 were males. When the hermaphrodite was counted as a male, 382 frogs were females and 412 (51.9%) were males in total of the juvenile and mature ones.

TABLE 16

Sex of inter- and intraspecific hybrids between female *Rana dybowskii* from Korea males of five species and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs						Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1970	*dyb.* K	*dyb.* K	934	535	260	0	1	0	274	259	122	137	794	382	412(51.9)
		dyb. T	1140	619	300	7	8	0	304	167	81	86	786	388	398(50.6)
		jap.	63	36	0	0	4	0	32	5	0	5	41	0	41
		ornat.	669	504	0	4	61	4	435	111	0	111	615	4	611(99.3)
		chen.	468	374	0	18	21	23	312	26	0	26	400	18	382(95.5)
		tsu.	20	14	0	0	1	0	13	1	0	1	15	0	15

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries
⚥, Hermaphrodites ♂R, Males with rudimentary testes
♂N, Males with normal testes * Including hermaphrodites

b. *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Tsushima♂

Of 1140 normally metamorphosed frogs produced in 1970 from crosses between female *Rana dybowskii* collected from Korea and male *Rana dybowskii* from Tsushima, the sex of 786 was examined at the juvenile or mature stage (Table 16). At the juvenile stage, 300 of 619 frogs were females with normal ovaries, seven others were females with underdeveloped ovaries, in addition eight others were hermaphrodites with gonads transforming from ovaries into testes and the remaining 304 were males with normal testes. At the mature stage, 81 of 167 frogs were females and the other 86 were males. When the hermaphrodites were counted as males, 388 frogs were females and 398 (50.6%) were males in total of the juvenile and mature ones.

c. *Rana dybowskii* from Korea♀ × *Rana japonica*♂

The sex of 41 of 63 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Korea and male *Rana japonica* in 1970, was examined at the juvenile or mature stage (Table 16). At the juvenile stage, 32 of 36 hybrids were males and the other four were hermaphrodites, while five mature hybrids were all males. When the hermaphrodites were counted as males, the 41 hybrids in total were all males.

d. *Rana dybowskii* from Korea♀ × *Rana ornativentris*♂

Of 669 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Korea and male *Rana ornativentris* in 1970, the sex of 615 was examined at the juvenile or mature stage (Table 16). At the juvenile stage, 435 of 504 hybrids were males with apparently normal testes, four others were males with rudimentary testes, in addition 61 others were hermaphrodites and the remaining four were females with underdeveloped ovaries. At the mature stage, 111 hybrids were all males. When the hermaphrodites were counted as males, 611 (99.3%) of the 615 hybrids in total were males. The four females with underdeveloped ovaries were assumed to become males before long by sex reversal.

e. *Rana dybowskii* from Korea♀ × *Rana chensinensis*♂

Of 468 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Korea and male *Rana chensinesis* in 1970, the sex of 400 was examined at the juvenile or mature stage (Table 16). At the juvenile stage, 312 of 374 hybrids were males with apparently normal testes, 23 others were males with rudimentary testes, in addition 21 others were hermaphrodites with gonads transforming from ovaries into testes and the remaining 18 were females with underdeveloped ovaries. At the mature stage, 26 hybrids were all males. When the hermaphrodites were counted as males, 382 (95.5%) of the 400 hybrids in total were males. The other 18 females with underdeveloped ovaries were assumed to become males before long by sex reversal.

f. *Rana dybowskii* from Korea♀ × *Rana tsushimensis*♂

The sex of 15 of 20 normally metamorphosed frogs produced from crosses between female *Rana dybowskii* collected from Korea and male *Rana tsushimensis* in 1970 was examined at the juvenile or mature stage (Table 16). At the juvenile stage, 13 of 14 hybrids were males and the remaining was a hermaphrodite, while one mature hybrid was a male. When the hermaphrodite was counted as a male, the 15 hybrids in total were all males.

7. Control *Rana amurensis coreana*

As no hybrids raised from eggs of *Rana amurensis coreana* could complete metamorphosis, the sex of the hybrids was not examined. Of 167 normally metamorphosed frogs produced from control matings in 1970, the sex of 164 was examined at the juvenile or mature stage (Table 17). At the juvenile stage, 74 of 153 frogs were females with normal ovaries, seven were hermaphrodites

with gonads transforming from ovaries into testes and the remaining 72 were males with normal testes. At the mature stage five of 11 frogs were females and the other six were males. When the hermaphrodites were counted as males, 79 frogs were females and 85 (51.8%) were males in total of the juvenile and mature ones.

8. Hybrids between female *Rana longicrus* and males of two species

a. Control *Rana longicrus*

Of 389 normally metamorphosed frogs produced from control matings in 1981, the sex of 355 was examined at the juvenile or mature stage (Table 17). At the juvenile stage, 171 of 300 frogs were females with normal testes, 52 were hermaphrodites with gonads transforming from ovaries into testes and the remaining 77 were males with normal testes. At the mature stage, 25 of 55 frogs were females and the other 30 were males. When the hermaphrodites were counted as males, 196 frogs were females and 159 (44.8%) were males in total of the juvenile and mature ones.

TABLE 17

Sex of control *Rana amurensis coreana*, control *Rana temporaria*, hybrids between female *Rana longicrus* and males of two species and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs						Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1970	*amur.*	*amur.*	167	153	74	0	7	0	72	11	5	6	164	79	85 (51.8)
1981	*long.*	*long.*	389	300	171	0	52		77	55	25	30	355	196	159 (44.8)
		jap.	342	263	0	0	0	0	263	69	0	69	332	0	332
		ornat.	5	5	0	0	0	0	5	—	—	—	5	0	5
1963	*temp.*	*temp.*	169	124	52	0	7	0	65	43	15	28	167	67	100 (59.9)

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries
⚥, Hermaphrodites ♂R, Males with rudimentary testes
♂N, Males with normal testes * Including hermaphrodites

b. *Rana longicrus*♀ × *Rana japonica*♂

Of 342 normally metamorphosed frogs produced from crosses between female *Rana longicrus* and male *Rana japonica* in 1981, the sex of 332 was examined at the juvenile or mature stage (Table 17). It was found that the hybrids including 263 juvenile and 69 mature hybrids were all males.

c. *Rana longicrus*♀ × *Rana ornativentris*♂

Five normally metamorphosed frogs produced from a cross between a female *Rana longicrus* and a male *Rana ornativentris* in 1981 were all males with apparently normal testes when their sex was examined shortly after metamorphosis (Table 17).

9. Control *Rana temporaria*

As no hybrids raised from eggs of *Rana temporaria* could complete metamorphosis,

the sex of the hybrids was not examined. Of 169 normally metamorphosed frogs produced from control matings in 1963, the sex of 167 was examined at the juvenile or mature stage (Table 17). At the juvenile stage, 52 of 124 frogs were females with normal testes, seven others were hermaphrodites with gonads transforming from ovaries into testes and the remaining 65 were males with normal testes. At the mature stage, 15 of 43 frogs were females and the other 28 were males. When the hermaphrodites were counted as males, 67 frogs were females and 100 (59.9%) were males in total of the juvenile and mature ones.

10. Hybrids between female *Rana arvalis* and males of six species

a. Control *Rana arvalis*

Of 416 normally metamorphosed frogs produced from control matings in 1962, 1963, 1966 and 1976, the sex of 382 was examined at the juvenile or mature stage (Table 18). At the juvenile stage, 117 of 247 frogs were females with normal ovaries, five others were hermaphrodites with gonads transforming from ovaries into testes and the remaining 125 were males with normal testes. At the mature stage, 63 of 135 frogs were females and the other 72 were males. When the hermaphrodites were counted as males, 180 forgs were females and 202 (52.9%) were males in total of the juvenile and mature ones.

TABLE 18

Sex of hybrids between female *Rana arvalis* and males of six species and the controls

Year	Parents		No. of metamorphosed frogs	Juvenile frogs						Mature frogs			All frogs examined		
	Female	Male		Number	♀N	♀U	⚥	♂R	♂N	Number	♀	♂	Number	♀	♂(%)*
1962	*arv.*	*arv.*	154	114	55	0	2	0	57	39	17	22	153	72	81 (52.9)
		jap.	47	32	0	0	3	0	29	13	0	13	45	0	45
		ornat.	84	75	0	4	15	0	56	9	0	9	84	4	80 (95.2)
		temp.	3	3	0	0	1	0	2	—	—	—	3	0	3
1963	*arv.*	*arv.*	112	91	41	0	2	0	48	13	7	6	104	48	56 (53.8)
1966	*arv.*	*arv.*	32	13	5	0	1	0	7	9	5	4	22	10	12 (54.5)
		chen.	5	2	0	0	0	0	2	3	0	3	5	0	5
		dyb. T	3	3	0	0	0	0	3	—	—	—	3	0	3
1976	*arv.*	*arv.*	118	29	16	0	0	0	13	74	34	40	103	50	53 (51.5)
		jap.	3	3	0	0	0	0	3	—	—	—	3	0	3
		ornat.	6	4	0	0	0	0	4	2	0	2	6	0	6
		chen.	8	2	0	0	0	0	2	6	0	6	8	0	8
		dyb. T	1	1	0	0	0	0	1	—	—	—	1	0	1
1977	*arv.*	*tsu.*	3	—	—	—	—	—	—	1	0	1	1	0	1
Total	*arv.*	*arv.*	416	247	117	0	5	0	125	135	63	72	382	180	202 (52.9)
		jap.	50	35	0	0	3	0	32	13	0	13	48	0	48
		ornat.	90	79	0	4	15	0	60	11	0	11	90	4	86 (95.6)
		chen.	13	4	0	0	0	0	4	9	0	9	13	0	13
		tsu.	3	—	—	—	—	—	—	1	0	1	1	0	1
		dyb. T	4	4	0	0	0	0	4	—	—	—	4	0	4
		temp.	3	3	0	0	1	0	2	—	—	—	3	0	3

♀N, Females with normal ovaries ♀U, Females with underdeveloped ovaries
⚥, Hermaphrodites ♂R, Males with rudimentary testes
♂N, Males with normal testes * Including hermaphrodites

b. *Rana arvalis*♀ × *Rana japonica*♂

The sex of 48 of 50 normally metamorphosed frogs produced from crosses between female *Rana arvalis* and male *Rana japonica* in 1962 and 1976 was examined at the juvenile or mature stage (Table 18). It was found that 32 of 35 juvenile hybrids were males and the other three were hermaphrodites, while 13 mature hybrids were all males. When the hermaphrodites were counted as males, the 48 hybrids in total were all males.

c. *Rana arvalis*♀ × *Rana ornativentris*♂

The sex of 90 normally metamorphosed frogs produced from crosses between female *Rana arvalis* and male *Rana ornativentris* in 1962 and 1976 was examined at the juvenile or mature stage (Table 18). At the juvenile stage, 60 of 79 frogs were males, 15 others were hermaphrodites and the remaining four were females with underdeveloped ovaries. At the mature stage, 11 hybrids were all males. When the hermaphrodites were counted as males, 86 (95.6%) of the 90 hybrids in total were males and the remaining four were females. These females with underdeveloped ovaries were assumed to become males before long by sex reversal.

d. *Rana arvalis*♀ × *Rana chensinensis*♂

The sex of 13 hybrids produced from crosses between female *Rana arvalis* and male *Rana chensinensis* in 1966 and 1976 was examined at the juvenile or mature stage (Table 18). The results showed that the 13 hybrids including four juvenile and nine mature ones were all males.

e. *Rana arvalis*♀ × *Rana tsushimensis*♂

A mature hybrid between a female *Rana arvalis* and a male *Rana tsushimensis* was a male (Table 18).

f. *Rana arvalis*♀ × *Rana dybowskii* from Tsushima♂

Four hybrids produced from crosses between female *Rana arvalis* and male *Rana dybowskii* collected from Tsushima were all males when their sex was examined shortly after metamorphosis (Table 18).

g. *Rana arvalis*♀ × *Rana temporaria*♂

The sex of three hybrids produced from crosses between female *Rana arvalis* and male *Rana temporaria* in 1962 was examined at the juvenile stage (Table 18). It was found that two hybrids were males and the other was a hermaphrodite. When the hermaphrodite was counted as a male, the three hybrids in total were all males.

III. External characters of mature frogs

1. Field-caught frogs used in crossing experiments

a. *Rana japonica*

Three females and four males were 56.1 mm and 47.1 mm in mean body length, respectively. Twelve females and eleven males observed had a slender body and fairly long hind legs. The head had a pointed snout. The dorsal skin was smooth. Although it was sparsely or densely covered with minute granules, these were low and flat. There were no distinct warts on the back. Some frogs had some indistinct blackish spots on the dorsal and lateral surfaces of the body, while such spots were very scarce in other frogs. There was no vertebral stripe. The dorsolateral folds ran nearly parallel with each other from the upper eyelid to the groin. The upper lip was obscurely edged with

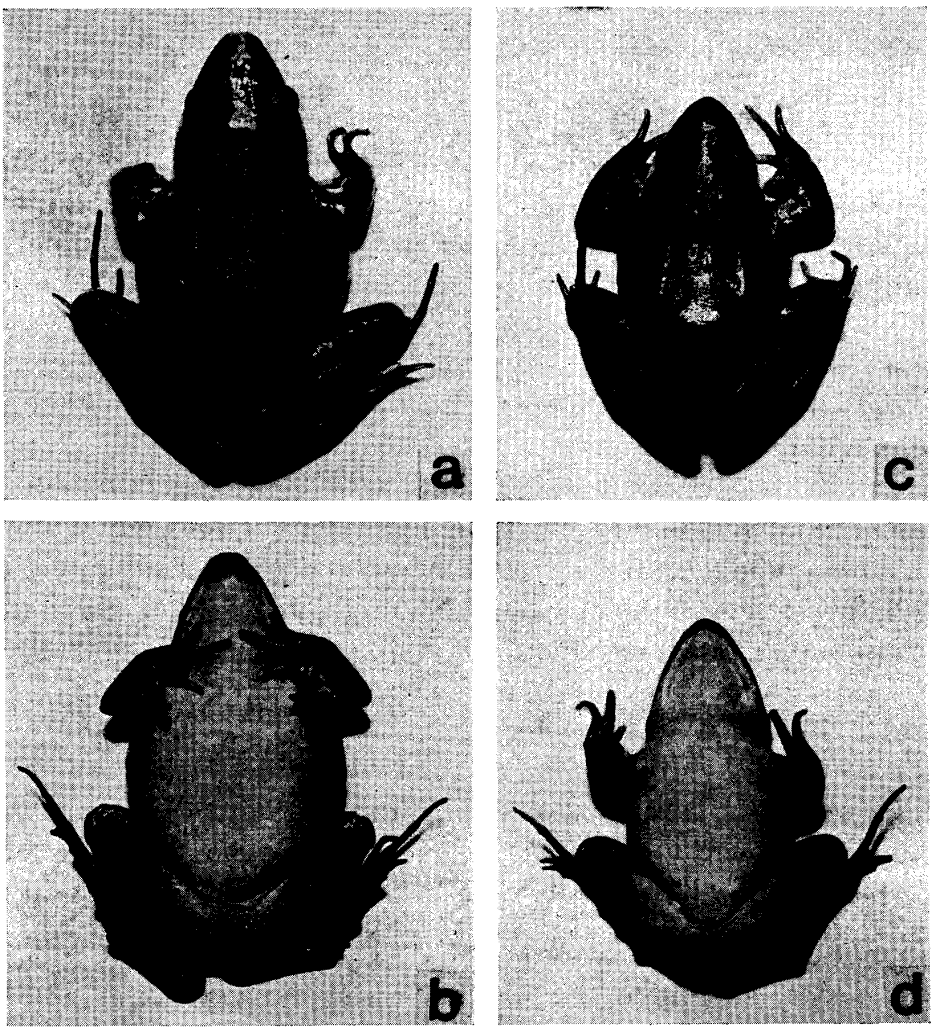


Fig. 7. Dorsal and ventral views of *Rana japonica* collected from Hiroshima, Japan. ×0.8
a, b. Female c, d. Male

dark spots. The ventral surface of the body was white or grayish white and sometimes partly mottled with dark color. The hind legs were distinctly or indistinctly barred with dark color. The dark bars on the tibia were usually five or six in number. The inner metatarsal tubercles were smaller than those of *Rana ornativentris* and *Rana chensinensis* (Table 19; Fig. 7).

b. *Rana ornativentris*

Four females and five males were 66.8 mm and 50.1 mm in mean body length, respectively. Ten females and eight males observed had a stocky body and fairly long hind legs. The head had a somewhat blunt snout. The dorsal skin was smooth, although it was covered with minute granules. There were several distinct dot- or rod-shaped warts on the dorsal and lateral surfaces of the body. Each wart was covered with a blackish spot. On the dorsal surface of the trunk there was a distinctly or obscurely pale vertebral stripe which was

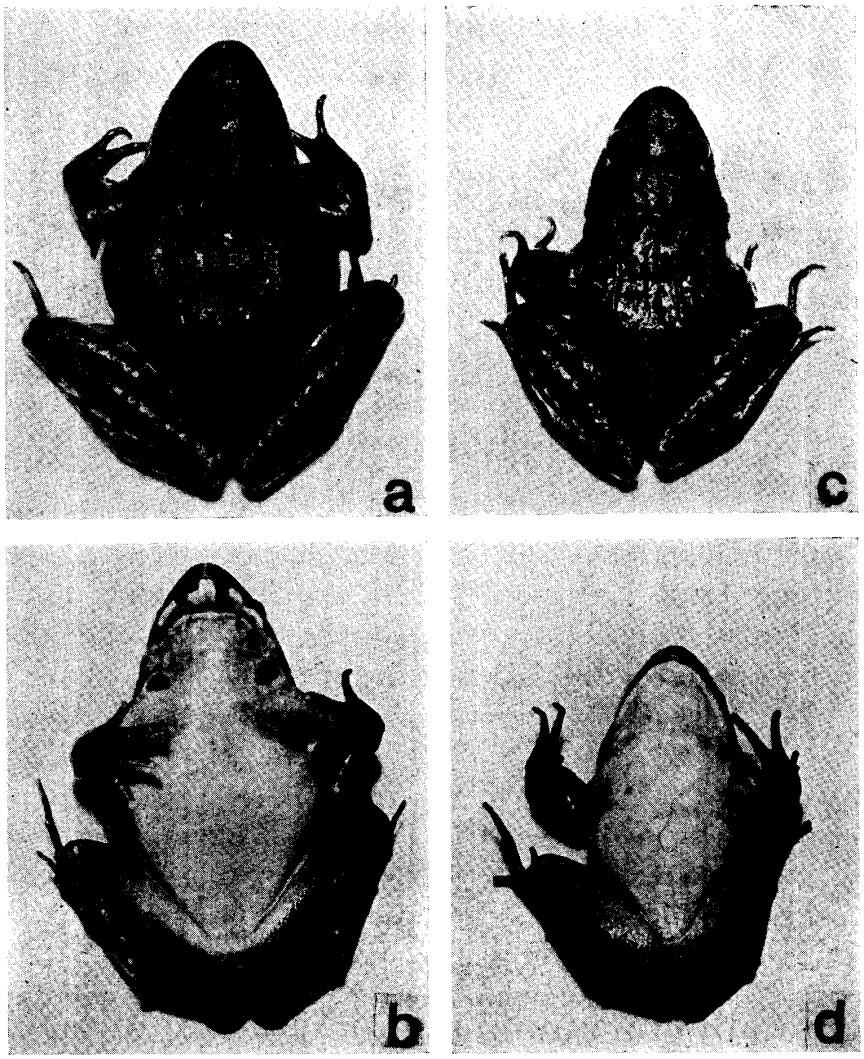


Fig. 8. Dorsal and ventral views of *Rana ornativentris* collected from Hiroshima Prefecture, Japan. ×0.8

a, b. Female c, d. Male

TABLE 19

Measurements of various body sites of twelve brown frog species collected from the field. An additional

Kind	*jap.* Wild		*ornat.* Wild		*chen.* Wild		*oki.* Wild		*tsu.* Wild	
Number of frogs	♀3	♂4	♀4	♂5	♀5	♂4	♀2	♂2	♀5	♂4
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
Body length	56.1	47.1	66.8	50.1	62.0	56.8	46.8	40.6	41.7	35.6
Head length	17.6	14.6	18.6	15.9	16.8	15.3	14.4	12.9	11.4	10.4
Head length / Body length	0.31	0.31	0.28	0.32	0.27	0.27	0.31	0.32	0.28	0.29
Head width	17.0	14.9	22.4	17.0	18.9	18.6	13.5	12.5	13.1	11.3
Head width / Head length	0.97	1.02	1.20	1.07	1.13	1.22	0.94	0.97	1.14	1.09
Snout length	6.8	5.8	7.7	6.4	7.0	6.0	6.7	5.0	4.5	3.6
Distance between orbitals	3.1	2.2	3.9	3.0	3.8	3.4	3.9	3.4	3.0	2.4
Distance between nostrils	3.1	2.8	3.4	3.0	3.9	3.8	3.5	3.0	3.0	2.7
Diameter of tympanum	3.7	3.6	4.1	3.1	3.2	3.0	3.5	3.2	2.2	1.9
Arm length	32.2	29.2	38.5	31.6	37.3	33.3	28.3	22.8	25.9	21.0
Arm length / Body length	0.57	0.62	0.58	0.63	0.60	0.59	0.60	0.56	0.62	0.59
Hind leg length	99.1	85.1	119.3	92.6	95.9	94.0	83.9	67.6	73.8	63.3
Hind leg length / Body length	1.77	1.81	1.79	1.85	1.55	1.65	1.79	1.67	1.77	1.78
Outer metatarsal tubercle	None	None or dot	None	None or dot	None or dot	None or dot	1.0	1.0	Dot	Dot
Length of inner metatarsal tubercle	1.9	2.0	3.7	2.9	3.2	3.3	1.8	1.5	2.0	1.8
Length of inner metatarsal tubercle / Body length	0.03	0.04	0.06	0.06	0.05	0.06	0.04	0.04	0.05	0.05

jap., *Rana japonica* *ornat.*, *Rana ornativentris* *chen.*, *Rana chensinesis* *tsu.*, *Rana tsushimensis* *temp.*, *Rana temporaria* *arv.*, *Rana arvalis* Wild, field-caught

usually accompanied with two parallel rows of warts. Dorsolateral folds were curved outward and partially cut off in the shoulder region. The upper lip was distinctly edged with dark spots. There were usually some distinct, blackish spots on the throat. The venter was white. The hind legs were distinctly barred with dark color. The dark bars on the tibia were usually five to eight in number. The inner metatarsal tubercles were fairly large (Table 19; Fig. 8).

c. *Rana chensinensis*

Five females and four males were 62.0 mm and 56.8 mm in mean body length, respectively. Seven females and ten males observed had a stocky body and comparatively short hind legs. The head had a blunt or rounded snout. The dorsal skin was either smooth or rough and covered with minute granules all over the surface. Various number of warts were sparsely distributed on the dorsal and lateral surfaces of the body. Each wart was generally covered with a blackish spot. Some specimens had a pale vertebral stripe accompanied with two parallel rows of warts on the posterior part of the back. The dorsolateral folds were curved outward without being cut off in the shoulder region. The

Rana temporaria and two additional *Rana arvalis* specimens were produced in the laboratory

amur. Wild		*long.* Wild		*lato.* Wild	*temp.* Wild		63 *temp.* ♀ × *temp.* ♂	*arv.* Wild		76*arv.* ♀ × *arv.* ♂	*dalm.* Wild	*macr.* Wild
♀3	♂3	♀5	♂4	♂3	♀2	♂3	♂1	♀3	♂3	♂2	♂1	♂1
mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
45.7	36.4	47.5	42.5	40.2	73.8	63.3	67.0	55.9	52.5	51.9	51.5	60.5
13.5	11.2	15.6	15.0	13.6	19.0	17.5	18.0	16.2	16.3	15.9	16.0	17.5
0.30	0.31	0.33	0.35	0.34	0.26	0.28	0.27	0.29	0.31	0.31	0.31	0.29
13.8	12.0	12.3	11.9	12.3	23.0	20.7	22.5	19.0	17.7	17.1	18.51	23.0
1.02	1.07	0.79	0.79	0.90	1.21	1.18	1.25	1.17	1.09	1.08	1.16	1.31
4.7	4.3	6.3	6.0	5.3	8.0	6.8	6.5	6.3	5.9	5.3	6.5	6.5
3.1	2.6	3.0	3.0	3.3	5.3	4.1	4.0	4.0	4.0	3.9	4.0	3.5
2.9	2.1	2.8	2.6	4.1	4.7	3.7	4.5	3.1	3.2	3.2	3.0	4.5
2.5	2.0	2.7	2.5	3.0	4.3	4.2	5.5	3.3	2.9	3.0	3.5	4.0
27.8	20.8	27.4	25.7	24.3	46.7	41.5	35.0	33.3	33.1	30.8	35.0	35.0
0.61	0.57	0.58	0.60	0.60	0.63	0.66	0.52	0.60	0.63	0.59	0.68	0.58
76.3	55.4	86.2	80.5	61.9	120.5	109.7	101.0	96.1	94.2	85.4	106.0	107.5
1.67	1.52	1.82	1.89	1.54	1.63	1.73	1.51	1.72	1.79	1.65	2.06	1.77
None or dot	None	Dot	Dot	1.1	None	None	None	Dot	None or dot	Dot or none	None	1.5
2.0	1.2	1.9	2.1	2.0	4.1	3.1	4.5	3.5	3.5	3.4	3.0	3.5
0.04	0.03	0.04	0.05	0.05	0.06	0.05	0.07	0.06	0.07	0.07	0.06	0.06

oki., *Rana okinavana* *amur.*, *Rana amurensis coreana* *long.*, *Rana longicrus* *lato.*, *Rana latouchii*

dark spots on the upper lip were not so distinct as those of *Rana ornativentris* but more distinct than those of *Rana japonica*. The ventral surface of the body was evenly white or gray, or suffused with brownish gray or orange marks. The hind legs were indistinctly barred with dark color. The inner metatarsal tubercles were larger than those of *Rana japonica* (Table 19; Fig. 9).

d. *Rana okinavana*

Two females and two males were 46.8 mm and 40.6 mm in mean body length, respectively. They had a pointed head and a slender body. The dorsal skin was rough due to distribution of minute projecting granules all over the surface. There was no vertebral stripe. The dorsolateral folds were parallel with each other. They were either continued or slightly interrupted from the upper eyelids. The upper lip was edged with dark spots. Many small warts were distributed on the dorsal and lateral surfaces of the trunk. Blackish spots were rather rare on the back. The ventral surface of the body was grayish white in ground color, while the throat, thorax and lateral parts of the venter were suffused with brownish gray spots. The hind legs were barred with dark color. The dark

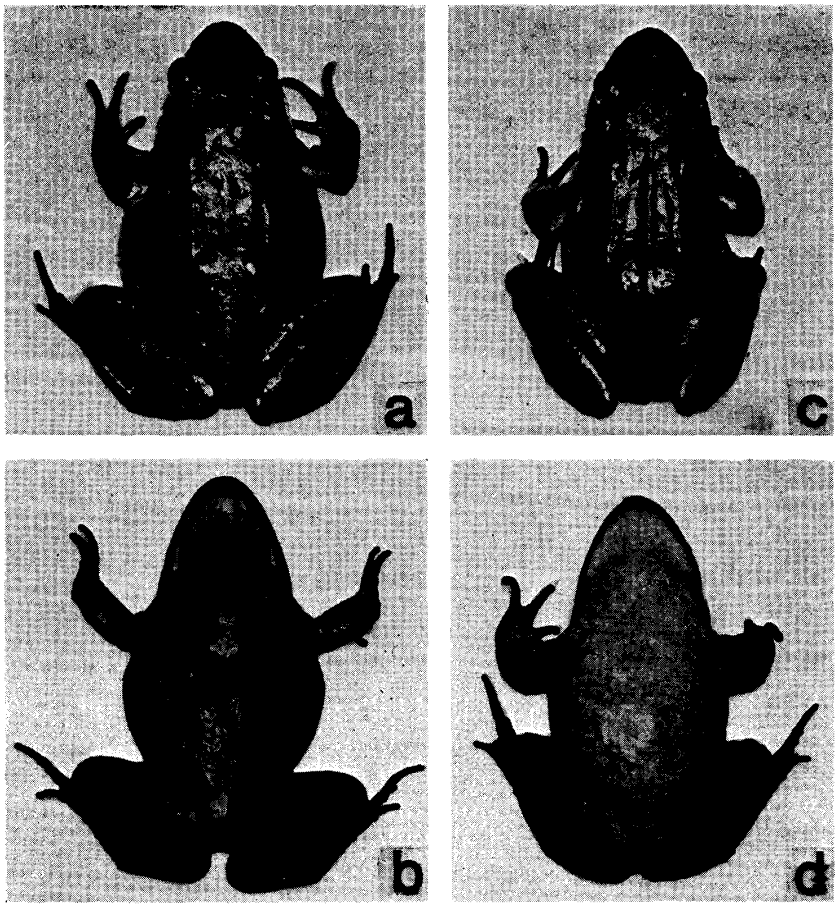


Fig. 9. Dorsal and ventral views of *Rana chensinensis* collected from Sapporo, Hokkaido, Japan. ×0.7

a, b. Female c, d. Male

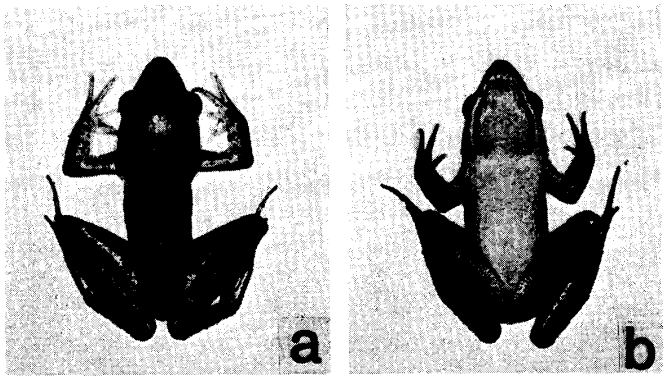


Fig. 10. Dorsal and ventral views of *Rana okinavana* collected from Okinawa Island, Japan. ×0.7

a, b. Male

bars were narrow and six or more in number on the tibia. The inner metatarsal tubercles were comparatively small, while the outer metatarsal tubercles were always distinct (Table 19; Fig. 10).

e. *Rana tsushimensis*

Five females and four males were 41.7 mm and 35.6 mm in mean body length, respectively. Ten females and sixteen males observed had a somewhat slender body and fairly long hind legs. The head had a pointed snout. The dorsal skin of the body was rough due to distribution of minute projecting granules all over the surface. There were no distinct warts on the area between the dorsolateral folds except that some specimens had a few warts which were arranged in short rods on the level of the forelegs. There was no vertebral stripe. The dorsolateral folds were curved outward in the shoulder region, where the folds were either cut off or intact. The upper lip was distinctly edged with dark spots. The throat, thorax and anterior part of the venter were suffused with brownish gray spots, while the posterior part of the venter was white. The hind legs were distinctly barred with dark color. The dark bars were usually five to seven in number on the tibia. The inner metatarsal tubercles were comparatively large. The outer metatarsal tubercles were present as a small dot-like protuberance (Table 19; Fig. 11).

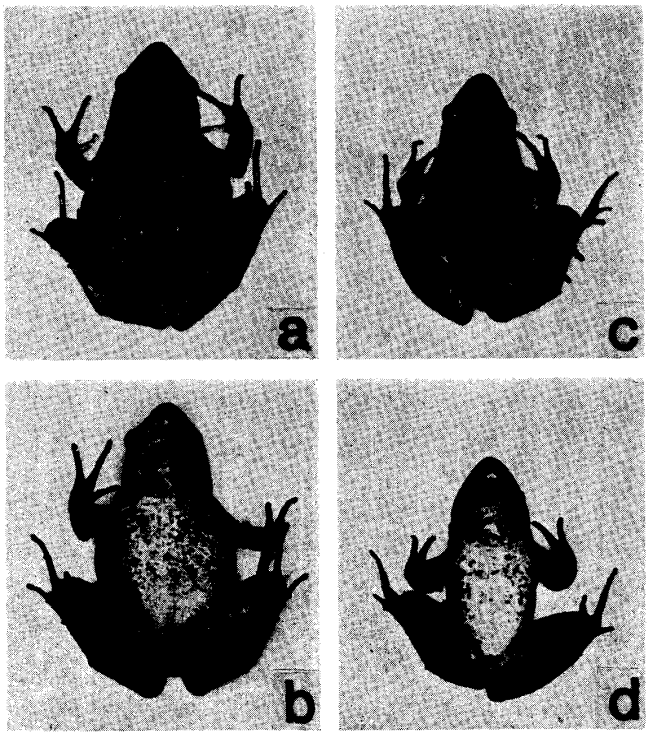


Fig. 11. Dorsal and ventral views of *Rana tsushimensis* collected from Tsushima Island, Japan. ×0.8

a, b. Female c, d. Male

f. *Rana dybowskii* from Tsushima

Five females and four males were 75.9 mm and 62.2 mm in mean body length, respectively. Nine females and nine males observed had a stocky body and fairly long hind legs. The head had a blunt snout. The dorsal skin was smooth and covered with minute flat granules all over the surface. There were a few small,

irregularly shaped warts on the back. Each wart was usually covered with a dark spot. There was no vertebral stripe. The dorsolateral folds were slightly curved outward and usually interrupted in the shoulder region. The upper lip was edged with dark spots. The ventral surface of the body was white or reddish orange in ground color. The throat and thorax were often mottled with gray color. The hind legs were distinctly barred with dark color. The inner metatarsal tubercles were comparatively large (Table 21; Fig. 12).

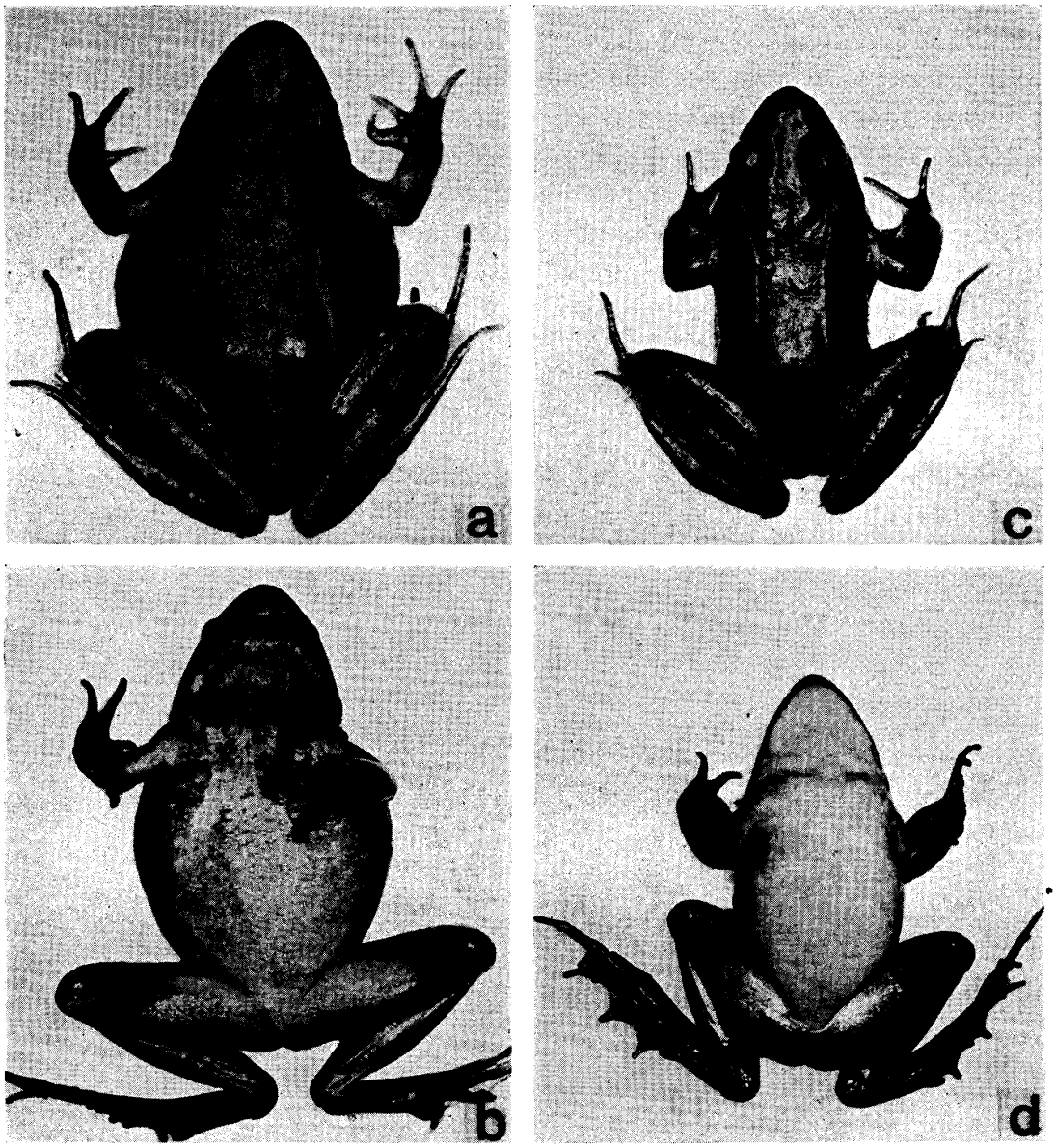


Fig. 12. Dorsal and ventral views of *Rana dybowskii* collected from Tsushima Island, Japan. ×0.7

a, b. Female c, d. Male

g. *Rana dybowskii* from Korea

Three females and three males were 74.5 mm and 55.0 mm in mean body length, respectively. Seven females and eight males observed were very similar

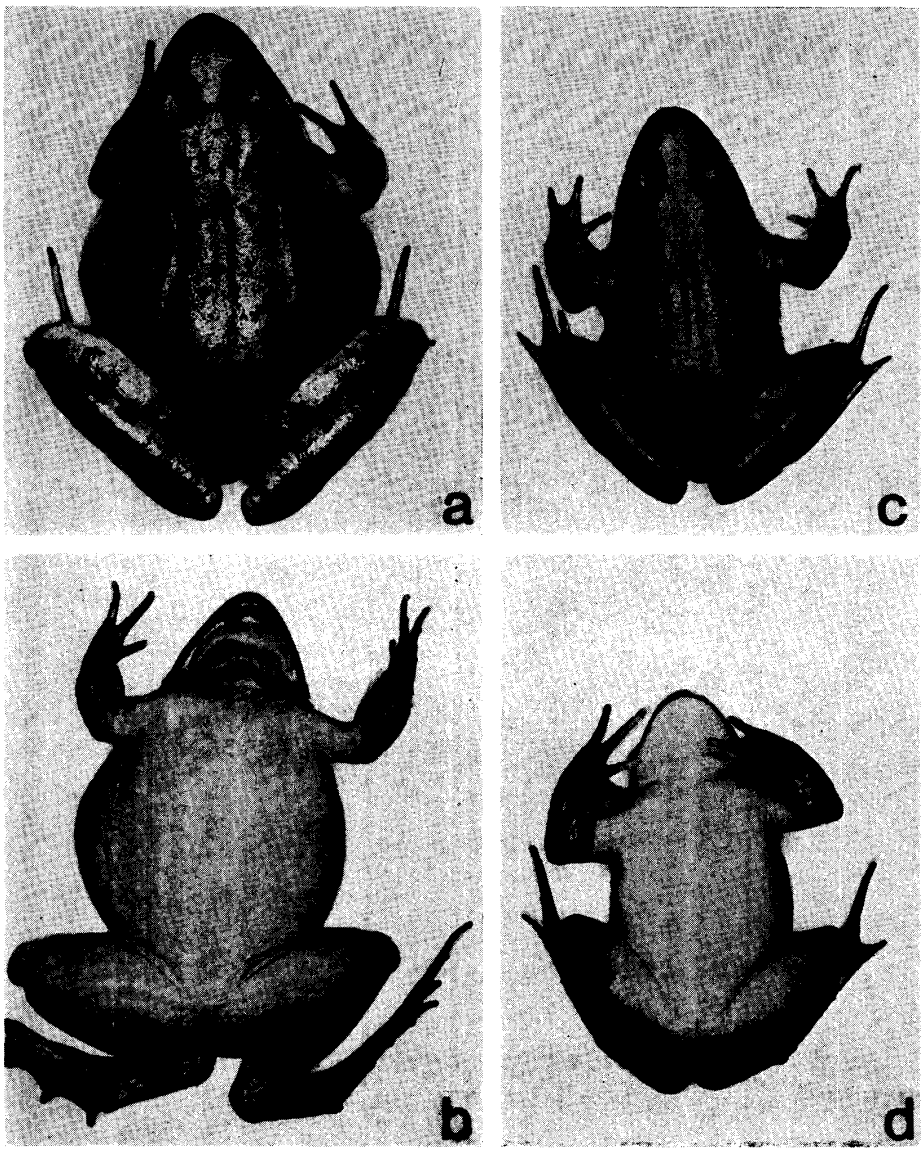


Fig. 13. Dorsal and ventral views of *Rana dybowskii* collected from Seoul, Korea. ×0.7

a, b. Female c, d. Male

to *Rana dybowskii* from Tsushima in various respects. These two populations were morphologically indistinguishable from each other. (Table 21; Fig. 13).

h. *Rana amurensis coreana*

Three females and three males were 45.7 mm and 36.4 mm in mean body length, respectively. Five females and five males observed had a somewhat slender body and comparatively short legs. The head had a pointed snout. The dorsal skin was rather rough due to distribution of minute projecting granules and small warts all over the surface. Each wart was usually covered with dark color. A pale vertebral stripe was either present or absent. This stripe was usually accompanied with rows of dark small warts arranged along the stripe.

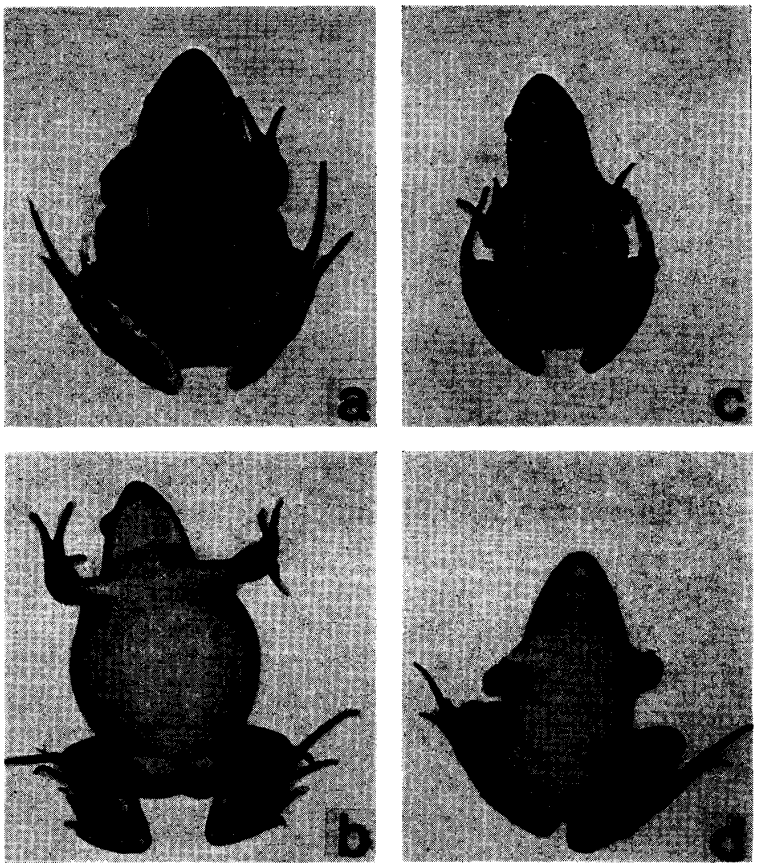


Fig. 14. Dorsal and ventral views of *Rana amurensis coreana* collected from Suwon, Korea. ×0.8

a, b. Female c, d. Male

The dorsolateral folds were slightly curved outward in the shoulder region. They were either interrupted or faintly continued from the upper eyelids. The upper lip had no dark spots. The ventral surface of the body was wholly or partly white. The thorax and the lateral parts of the venter were suffused with minute gray spots in some specimens. The hind legs were barred with dark color. The dark bars were narrow and usually seven in number. The inner metatarsal tubercles were comparatively small (Table 19; Fig. 14).

i. *Rana longicrus*

Five females and four males were 47.5 mm and 42.5 mm in mean body length, respectively. They had a slender body and long legs. The head had a sharply pointed snout. The dorsal skin was rough due to distribution of minute projecting granules all over the surface. There was no vertebral stripe. The dorsolateral folds were almost parallel with each other and continuous from the upper eyelids. There were a few blackish spots on the back. The upper lip was edged with fairly distinct blackish spots. The ventral surface of the body was wholly or partly white. In some specimens, the marginal parts of the throat, thorax and venter were distributed with small blackish spots or marbled with gray color.

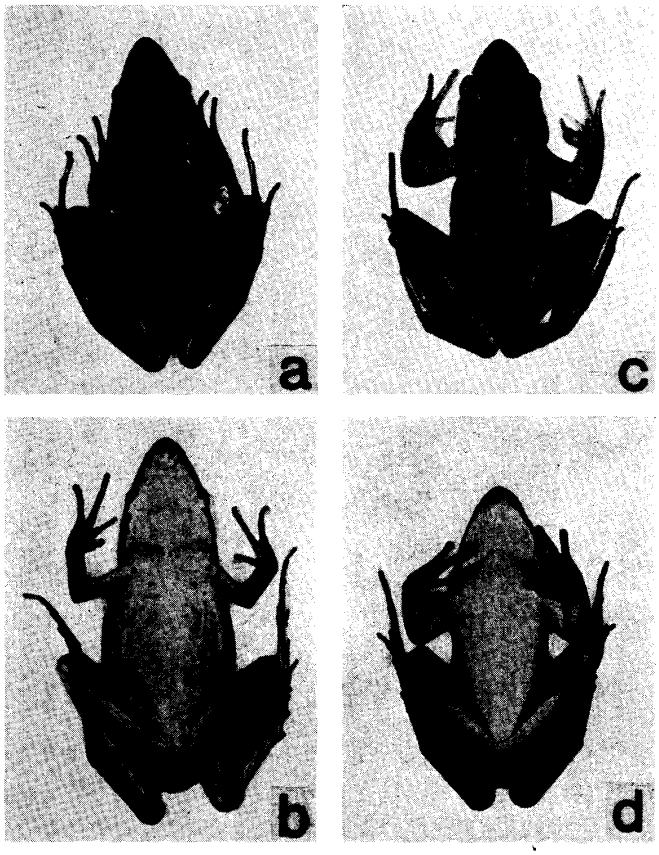


Fig. 15. Dorsal and ventral views of *Rana longicrus* collected from Taipei, Formosa. ×0.7
a, b. Female c, d. Male

The hind legs were obscurely barred with dark color. The outer metatarsal tubercles were present as a small dot-like protuberance (Table 19; Fig. 15).

j. *Rana latouchii*

Three males were 40.2 mm in mean body length. Two females and three males observed had a slender body and short hind legs. The head had a somewhat blunt snout. The dorsal skin was rough due to distribution of minute projecting granules and small warts all over the surface. Various number of large dark spots existed on the back. There was no vertebral strip on the back except for the most posterior part. The dorsolateral folds were parallel with each other and continued with the upper eyelids. There were several well-defined blackish spots on the lateral surfaces of the body. The upper lip was edged with dark spots. The ventral surface of the body was whitish, although the marginal parts were mottled with gray color. The hind legs were distinctly barred with dark color. The bars were about four in number on the tibia. The outer metatarsal tubercles were distinct (Table 19; Fig. 16).

k. *Rana temporaria*

Two females and three males were 73.8 mm and 63.3 mm in mean body

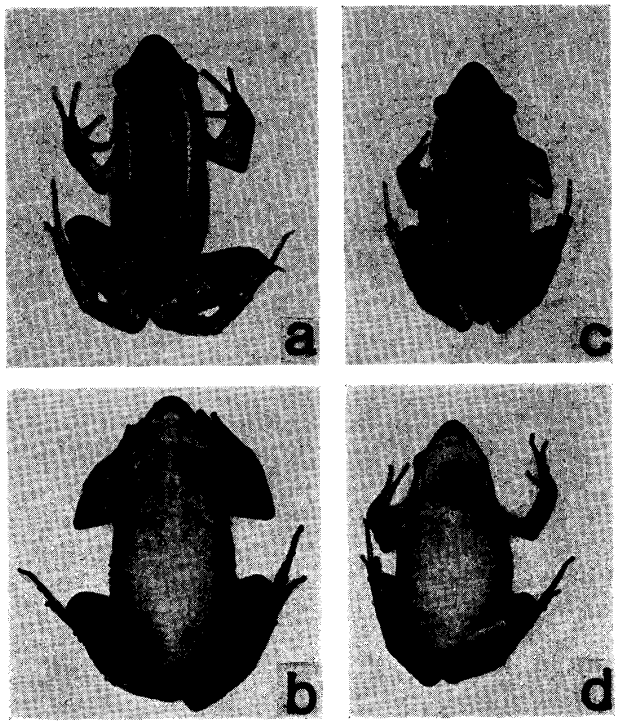


Fig. 16. Dorsal and ventral views of *Rana latouchii* collected from Taipei, Formosa. ×0.7

a, b. Female c, d. Male

length, respectively. Three females and four males observed were very similar to *Rana chensinensis* in shape, color, and skin texture. The body was stocky. The head had a blunt or rounded snout. The dorsal skin was either smooth or somewhat rough due to distribution of minute projecting granules all over the surface. There were various number of dark spots each of which usually surrounded a wart. An obscure vertebral stripe was either present or absent on the back. When a vertebral stripe was present, it was accompanied with two parallel rows of blackish warts. The dorsolateral folds were curved outward in the shoulder region and continued from the upper eyelids without interruption. A few dark spots were arranged along the outside of the dorsolateral folds. The upper lips of five frogs had no dark spots, while those of the other two were distinctly edged with such spots. The ventral surface of the body was wholly or mostly grayish white. The throat, thorax and anterior part of the venter were suffused with irregular brownish speckles in some specimens. The hind legs were irregularly barred with dark color. There were no outer metatarsal tubercles, while the inner metatarsal tubercles were similar in size to those of *Rana ornativentris* and *Rana chensinensis* (Table 19; Fig. 17).

1. *Rana arvalis*

Three females and three males were 55.9 mm and 52.5 mm in mean body length, respectively. Five females and six males observed had a rather stocky body and fairly long hind legs. The head had a pointed snout. The dorsal

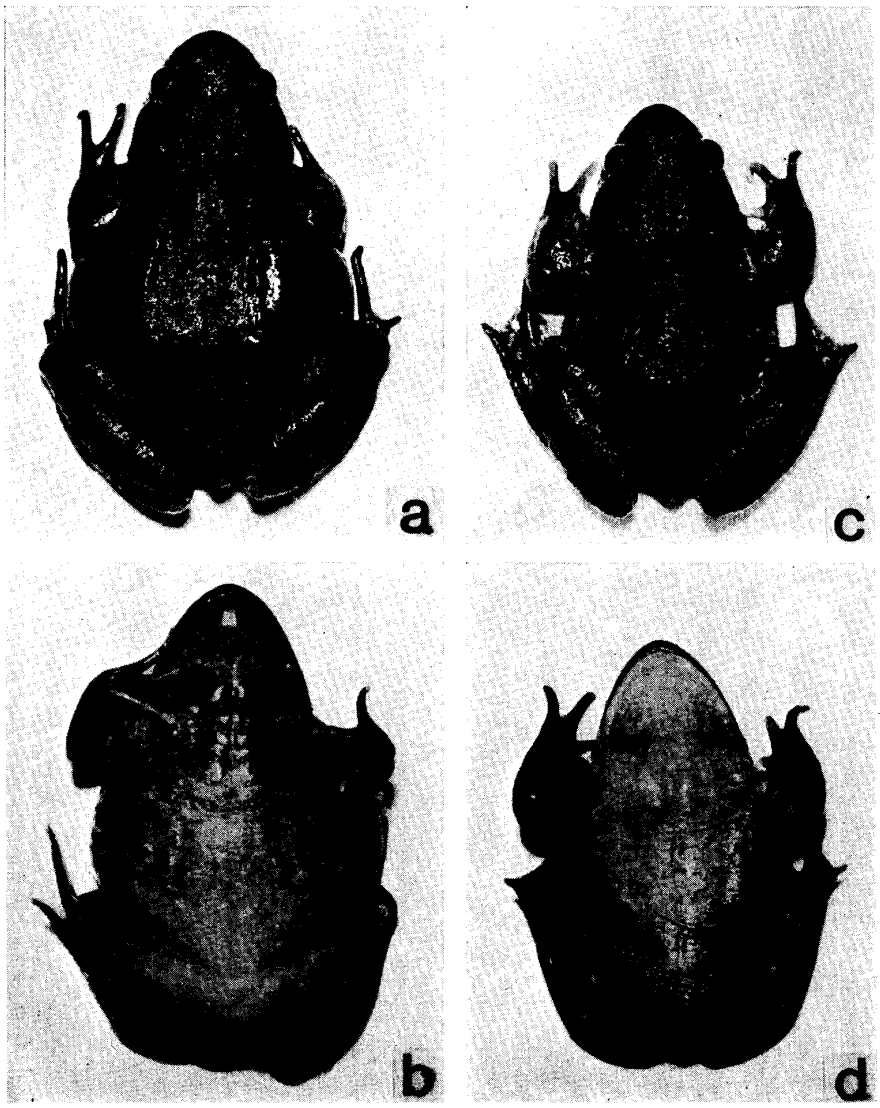


Fig. 17. Dorsal and ventral views of *Rana temporaria* collected from Saxony, Germany. ×0.7

a, b. Female c, d. Male

skin was smooth and covered with minute flat granules all over the surface. A pale vertebral stripe that was usually very distinct was either present or absent on the back. When this stripe existed, it was interposed between two rows of fairly large, irregularly shaped warts, each of which was usually covered with a dark spot. When the stripe was absent, a small number of fairly large warts were scattered on the back. In this case, the warts usually were not dark. The dorsolateral folds were continued from the upper eyelids without interruption and slightly curved outward in the shoulder region. The upper lip had no dark spots. The ventral surface of the body was white, although irregularly shaped, gray-brown or dark-brown spots were distributed on the throat and the lateral parts of the venter in some specimens. The hind legs were distinctly or obscurely barred with dark color. The bars were mostly three or four in number on the tibia. The inner metatarsal tubercles were comparatively large (Table 19;

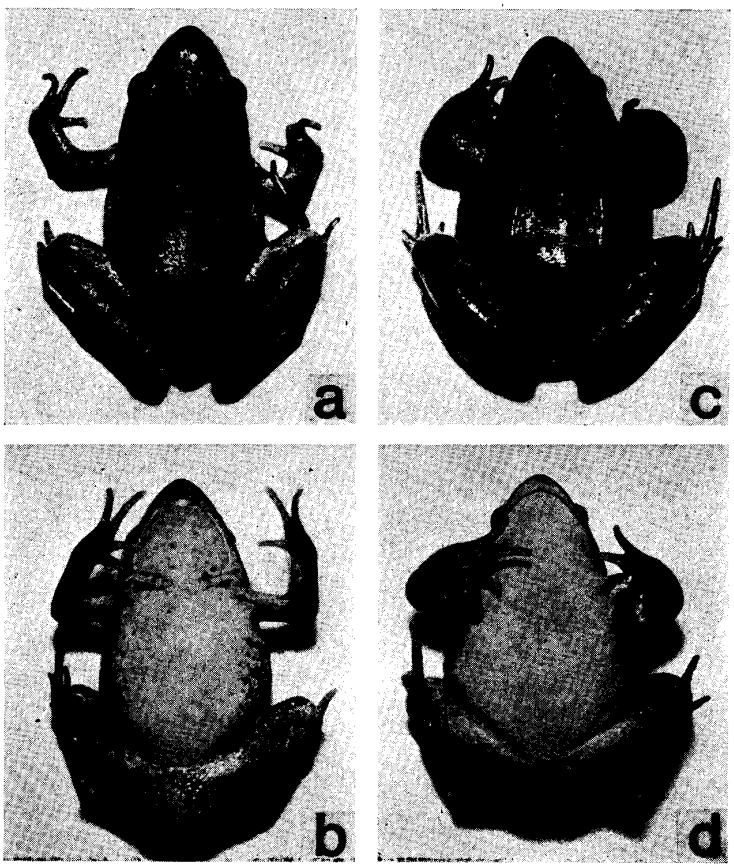


Fig. 18. Dorsal and ventral views of *Rana arvalis* collected from Luxembourg. ×0.7

a, b. Female c, d. Male

Fig. 18).

m. *Rana dalmatina*

A male was 51.5 mm in body length. One female and two males observed had a stocky body and remarkably long hind legs. The head had a somewhat blunt snout. The dorsal skin was rough due to distribution of minute projecting granules all over the surface. On the back, there were several warts each of which was covered with a dark spot. There was no vertebral stripe. The dorsolateral folds were slightly curved outward in the shoulder region and continued from the upper eyelids without interruption. On the lateral surfaces of the body, there were a few dark spots. The upper lip was edged with dark spots. The ventral surface of the body was white, although the throat and the lateral parts of the venter were speckled with brownish color. The hind legs were barred with dark color. The bars were about four in number on the tibia. The inner metatarsal tubercles were comparatively large (Table 19; Fig. 19).

n. *Rana macrocnemis*

A male was 60.5 mm in body length. This male had a somewhat stocky body

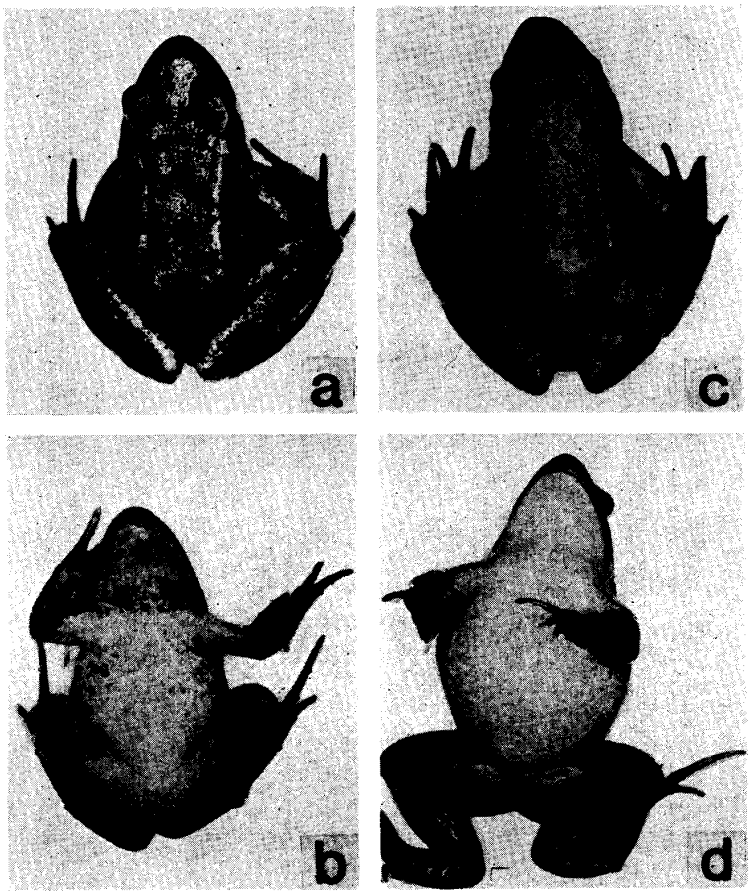


Fig. 19. Dorsal and ventral views of *Rana dalmatina* collected from Austria and Italy. ×0.8

a, b. Female from Austria c, d. Male from Italy

and fairly long hind legs. The head had a rather blunt snout. The dorsal skin was rough due to distribution of minute projecting granules. There were many warts on the dorsal and lateral surfaces of the body. Each wart was usually covered with a dark spot. There was an obscure vertebral stripe. The dorsolateral folds were slightly curved outward over the tympanum and continued from the upper eyelids. Two rows of dark roundish spots were arranged between the dorsolateral folds. The upper lip was scarcely edged with dark spots. The ventral surface of the body was white. The hind legs were distinctly barred with dark color. There were three complete bars on the tibia. The outer metatarsal tubercles were present. The inner metatarsal tubercles were comparatively large (Table 19).

2. Interspecific hybrids between female *Rana japonica* and males of five species

a. Hybrids, *Rana japonica*♀ × *Rana ornativentris*♂

Three males were 51.0 mm in mean body length. Sixteen males including these three were intermediate as a whole between the two parental species in various external characters. The ventral surface of the body was white. The

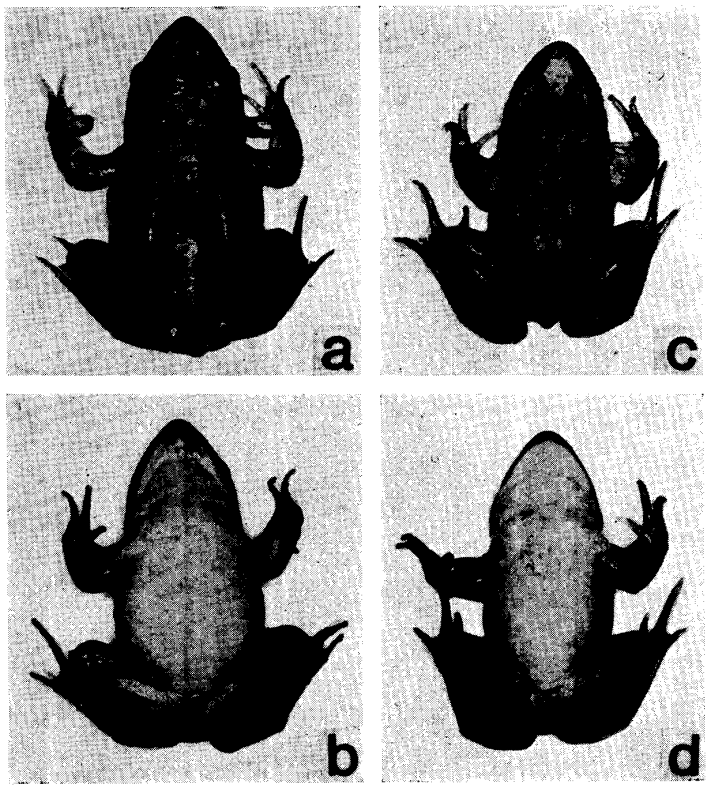


Fig. 20. Dorsal and ventral views of male hybrids between a female *Rana japonica* and a male *Rana ornativentris* or *Rana chensinensis*. All the hybrids were two years old. ×0.7

a, b. Hybrid, *Rana japonica* ♀ × *Rana ornativentris* ♂, produced in 1976.
c, d. Hybrid, *Rana japonica* ♀ × *Rana chensinensis* ♂, produced in 1976.

hind legs were abnormally short probably due to effects of captivity throughout life (Table 20; Fig. 20a, b).

b. Hybrids, *Rana japonica*♀ × *Rana chensinensis*♂

Five males were 43.6 mm in mean body length. Ten males including these five were intermediate as a whole between the two parental species in various external characters. The warts and dark spots on the back were similar to those of *Rana chensinensis*. The ventral surface of the body was white (Table 20; Fig. 20c, d).

c. Hybrids, *Rana japonica*♀ × *Rana longicrus*♂

Four males were 43.4 mm in mean body length. Nine males including these four were intermediate as a whole between the two parental species in various external characters. The dark spots on the back were similar to those of *Rana longicrus*. The ventral surface of the body was white (Table 20; Fig. 21a, b).

d. Hybrids, *Rana japonica*♀ × *Rana temporaria*♂

Five males were 47.6 mm in mean body length. Fifteen males including these five were intermediate as a whole between the two parental species in various

TABLE 20

Measurements of various body sites of hybrids between female *Rana japonica* and males of five species and between a female *Rana ornativentris* and a male *Rana temporaria*

Kind	76 *jap.* ♀ × *ornat.* ♂	76 *jap.* ♀ × *chen.* ♂	81 *jap.* ♀ × *long.* ♂	76 *jap.* ♀ × *temp.* ♂	76 *jap.* ♀ × *arv.* ♂	75 *ornat.* ♀ × *temp.* ♂
Number of frogs	♂3	♂5	♂4	♂5	♂10	♂2
	mm	mm	mm	mm	mm	mm
Body length	51.0	43.6	43.4	47.6	43.0	50.7
Head length	16.9	14.9	15.0	15.4	14.8	19.3
Head length / Body length	0.33	0.34	0.35	0.32	0.34	0.38
Head width	17.4	15.0	14.3	16.5	15.2	20.8
Head width / Head length	1.03	1.01	0.95	1.07	1.03	1.08
Snout length	7.2	5.4	5.6	5.6	5.2	7.1
Distance between orbitals	3.1	3.2	2.7	2.9	2.9	3.8
Distance between nostrils	3.0	3.1	2.7	2.8	3.1	4.1
Diameter of tympanum	4.1	2.8	2.9	3.2	3.5	4.1
Arm length	27.8	26.3	26.7	30.0	24.7	32.7
Arm length / Body length	0.55	0.60	0.62	0.63	0.57	0.64
Hind leg length	73.1	66.3	71.9	78.8	64.7	93.1
Hind leg length / Body length	1.43	1.52	1.66	1.66	1.50	0.84
Outer metatarsal tubercle	None	None or dot	Dot or none	None	None or dot	Dot or none
Length of inner metatarsal tubercle	2.0	2.0	2.2	2.7	2.8	2.8
Length of inner metatarsal tubercle / Body length	0.04	0.05	0.05	0.06	0.07	0.06

jap., *Rana japonica* *ornat.*, *Rana ornativentris* *long.*, *Rana longicrus* *chen.*, *Rana chensinensis* *temp.*, *Rana temporaria* *arv.*, *Rana arvalis*

external characters. The dark spots on the upper and lateral surfaces of the body were very distinct. They were usually more distinct than those of *Rana temporaria*. The ventral surface of the body was intermediate in color between the two parental species. The outer metatarsal tubercles were large and similar to those of *Rana temporaria* (Table 20; Fig. 21c, d).

e. Hybrids, *Rana japonica*♀ × *Rana arvalis*♂

Ten males were 43.0 mm in mean body length. They were as a whole intermediate between the two parental species or more similar to *Rana arvalis* in various external characters. The dark spots on the dorsal surface of the body were more distinct than those of *Rana arvalis*. The ventral surface of the body was white. The inner metatarsal tubercles were large and similar to those of *Rana arvalis* (Table 20; Fig. 21e, f).

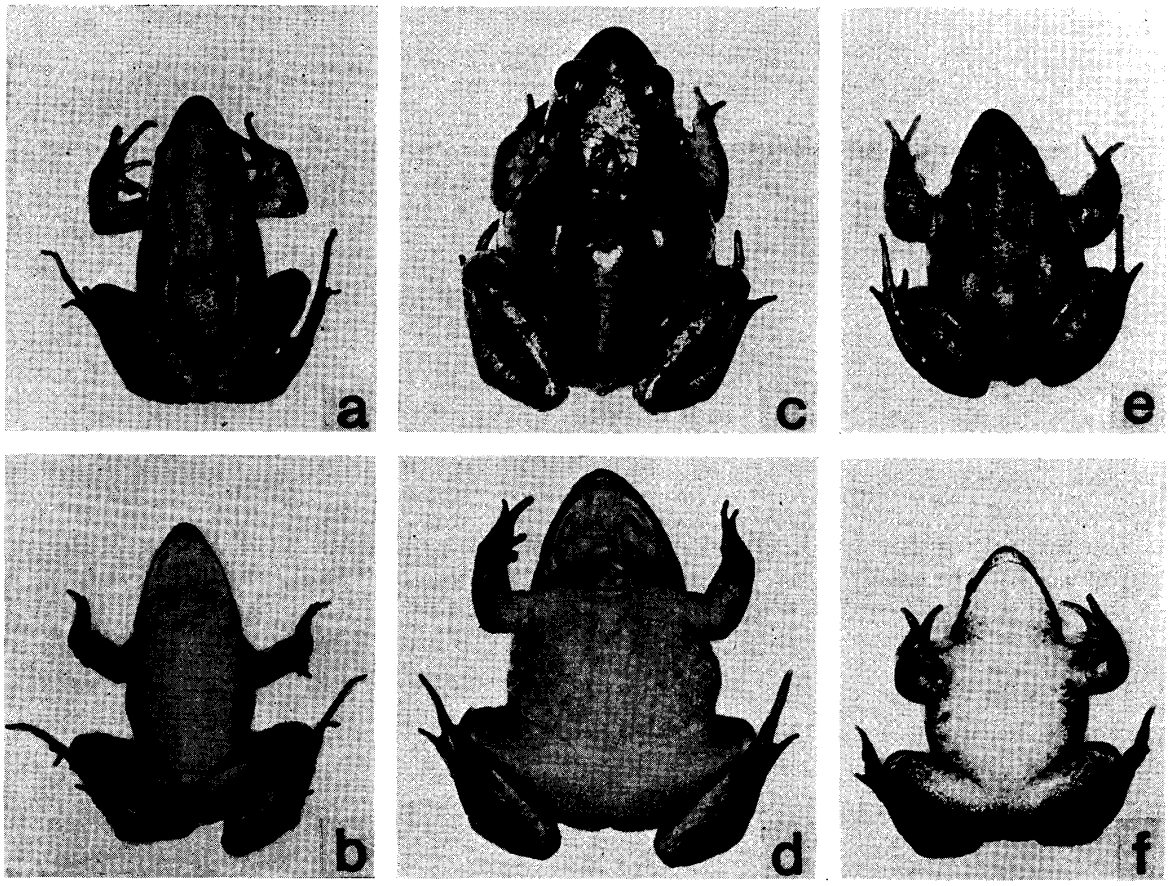


Fig. 21. Dorsal and ventral views of male hybrids between female *Rana japonica* and males of three species. ×0.8

a, b. Hybrid, *Rana japonica* ♀ × *Rana longicrus* ♂, produced in 1981. Eight months old.
c, d. Hybrid, *Rana japonica* ♀ × *Rana temporaria* ♂, produced in 1975. Two years old.
e, f. Hybrid, *Rana japonica* ♀ × *Rana arvalis* ♂, produced in 1976. Two years old.

3. Interspecific hybrids between a female *Rana ornativentris* and a male *Rana temporaria*

Two males were 50.7 mm in mean body length. Twelve males including these two were intermediate as a whole between the two parental species or more similar to *Rana ornativentris* in various external characters. The upper lip was distinctly edged with dark spots as that of *Rana ornativentris*. There were also some dark spots on the throat. The venter was white as that of *Rana ornativentris* (Table 20; Fig. 22c, d).

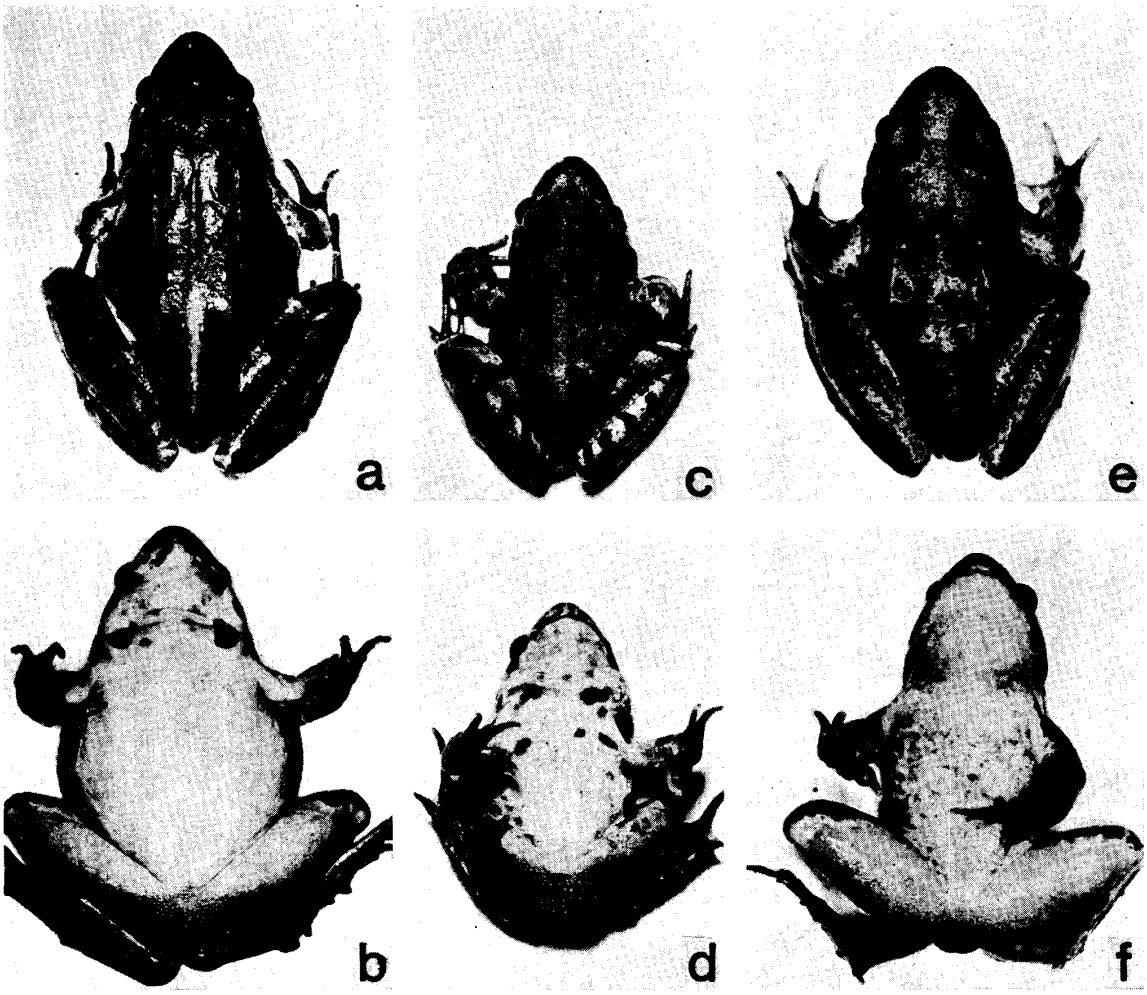


Fig. 22. Dorsal and ventral views of a male hybrid between a female *Rana ornativentris* and a male *Rana temporaria*, and the controls. ×0.7

a, b. Control female, *Rana ornativentris* ♀ × *Rana ornativentris* ♂, produced in 1962. Two years old.

c, d. Male hybrid, *Rana ornativentris* ♀ × *Rana temporaria* ♂, produced in 1962. Two years old.

e, f. Control male, *Rana temporaria* ♀ × *Rana temporaria* ♂, produced in 1963. One year old.

4. Intraspecific hybrids of *Rana dybowskii*

a. Controls

i) *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Tsushima♂

Two females and two males were 61.5 mm and 52.6 mm in mean body length, respectively. Five females and seven males observed were very similar to field-caught specimens from Tsushima in various external characters except that their hind legs were somewhat shorter (Table 21).

ii) *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Korea♂

Three females and three males were 59.8 mm and 51.9 mm in mean body length, respectively. Six females and seven males observed were very similar to field-caught specimens from Korea in various external characters except that their hind legs were somewhat shorter (Table 21; Fig. 23a, b).

TABLE 21

Measurements of various body sites of intraspecific hybrids between *Rana dybowskii* from Tsushima and *Rana dybowskii* from Korea, the controls and field-caught frogs

Kind	*dyb.* T Wild		78 *dyb.* T ♀ × *dyb.* T ♂		*dyb.* K Wild		70 *dyb.* K ♀ × *dyb.* K ♂		70 *dyb.* T ♀ × *dyb.* K ♂		70 *dyb.*K ♀ × *dyb.*T ♂	
Number of frogs	♀5	♂4	♀2	♂2	♀3	♂3	♀3	♂3	♀3	♂3	♀3	♂3
	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm	mm
Body length	75.9	62.2	61.5	52.6	75.4	55.0	59.8	51.9	58.1	48.8	58.3	47.3
Head length	20.6	17.6	17.8	15.8	21.5	16.9	17.1	16.5	16.7	15.0	17.5	14.6
Head length / Body length	0.27	0.28	0.29	0.30	0.29	0.31	0.29	0.32	0.29	0.31	0.30	0.31
Head width	25.2	20.6	20.3	19.3	25.7	19.0	19.1	19.8	19.0	18.8	19.7	18.6
Head width / Head length	1.22	1.17	1.14	1.22	1.20	1.12	1.12	1.20	1.14	1.25	1.13	1.27
Snout length	8.1	7.3	7.1	6.5	8.4	7.8	7.1	6.0	6.8	6.1	6.8	5.8
Distance between orbitals	5.3	4.1	4.0	3.4	4.9	3.7	3.9	3.1	3.8	3.0	3.7	2.9
Distance between nostrils	4.2	4.3	4.0	3.4	4.1	3.6	4.0	3.1	3.7	3.0	3.8	2.8
Diameter of tympanum	4.6	4.0	4.0	3.5	4.7	3.5	4.0	3.1	3.4	2.7	3.9	3.2
Arm length	43.9	38.7	34.0	33.0	41.7	37.3	31.2	30.8	32.7	29.8	30.8	29.0
Arm length / Body length	0.58	0.62	0.55	0.63	0.55	0.68	0.52	0.59	0.56	0.61	0.53	0.61
Hind leg length	134.6	113.3	99.8	92.3	128.8	101.7	91.9	84.7	92.2	81.0	93.0	79.4
Hind leg length / Body length	1.77	1.82	1.62	1.75	1.71	1.85	1.54	1.63	1.59	1.66	1.60	1.68
Outer metatarsal tubercle	None or dot	None or dot	Dot or none	Dot	Dot or none	None or dot	Dot	Dot	Dot	None or dot	Dot or none	Dot
Length of inner metatarsal tubercle	4.1	4.0	4.4	3.8	4.3	3.5	3.9	3.2	3.8	2.9	2.9	2.7
Length of inner metatarsal tubercle / Body length	0.05	0.06	0.07	0.07	0.06	0.06	0.07	0.06	0.07	0.06	0.05	0.06

dyb. T, *Rana dybowskii* from Tsushima *dyb.* K, *Rana dybowskii* from Korea Wild, field-caught

b. Intraspecific hybrids

i) *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Korea♂

Three females and three males were 58.1 mm and 48.8 mm in mean body length, respectively. Eight females and seven males observed were very similar to both kinds of controls in varous external characters (Table 21; Fig. 24a, b).

ii) *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Tsushima♂

Three females and three males were 58.3 mm and 47.3 mm in mean body length, respectively. They were very similar to the two kinds of controls in various external characters (Table 21; Fig. 23c~f).

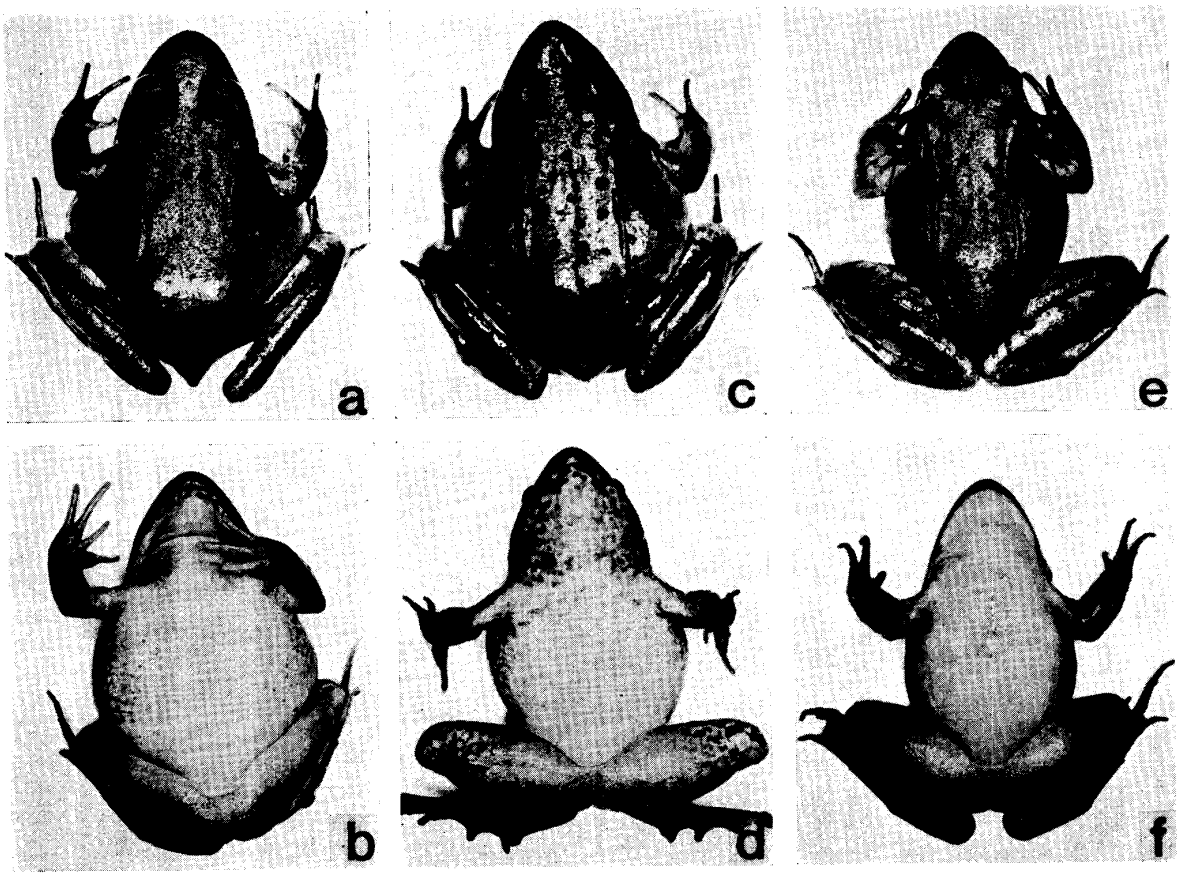


Fig. 23. Dorsal and ventral views of intraspecific hybrids between female *Rana dybowskii* from Korea and male *Rana dybowskii* from Tsushima, and the control female. All the hybrids were two years old. ×0.8

a, b. Control female, *Rana dybowskii* from Korea ♀ × *Rana dybowskii* from Korea ♂, produced in 1970.

c, d. Female hybrid, *Rana dybowskii* from Korea ♀ × *Rana dybowskii* from Tsushima ♂, produced in 1970.

e, f. Male hybrid, *Rana dybowskii* from Korea ♀ × *Rana dybowskii* from Tsushima ♂, produced in 1970.

5. Interspecific hybrids between female *Rana dybowskii* from Tsushima and males of four species

a. Hybrids, *Rana dybowskii* from Tsushima ♀ × *Rana japonica* ♂

Seven males were 47.7 mm in mean body length. They were intermediate as a whole between the two parental species in various external characters. The ventral surfaces of the body was almost white. The hind legs were abnormally short when compared with the other hybrids of *Rana dybowskii* from Tsushima (Table 22; Fig. 24c, d).

In an exceptional female hybrid whose gonads had completely degenerated, the dark spots on the dorsal and lateral surfaces of the body were more distinct than those of the two parental species (Table 22, Fig. 24e, f).

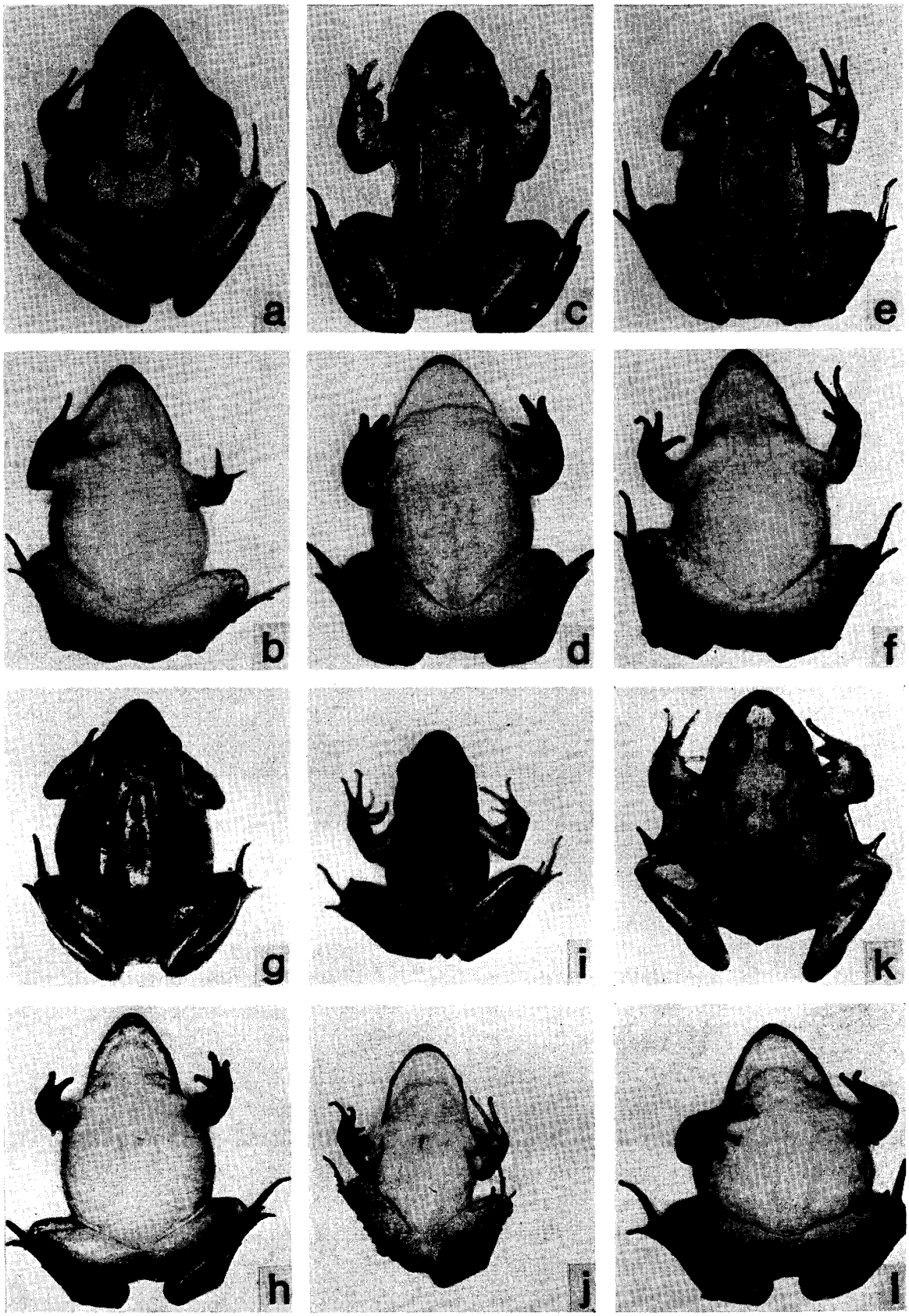


Fig. 24. Dorsal and ventral views of hybrids between female *Rana dybowskii* from Tsushima and males of five species. All the hybrids were two years old.

b. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana ornativentris*♂

Seven males were 55.1 mm in mean body length. Nine males including these seven were intermediate as a whole between the two parental species in various external characters. The ventral surface of the body was white (Table 22; Fig. 24g, h).

TABLE 22

Measurements of various body sites of hybrids between female *Rana dybowskii* from Tsushima or Korea and males of four species and between a female *Rana longicrus* and a male *Rana japonica*

Kind	75, 78 *dyb.* T♀ × *jap.*♂		75, 78 *dyb.* T♀ × *ornat.*♂	75 *dyb.* T♀ × *chen.*♂	75 *dyb.* T♀ × *temp.*♂	70 *dyb.* K♀ × *jap.*♂	70 *dyb.* K♀ × *ornat.*♂	70 *dyb.* K♀ × *chen.*♂	81 *long.* ♀ × *jap.*♂
Number of frogs	♀1*	♂7	♂7	♂2	♂2	♂2	♂5	♂3	♂5
	mm	mm	mm	mm	mm	mm	mm	mm	mm
Body length	49.5	47.7	55.1	44.3	53.0	42.8	47.2	47.2	39.2
Head length	16.0	16.1	17.4	18.5	20.8	13.0	15.6	15.6	13.9
Head length / Body length	0.32	0.34	0.32	0.42	0.39	0.30	0.33	0.33	0.35
Head width	14.0	16.4	19.3	21.2	22.5	14.4	17.4	16.8	12.2
Head width / Head length	0.88	1.02	1.11	1.15	1.08	1.11	1.12	1.08	0.88
Snout length	5.5	6.1	6.9	6.0	7.1	4.7	6.1	5.7	5.7
Distance between orbitals	4.0	3.1	3.5	3.0	4.0	2.9	2.8	2.7	2.8
Distance between nostrils	3.0	2.6	3.2	3.2	4.3	2.5	2.9	2.8	2.6
Diameter of tympanum	3.0	3.7	4.3	3.8	4.0	2.3	2.6	2.0	2.6
Arm length	28.5	25.6	30.2	30.1	33.9	26.5	27.9	30.8	24.2
Arm length / Body length	0.58	0.54	0.55	0.68	0.64	0.62	0.59	0.65	0.62
Hind leg length	83.0	70.1	88.1	80.6	83.9	69.7	74.5	80.0	63.0
Hind leg length / Body length	1.68	1.47	1.60	1.82	1.58	1.63	1.58	1.69	1.61
Outer metatarsal tubercle	1.0	None or dot	None or dot	None	None	None	Dot or none	Dot or none	Dot
Length of inner metatarsal tubercle	2.5	2.7	3.8	4.0	3.9	2.0	2.8	2.9	2.0
Length of inner metatarsal tubercle / Body length	0.05	0.06	0.07	0.09	0.07	0.05	0.06	0.06	0.05

dyb. T, *Rana dybowskii* from Tsushima *dyb.* K, *Rana dybowskii* from Korea *jap.*, *Rana japonica* *ornat.*, *Rana ornativentris* *chen.*, *Rana chensinensis* *temp.*, *Rana temporaria* *long.*, *Rana longicrus*

* Abnormal female whose gonads have completely degenerated

a, b. Female intraspecific hybrid, *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Korea♂, produced in 1970. ×0.8

c, d. Male interspecific hybrid, *Rana dybowskii* from Tsushima♀ × *Rana japonica*♂, produced in 1970. ×0.9

e, f. Female interspecific hybrid, *Rana dybowskii* from Tsushima♀ × *Rana japonica*♂, having no gonads, produced in 1978. ×0.9

g, h. Male interspecific hybrid, *Rana dybowskii* from Tsushima♀ × *Rana ornativentris*♂, produced in 1970. ×0.7

i, j. Male interspecific hybrid, *Rana dybowskii* from Tsushima♀ × *Rana chensinensis*♂, produced in 1970. ×0.7

k, l. Male interspecific hybrid, *Rana dybowskii* from Tsushima♀ × *Rana temporaria*♂, produced in 1970. ×0.7

c. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana chensinensis*♂

Two males were 44.3 mm in mean body length. Ten males including these two were intermediate as a whole between the two parental species in various external characters. The ventral surface of the body was white. The inner metatarsal tubercles were remarkably large (Table 22; Fig. 24i, j).

d. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana temporaria*♂

Two males were 53.0 mm in mean body length. Four males including these two were intermediate as a whole between the two parental species in various external characters. The ventral surface of the body was white (Table 22; Fig. 24. k, 1).

6. Interspecific hybrids between female *Rana dybowskii* from Korea and males of four species

a. Hybrids, *Rana dybowskii* from Korea♀ × *Rana japonica*♂

Two males were 42.8 mm in mean body length. Five males including these two were intermediate as a whole between the two parental species in various external characters. It was very curious that there were many roundish spots and blotches of faded color on the dorsal surface of the body and four legs. Such spots or blotches were never found in the control *Rana dybowskii* from Korea as well as in the hybrids of a female *Rana dybowskii* from Tsushima mated with male *Rana japonica*. The ventral surface of the body was white (Table 22; Fig. 25c, d).

b. Hybrids, *Rana dybowskii* from Korea♀ × *Rana ornativentris*♂

Five males were 47.2 mm in mean body length. Seventeen males including these five were intermediate as a whole between the two parental species in various external characters. These hybrids had many roundish spots and blotches of faded color on the dorsal surface of the body and four legs just as the above hybrids mated with male *Rana japonica* had. Such spots and blotches were not found in the hybrids of female *Rana dybowskii* from Tsushima mated with *Rana ornativentris*. The ventral surface of the body was white (Table 22; Fig. 25e, f).

c. Hybrids, *Rana dybowskii* from Korea♀ × *Rana chensinensis*♂

Three males were 47.2 mm in mean body length. Eight males including

Fig. 25. Dorsal and ventral views of male hybrids between female *Rana dybowskii* from Korea and males of four species, and the controls. All the hybrids were two years old. ×0.8

a, b. Control female, *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Korea♂, produced in 1970.

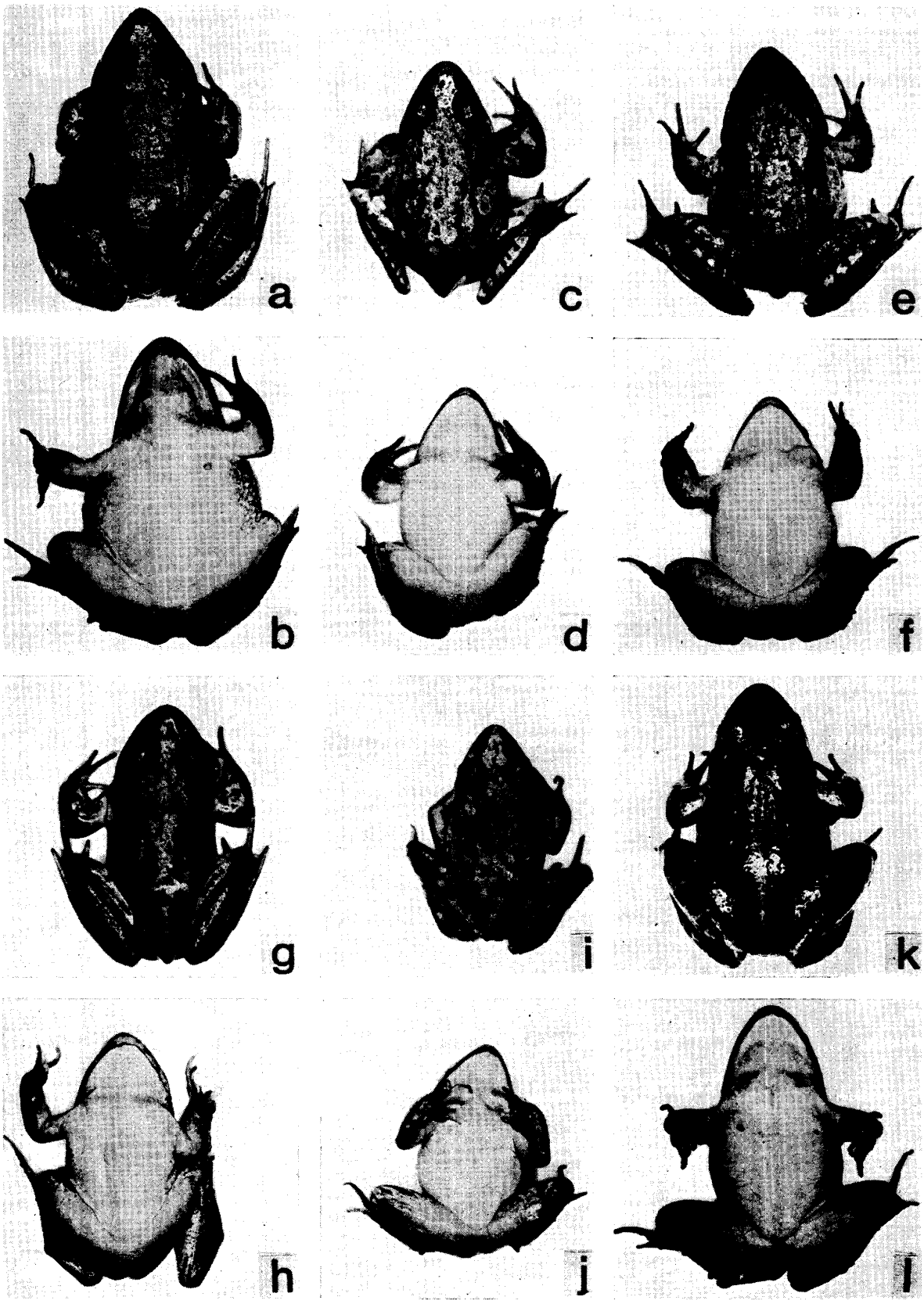
c, d. Hybrid, *Rana dybowskii* from Korea♀ × *Rana japonica*♂, produced in 1970.

e, f. Hybrid, *Rana dybowskii* from Korea♀ × *Rana ornativentris*♂, produced in 1970.

g, h. Hybrid, *Rana dybowskii* from Korea♀ × *Rana chensinensis*♂, produced in 1970.

i, j. Hybrid, *Rana dybowskii* from Korea♀ × *Rana tsushimensis*♂, produced in 1970.

k, l. Control male, *Rana ornativentris*♀ × *Rana ornativentris*♂, produced in 1970.


a
c
e
b
d
f
g
i
k
h
j
l

these three were intermediate as a whole between the two parental species in various external characters. These hybrids had many roundish spots and blotches of faded color on the dorsal surfaces of the body and four legs just as the above hybrids had. Such spots and blotches were never found in the hybrids of female *Rana dybowskii* from Tsushima mated with male *Rana chensinensis*. The ventral surface of the body was white (Table 22; Fig. 25g, h).

d. Hybrid, *Rana dybowskii* from Korea♀ × *Rana tsushimensis*♂

A male was 37.5 mm in body length. This male was intermediate as a whole between the two parental species in various external characters. There were many roundish spots and blotches of faded color on the dorsal surface of the body and four legs. The ventral surface of the body was white (Fig. 25i, j).

7. Interspecific hybrids between female *Rana longicrus* and male *Rana japonica*

Five males were 39.2 mm in body length. They were intermediate as a whole

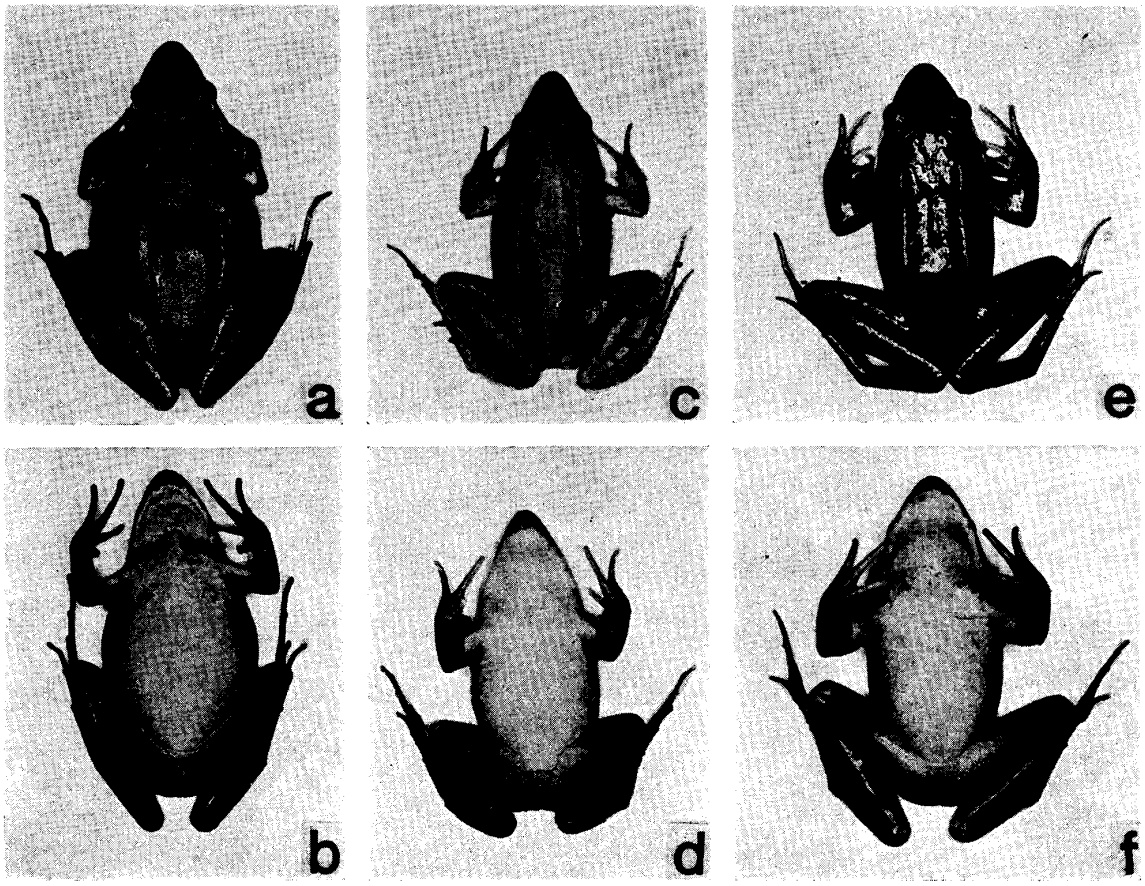


Fig. 26. Dorsal and ventral views of a male hybrid between a female *Rana longicrus* and a male *Rana japonica*, and the controls. All the frogs were 8 months old.

a, b. Control female, *Rana longicrus*♀ × *Rana longicrus*♂, produced in 1981. ×0.9
c, d. Male hybrid, *Rana longicrus*♀ × *Rana japonica*♂, produced in 1981. ×0.8
e, f. Control male, *Rana japonica*♀ × *Rana japonica*♂, produced in 1981. ×0.8

between the two parental species in various external characters. The ventral surface of the body was white (Table 22; Fig. 26a~f).

8. Interspecific hybrids between female *Rana arvalis* and males of three species

a. Hybrids, *Rana arvalis*♀ × *Rana ornativentris*♂

A male was 46.0 mm in body length. Five males including this one were intermediate as a whole between the two parental species in various external characters. The head had a somewhat blunt snout which was similar to that of the control *Rana arvalis*. It was remarkable that the controls had a blunt snout in contrast to field-caught specimens. The dorsolateral folds were very similar in shape to those of *Rana ornativentris*. The dark spots on the back were also very similar to those of *Rana ornativentris*. The ventral surface of the body was almost white (Table 23; Fig. 27g. h).

TABLE 23

Measurements of various body sites of hybrids between female *Rana arvalis* and males of three species

Kind	76 *arv.*♀ × *ornat.*♂	76 *arv.*♀ × *chen.*♂	76 *arv.*♀ × *tsu.*♂
Number of frogs	♂1	♂6	♂1
Body length	46.0 mm	51.9 mm	42.0 mm
Head length	16.0	17.0	15.0
Head length / Body length	0.35	0.33	0.36
Head width	17.0	19.2	16.0
Head width / Head length	1.06	1.13	1.07
Snout length	5.5	6.0	6.0
Distance between orbitals	3.0	3.1	2.5
Distance between nostrils	3.0	3.0	2.5
Diameter of tympanum	3.5	3.4	3.0
Arm length	29.0	32.2	23.0
Arm length / Body length	0.63	0.62	0.55
Hind leg length	75.0	87.1	69.0
Hind leg length / Body length	1.63	1.68	1.64
Outer metatarsal tubercle	None	None	None
Length of inner metatarsal tubercle	3.5	3.8	3.0
Length of inner metatarsal tubercle / Body length	0.08	0.07	0.07

arv., *Rana arvalis* *ornat.*, *Rana ornativentris* *chen.*, *Rana chensinensis* *tsu.*, *Rana tsushimensis*

b. Hybrids, *Rana arvalis*♀ × *Rana chensinensis*♂

Six males were 51.9 mm in body length. Nine males including these six were intermediate as a whole between the two parental species in various external characters. The ventral surface of the body was white or pale orange (Table 23; Fig. 27i, j).

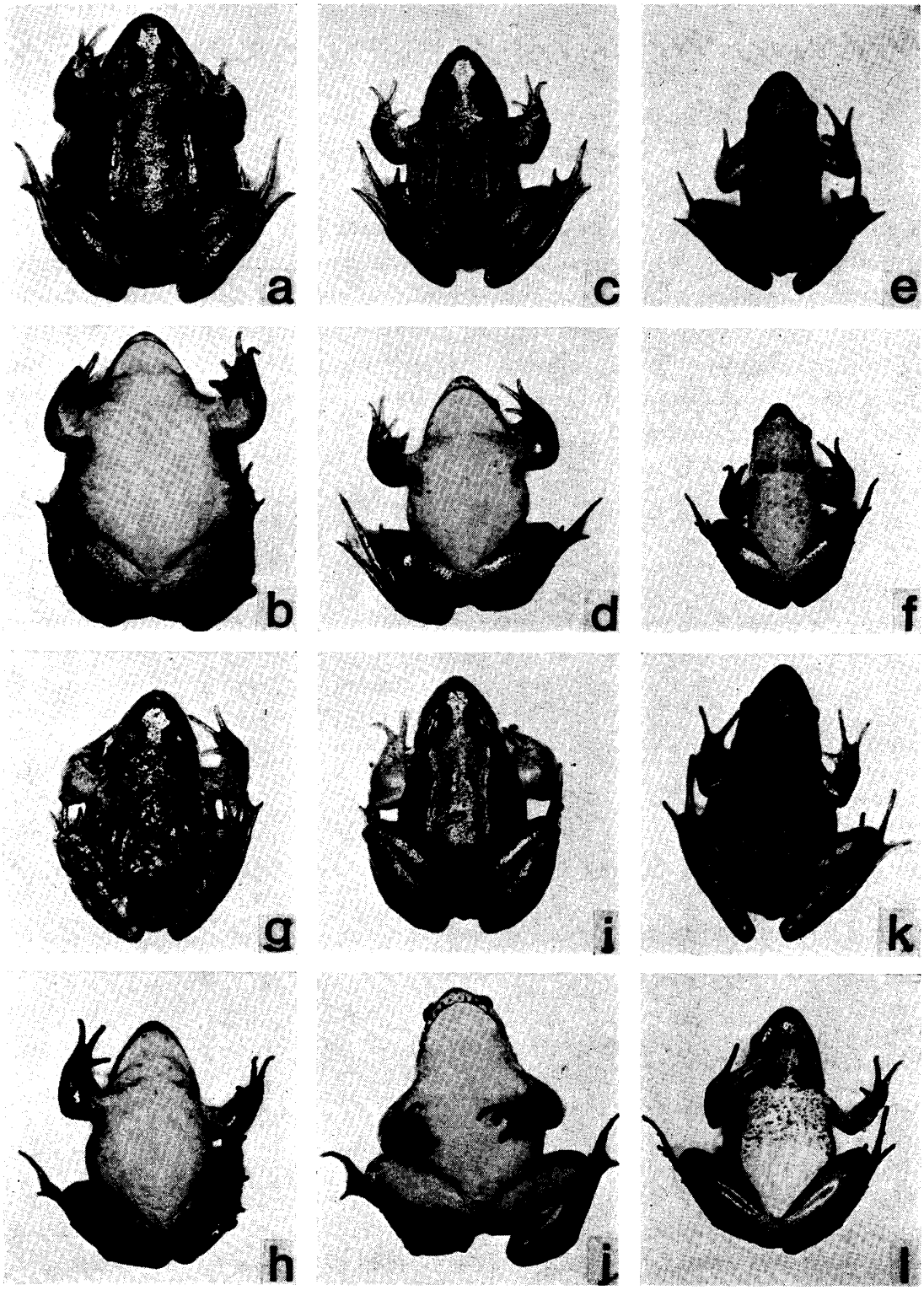


Fig. 27. Dorsal and ventral views of male hybrids between female *Rana arvalis* and males of three species, and the controls. ×0.7

a, b. Control male, *Rana arvalis* ♀ × *Rana arvalis* ♂, produced in 1976. One year old.
c, d. Male hybrid, *Rana arvalis* ♀ × *Rana tsushimensis* ♂, produced in 1977. One year old.
e, f. Control male, *Rana tsushimensis* ♀ × *Rana tsushimensis* ♂, produced in 1976. Two years old.
g, h. Male hybrid, *Rana arvalis* ♀ × *Rana ornativentris* ♂, produced in 1976. Two years old.
i, j. Male hybrid, *Rana arvalis* ♀ × *Rana chensinensis* ♂, produced in 1976. One year old.
k, l. Control female, *Rana tsushimensis* ♀ × *Rana tsushimensis* ♂, produced in 1976. Two years old.

c. Hybrid, *Rana arvalis*♀ × *Rana tsushimensis*♂

A male was 42.0 mm in body length. This male was intermediate as a whole between the two parental species in various external characters. The ventral surface of the body was white (Table 23; Fig. 27a~f, k, l).

IV. Gonads of field-caught frogs used in crossing experiments

1. Eggs of mature females

a. *Rana japonica*

During the years from 1962 to 1981, a total of 56 females were used in crossing experiments. Twelve of these females including three in 1963, five in 1967 and four in 1968 were 40.5~60.0 mm, 51.9 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 1.3~1.7 mm, 1.6 mm on the average, in diameter. Each egg was separated from the neighboring ones at intervals of 4.0~6.6 mm by swollen jelly envelopes, which were transparent and soft in quality.

b. *Rana ornativentris*

A total of 31 females were used in crossing experiments during the years from 1962 to 1981. Ten of them including three in 1963, three in 1964, one in 1965 and three in 1968 were 43.5~66.0 mm, 51.3 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 1.7~2.4 mm, 2.0 mm on the average, in diameter and separated from one another at intervals of 5.5~11.0 mm by swollen jelly envelopes, which were transparent and hard in quality.

c. *Rana chensinensis*

A total of 21 females were used in crossing experiments during the years from 1962 to 1981. Seven of them including five in 1963 and two in 1970 were 45.0~69.5 mm, 60.6 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 1.7~2.3 mm, 2.2 mm on the average, in diameter and separated from one another at intervals of 7.0~14.5 mm by swollen jelly layers, which were usually semitransparent and very hard in quality. However, one of the five females used in 1981 had exceptionally transparent jelly envelopes.

d. *Rana tsushimensis*

A total of 41 females were used in crossing experiments during the years from 1963 to 1981. Ten of them including two in 1963, one in 1967, two in 1968 and five in 1970 were 41.0~46.5 mm, 42.6 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 1.7~2.3 mm, 1.9 mm on the average, in diameter and separated from one another at intervals of 4.0~7.5 mm by swollen jelly envelopes, which were transparent

and soft in quality.

e. *Rana dybowskii* from Tsushima

A total of 22 females were used in crossing experiments during the years from 1966 to 1981. Nine of them including three in 1968 and six in 1970 were 58.5～84.0 mm, 72.8 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 2.0～2.2 mm, 2.1 mm on the average, in diameter and separated from one another at intervals of 5.0～9.5 mm by swollen jelly envelopes, which were transparent and hard in quality.

f. *Rana dybowskii* from Korea

Eight females used in 1970 were 73.5～80.0 mm, 76.5 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 1.9～2.1 mm, 2.0 mm on the average, in diameter and separated from one another at intervals of 5.0～9.0 mm by swollen jelly envelopes, which were transparent and hard in quality.

g. *Rana amurensis coreana*

Five females used in 1970 were 44.0～47.5 mm, 45.2 mm on the average, in bodty length. When eggs of these females were measured about 5 hours after laid in water, they were 1.6～1.8 mm, 1.7 mm on the average, in diameter and separated from one another at intervals of 2.0～4.5 mm by swollen jelly envelopes, which were transparent and soft in quality.

h. *Rana longicrus*

Five females used in 1981 were 43.5～55.0 mm, 47.4 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 1.5～1.7 mm, 1.6 mm on the average, in diameter and separated from one another at intervals of 4.0～5.5 mm by swollen jelly envelopes, which were transparent and soft in quality.

i. *Rana latouchii*

A female used in 1981 was 48.8 mm in body length. When eggs of this female were measured about 5 hours after laid in water, they were 1.7 mm in mean diameter and separated from one another at intervals of about 5.8 mm by swollen jelly envelopes, which were transparent and very soft. The eggs of *Rana latouchii* are unique in that they are soft and fragile.

j. *Rana temporaria*

Two females used in 1963 were 57.0 mm and 72.5 mm in body length. When eggs of these females were measured about 5 hours after laid in water, they were 2.1 mm and 2.3 mm on the average, in diameter and separated from one another at intervals of 7.5～11.5 mm by swollen jelly envelopes, which were transparent and very hard in quality.

k. *Rana arvalis*

Five females used in 1962 were 50.0～56.5 mm, 54.9 mm on the average, in body length. When eggs of these females were measured about 5 hours after laid in water, they were 1.6～1.9 mm, 1.7 mm on the average, in diameter and separated from one another at intervals of 4.0～6.5 mm swollen jelly envelopes, which were transparent and soft in quality.

2. Testes of mature males

a. *Rana japonica*

During the years from 1962 to 1981, a total of 56 males were used in crossing experiments. Eleven of them including three in 1963, five in 1967, one in 1968 and two in 1970 were 43.5～56.0 mm, 47.4 mm on the average, in body length. The left testes of these males were 3.0～4.5 mm, 3.6 mm on the average, in length and 2.0～3.0 mm, 2.6 mm on the average, in width, while the right testes were 3.0～4.0 mm, 3.4 mm on the average, in length and 2.0～3.0 mm, 2.5 mm on the average, in width.

b. *Rana ornativentris*

A total of 40 males were used in crossing experiments during the years from 1962 to 1981. Eight of them including three in 1963, three in 1964, 1965 and 1968, and two in 1970 were 45.0～60.5 mm, 52.7 mm on the average, in body length. The left testes of these males were 4.0～5.5 mm, 4.6 mm on the average, in length and 2.5～4.0 mm, 3.0 mm on the average, in width, while the right testes were 4.0～5.5 mm, 4.7 mm on the average, in length and 2.0～3.5 mm, 2.9 mm on the average, in width.

c. *Rana chensinesis*

A total of 27 males were used in crossing experiments during the years from 1962 to 1981. Ten of them including five in 1963, one in 1966, two in 1970 and two in 1975 were 51.5～60.0 mm, 55.9 mm on the average, in body length. The left testes of these males were 4.0～6.5 mm, 5.4 mm on the average, in length and 2.0～4.0 mm, 3.4 mm on the average, in width, while the right testes were 4.0～6.5 mm, 5.5 mm on the average, in length and 2.5～4.0 mm, 3.5 mm on the average, in width.

d. *Rana okinavana*

Three males including two in 1977 and one in 1978 were 36.5 mm, 38.0 mm and 40.5 mm, 38.3 mm on the average, in body length. The left and right testes were 2.0～3.5 mm, 3.0 mm on the average, in length and 1.5～2.0 mm, 1.8 mm on the average, in width.

e. *Rana tsushimensis*

A total of 47 males were used in crossing experiments during the years from 1963 to 1981. Fifteen of them including three in 1963, eight in 1964 and four

in 1970 were 32.5~38.0 mm, 35.6 mm on the average, in body length. The left testes of these males were 2.5~4.5 mm, 3.3 mm on the average, in length and 1.0~2.5 mm, 2.0 mm on the average, in width, while the right testes were 3.0~4.5 mm, 3.4 mm on the average, in length and 1.0~3.0 mm, 2.0 mm on the average, in width.

f. *Rana dybowskii* from Tsushima

A total of 17 males were used in crossing experiments during the years from 1966 to 1981. Nine of them including one in 1968, five in 1970, two in 1975 and one in 1976 were 55.0~69.0 mm, 61.9 mm on the average, in body length. The left testes of these males were 4.0~6.5 mm, 5.0 mm on the average, in length and 2.0~3.0 mm, 2.7 mm on the average, in width, while the right testes were 4.0~6.5 mm, 5.4 mm on the average, in length and 2.0~3.0 mm, 2.7 mm on the average, in width.

g. *Rana dybowskii* from Korea

A total of seven males including two in 1968 and five in 1970 were 51.5~64.0 mm, 57.8 mm on the average, in body length. The left and right testes were 4.0~7.5 mm, 4.9 mm on the average, in length and 2.0~3.5 mm, 2.6 mm on the average, in width.

h. *Rana amurensis coreana*

Five males used in 1970 were 35.5~40.5 mm, 37.4 mm on the average, in body length. The left and right testes were 2.0 mm in length and 1.0~1.5 mm, 1.2 mm on the average, in width.

i. *Rana longicrus*

Three males used in 1981 were 40.5~46.0 mm, 42.8 mm on the average, in body length. The left testes of these males were 2.5~3.0 mm, 2.8 mm on the average, in length and 1.5~2.0 mm, 1.7 mm on the average, in width, while the right testes were 3.0 mm in length and 1.5 mm in width, respectively.

j. *Rana latouchii*

A male used in 1981 was 41.5 mm in body length. The left and right testes were 4.0 mm and 4.5 mm in length and 2.0 mm and 2.0 mm in width, respectively.

k. *Rana temporaria*

Two males used in 1963 were 59.5 mm and 67.0 mm in body length. The left testes of these males were 11.0 mm in length and 5.5 mm and 6.0 mm in width, while the right testes were 11.5 mm and 10.0 mm in length and 5.5 mm and 5.0 mm in width.

l. *Rana arvalis*

A total of six males including one in 1963, one in 1966, two in 1976 and two in

1977 were 47.5～58.5 mm, 52.3 mm on the average, in body length. The left testes of these males were 3.5～5.0 mm, 4.1 mm on the average, in length and 2.5～3.0 mm, 2.9 mm on the average, in width, while the right testes were 3.0～5.0 mm, 4.1 mm on the average, in length and 2.0～3.5 mm, 2.8 mm on the average, in width.

m. *Rana dalmatina*

Two males used in 1975 and 1978 were 45.5 mm and 48.0 mm in body length. The left testes were 4.5 mm and 4.0 mm in length and 2.0 mm and 2.5 mm in width, while the right testes were 4.0 mm and 4.5 mm in length and 2.0 mm and 2.5 mm in width.

n. *Rana sylvatica*

A male used in 1972 was 40 mm in body length. The size of the testes was not measured.

V. Testes of mature male hybrids

1. Interspecific hybrids between female *Rana japonica* and males of five species

a. Controls, *Rana japonica*♀ × *Rana japonica*♂

Nine 1-year-old male hybrids including four (Nos. 1, 2, 5 and 6) produced in 1962 and five (Nos. 8～12) produced in 1976 were 40.5～45.0 mm, 42.9 mm on the average, in body length. The left testes of these males were 3.0～4.0 mm, 3.4 mm on the average, in length and 2.0～3.0 mm, 2.5 mm on the average, in width, while the right testes were 3.0～4.5 mm, 3.4 mm on the average, in length and 2.0～3.0 mm, 2.4 mm on the average, in width. Three 2-year-old males (Nos. 3, 4 and 7) produced in 1962 were 46.5～48.0 mm in body length. The left and right testes of these males were 3.5～4.5 mm in length and 3.0 mm and 3.5 mm in width, respectively (Table 24).

The testes of the above 12 males were all normal in inner structure. The seminiferous tubules were filled with compact bundles of normal spermatozoa (Fig. 28a).

b. Hybrids, *Rana japonica*♀ × *Rana ornativentris*♂

Four 1-year-old male hybrids including two (Nos. 1 and 2) produced in 1962 and two (Nos. 6 and 7) produced in 1976 were 40.5～48.0 mm, 44.3 mm on the average, in body length. The left and right testes of these males were 3.0～4.0 mm, 3.5 mm on the average, in length and 2.0～3.0 mm, 2.5 mm on the average, in width. Three 2-year-old male hybrids (Nos. 3～5) produced in 1962 were 43.5～49.5 mm in body length. The left testes of these males were 4.0～5.0 mm in length and 3.0 or 3.5 mm in width, while the right testes were 3.5 mm or 4.0 mm in length and 2.5 or 3.0 mm in width (Table 24).

TABLE 24

Testes of mature male hybrids between female *Rana japonica* and males of five species and between a female *Rana longicrus* and a male *Rana japonica*, and the controls

Year	Parents		Individual no.	Age year(s)	Body length mm	Size of testes Left mm	Size of testes Right mm	Remarks
	Female	Male						
1962	*jap.* No. 1	*jap.* No. 1	1	1	40.5	4.0×3.0	4.5×3.0	
			2	1	45.0	3.0×2.0	3.0×2.0	
			3	2	47.0	3.5×3.0	3.5×3.0	Fert. test in 1964
			4	2	46.5	4.0×3.5	4.0×3.5	Fert. test in 1964
1962	*jap.* No. 3	*jap.* No. 3	5	1	43.0	3.5×2.5	3.5×2.5	
			6	1	42.5	3.0×2.5	3.0×2.0	
			7	2	48.0	4.5×3.5	4.5×3.5	Fert. test in 1964
1976	*jap.* No. 2	*jap.* No. 2	8	1	43.5	3.5×2.5	3.5×3.0	
			9	1	42.0	3.5×3.0	3.5×2.5	
			10	1	44.5	3.5×2.5	3.5×2.5	
1976	*jap.* No. 3	*jap.* No. 3	11	1	42.5	3.0×2.0	3.0×2.0	
			12	1	43.0	3.5×2.5	3.5×2.5	
1962	*jap.* No. 1	*ornat.* No. 1	1	1	40.5	3.0×2.0	3.0×2.0	
			2	1	41.0	3.5×2.5	4.0×3.0	
			3	2	43.5	4.0×3.0	3.5×2.5	Fert. test in 1964
			4	2	46.0	4.5×3.0	4.0×3.0	Fert. test in 1964
			5	2	49.5	5.0×3.5	4.0×2.5	Fert test in 1964
1976	*jap.* No. 2	*ornat.* No. 2	6	1	47.5	4.0×3.0	4.0×2.5	
			7	1	48.0	3.5×2.5	3.5×2.5	
1962	*jap.* No. 1	*chen.* No. 1	1	1	39.5	3.5×2.5	3.0×2.0	
			2	1	42.0	3.5×3.0	3.5×2.5	
1962	*jap.* No. 3	*chen.* No. 3	3	2	47.0	3.5×3.0	4.0×3.5	Fert. test in 1964
			4	2	48.0	3.0×2.5	3.5×2.5	Fert. test in 1964
			5	2	47.5	2.5×2.0	3.0×2.0	Fert. test in 1964
1976	*jap.* No. 1	*chen.* No. 1	6	1	31.5	2.0×1.5	2.0×1.5	
			7	1	36.5	3.0×2.0	3.0×2.0	
			8	1	37.0	3.0×2.0	3.0×2.0	
			9	1	39.0	3.5×2.5	3.5×2.5	
			10	1	39.5	4.0×2.5	3.5×2.0	
1962	*jap.* No. 1	*temp.* No. 1 (♀)	1	1	32.5	2.0×0.5	2.0×0.5	
			2	1	35.0	1.0×0.5	1.0×0.5	
			3	2	55.5	7.0×4.0	2.0×0.5	Fert. test in 1964
1962	*jap.* No. 3	*temp.* No. 2	4	1	37.0	1.5×0.5	2.0×0.5	
			5	1	36.5	2.0×1.5	2.0×0.5	
			6	1	37.5	Very small	Very small	
			7	1	35.0	1.5×0.5	1.5×0.5	
			8	1	38.0	2.0×1.5	2.5×2.0	
			9	2	54.5	10.5×8.0	10.0×7.5	Fert. test in 1964
			10	2	53.5	8.5×7.0	9.0×7.5	Fert. test in 1964
			11	2	52.5	7.0×5.5	7.0×5.5	Fert. test in 1964
1976	*jap.* No. 1	*temp.* No. 1	12	1	43.5	2.5×1.5	3.0×1.5	
			13	1	40.0	3.0×2.0	3.5×1.5	
			14	1	39.0	2.5×1.5	2.5×1.5	
			15	1	41.5	2.5×1.5	2.5×1.5	
			16	1	43.0	3.0×2.0	3.0×2.0	
1962	*jap.* No. 1	*arv.* No. 1	1	2	42.0	4.0×3.0	5.0×3.5	Fert. test in 1964
			2	2	40.5	3.5×2.5	3.5×2.5	Fert. test in 1964
			3	2	49.0	4.5×3.0	5.0×3.0	Fert. test in 1964
1962	*jap.* No. 3	*arv.* No. 2	4	1	41.5	3.5×2.5	3.5×2.5	
			5	1	37.5	5.0×3.5	4.5×3.0	
1976	*jap.* No. 1	*arv.* No. 1	6	1	40.0	3.0×2.0	3.0×2.0	
			7	1	39.5	3.5×2.5	3.5×2.5	
			8	1	44.0	4.5×3.0	4.5×3.0	
			9	1	42.5	4.0×2.5	4.0×3.0	
			10	1	46.0	4.5×3.5	4.5×3.5	
1981	*jap.* No. 1	*long.* No. 1	1	0.7	35.5	3.0×2.0	3.0×2.0	
			2	0.7	37.0	3.0×2.5	3.0×2.5	
			3	0.7	34.0	2.5×2.0	2.5×2.0	
1981	*long.* No. 1	*jap.* No. 1	1	0.7	41.5	3.5×2.5	3.5×2.5	
			2	0.7	38.0	3.0×2.0	3.0×2.0	
			3	0.7	40.5	3.5×2.5	3.5×2.5	

The testes of these seven male hybrids were very abnormal in inner structure. The seminiferous tubules were filled with pycnotic nuclei and abnormal spermatozoa for the most part. There were some spermatogonia and first spermatocytes along the inner wall of seminiferous tubules, while normal spermatozoa were never found (Fig. 28b).

c. Hybrids, *Rana japonica*♀ × *Rana chensinensis*♂

Seven 1-year-old male hybrids including two (Nos. 1 and 2) produced in 1962 and five (Nos. 6～10) produced in 1976 were 31.5～42.0 mm, 37.9 mm on the average, in body length. The left testes of these males were 2.0～4.0 mm, 3.2 mm on the average, in length, and 1.5～3.0 mm, 2.3 mm on the average, in width, while the right testes were 2.0～3.5 mm, 3.1 mm on the average, in length and 1.5～2.5 mm, 2.1 mm on the average, in width. Three 2-year-old male hybrids (Nos. 3～5) produced in 1962 were 47.0～48.0 mm in body length. Their left testes were 2.5～3.5 mm in length and 2.0～3.0 mm in width, while their right testes were 3.0～4.0 mm in length and 2.0～3.5 mm in width (Table 24).

The testes of the above ten male hybrids were very abnormal in inner structure. The seminiferous tubules contained numerous pycnotic nuclei and abnormal spermatozoa. There were no normal spermatozoa, while some spermatogonia and first spermatocytes were found along the inner wall of seminiferous tubules (Fig. 28c).

d. Hybrids, *Rana japonica*♀ × *Rana longicrus*♂

Three 0.7-year-old male hybrids (Nos. 1～3) were 34.0～37.0 mm in body length. The left and right testes of these males were 2.5 or 3.0 mm in length and 2.0 or 2.5 mm in width (Table 24).

The testes of these males were very abnormal in inner structure. The seminiferous tubules contained numerous pycnotic nuclei and abnormal spermatozoa. Although normal spermatozoa were never found, there were some spermatogonia and first spermatocytes along the inner wall of seminiferous tubules. Spermatogenesis appeared to become abnormal at the metaphase or anaphase of the first meiotic division (Fig. 28d).

e. Hybrids, *Rana japonica*♀ × *Rana temporaria*♂

One of the two female *Rana japonica* used in 1962 was mated with a hermaphrodite *Rana temporaria* (No. 1), while the other was mated with a normal male *Rana temporaria* (No. 2). Seven 1-year-old male hybrids (Nos. 1, 2, 4, 5, 6, 7 and 8) produced in 1962 were 32.5～38.0 mm, 35.9 mm on the average, in body length. The testes of these males were comparatively small and in particular one of these hybrids had extremely small testes. The testes of the other six males were 1.0～2.0 mm, 1.7 mm on the average, in length and 0.5 or 1.5 mm, 0.8 mm on the average, in width, while the right testes were 1.0～2.5 mm, 1.8 mm on the average, in length and 0.5 or 2.0 mm, 0.8 mm on the average, in width.

The testes of above seven male hybrids were very abnormal in inner structure.

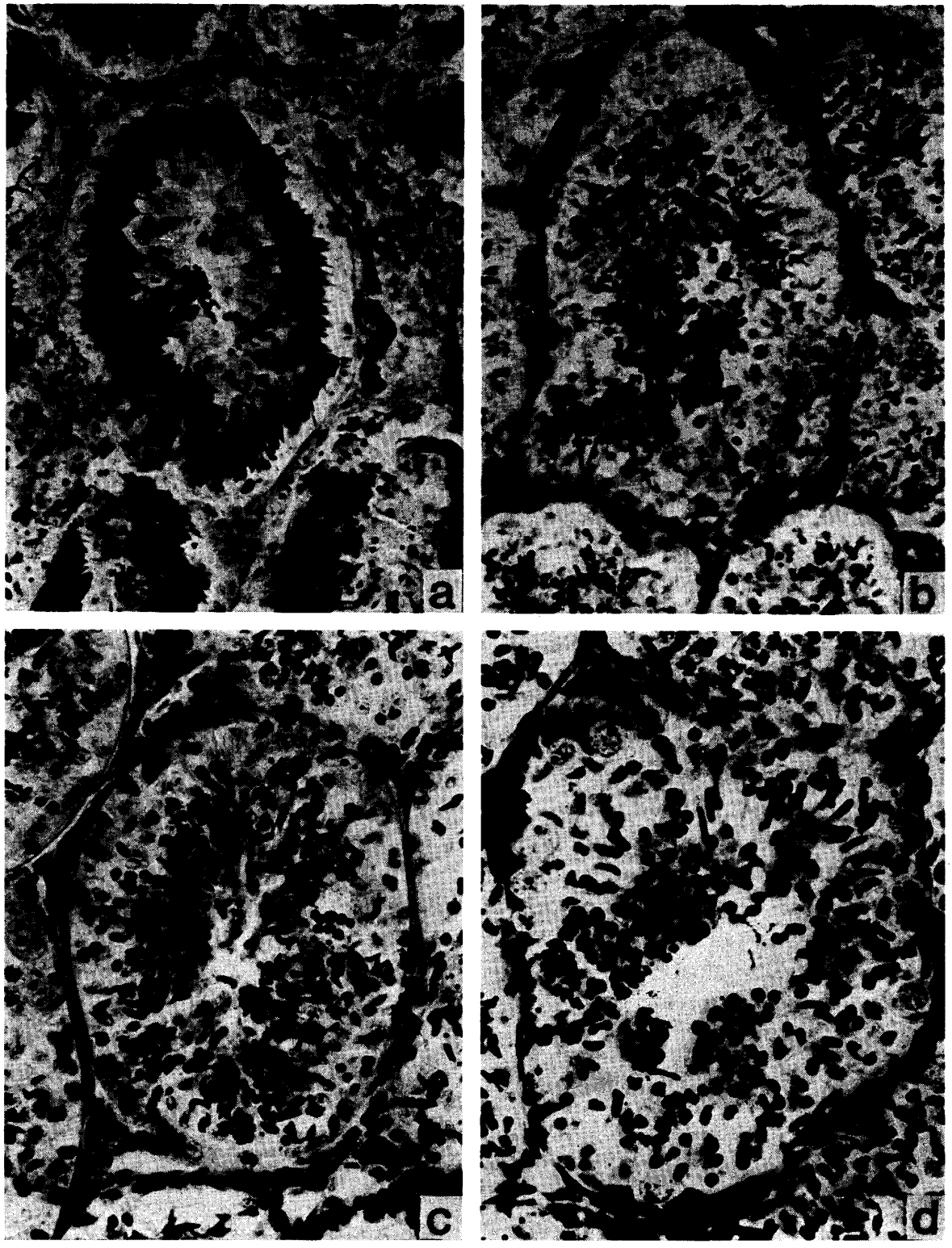


Fig. 28. Cross-sections of the testes of male hybrids between female *Rana japonica* and males of three species, and the control male.

a. Control *Rana japonica* ♂ No. 8, *Rana japonica* ♀ No. 2 × *Rana japonica* ♂ No. 2, produced in 1976. One year old. ×350
b. Hybrid ♂ No. 6, *Rana japonica* ♀ No. 2 × *Rana ornativentris* ♂ No. 2, produced in 1976. One year old. ×350
c. Hybrid ♂ No. 9, *Rana japonica* ♀ No. 1 × *Rana chensinensis* ♂ No. 1, produced in 1976. One year old. ×350
d. Hybrid ♂ No. 2, *Rana japonica* ♀ No. 1 × *Rana longicrus* ♂ No. 1, produced in 1981. Eight months old. ×400

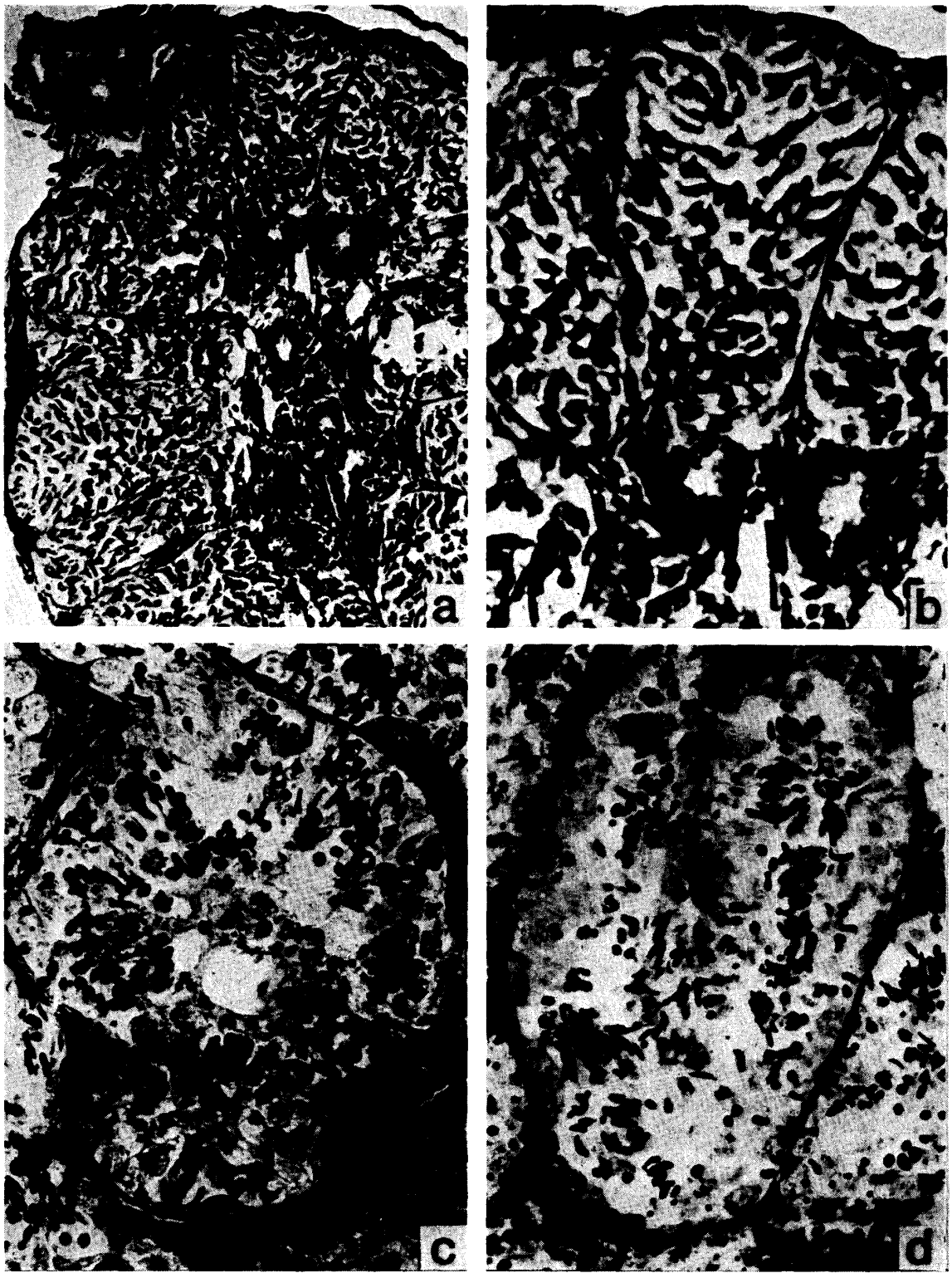


Fig. 29. Cross-sections of the testes of male hybrids between female *Rana japonica* and male *Rana temporaria* or *Rana arvalis*. All the hybrids were one year old.

a. Hybrid ♂ No. 1, *Rana japonica* ♀ No. 1 × *Rana temporaria* ♂ No. 1, produced in 1962. ×170
b. The same as (a). ×350
c. Hybrid ♂ No. 16, *Rana japonica* ♀ No. 1 × *Rana temporaria* ♂ No. 1, produced in 1976. ×350
d. Hybrid ♂ No. 6, *Rana japonica* ♀ No. 1 × *Rana arvalis* ♂ No. 1, produced in 1976. ×350

In the testes of hybrids, germ cells were scarce. The seminiferous tubules of these testes were filled with stromal cells (Fig. 29a, b). The seminiferous tubules of the other two males (Nos. 5 and 8) contained some pycnotic nuclei and abnormal spermatozoa. Although there were some spermatogonia and first spermatocytes along the inner wall of seminiferous tubules, normal spermatozoa were never found.

Of the hybrids produced in 1976, 64 were preserved at the age of one year. Many of them had very small or rudimentary testes which had almost completely degenerated. Five hybrids (Nos. 12～16) having testes of a measurable size were 39.0～43.5 mm, 41.4 mm on the average, in body length. The testes of these hybrids were 2.5 or 3.0 mm, 2.7 mm on the average, in length and 1.5 or 2.0 mm, 1.7 mm on the average, in width, while the right testes were 2.5～3.5 mm, 2.9 mm on the average, in length and 1.5 or 2.0 mm, 1.6 mm on the average, in width.

The testes of these five male hybrids were nearly the same in inner structure as those of the above two males, Nos. 5 and 8, produced in 1962. The seminiferous tubules contained some pycnotic nuclei and abnormal spermatozoa. There were no normal spermatozoa, while some spermatogonia and first spermatocytes were found along the inner wall of seminiferous tubules (Fig. 29c).

Four 2-year-old male hybrids produced in 1962 were 52.5～55.5 mm, 54.0 mm on the average, in body length, and had large testes. Their left testes were 7.0～10.5 mm, 8.3 mm on the average, in length and 4.0～8.0 mm, 6.1 mm on the average, in width. While the right testes of one (No. 3) of these frogs was 2.0 mm in length and 0.5 mm in width, those of the other three frogs were 7.0～10.0 mm in length and 5.5～7.5 mm in width.

The testes of these four male hybrids were very abnormal in inner structure in spite of their large size. The seminiferous tubules contained many pycnotic nuclei and abnormal spermatozoa. There were no normal spermatozoa. Some spermatogonia and first spermatocytes were found along the inner wall of the seminiferus tubules.

f. Hybrids, *Rana japonica*♀ × *Rana arvalis*♂

Seven 1-year-old male hybrids including two (Nos. 4 and 5) produced in 1962 and five (Nos. 6～10) produced in 1976 were 37.5～46.0 mm, 41.6 mm on the average, in body length. The left testes of these seven frogs were 3.0～5.0 mm, 4.0 mm on the average, in length and 2.0～3.5 mm, 2.8 mm on the average, in width, while the right testes were 3.0～4.5 mm, 3.9 mm on the average, in length and 2.0～3.5 mm, 2.8 mm on the average, in width (Table 24).

Three 2-year-old male hybrids (Nos. 1～3) produced in 1962 were 40.5～49.0 mm in body length. The left testes of these frogs were 3.5～4.5 mm in length and 2.5 or 3.0 mm in width, while the right testes were 3.5 or 5.0 mm in length and 2.5～3.5 mm in width (Table 24).

The testes of the above 10 male hybrids were very abnormal in inner structure. Normal spermatozoa were never found in the seminiferous tubules (Fig. 29d).

2. Interspecific hybrids between a female *Rana longicrus* and a male *Rana japonica*

Three 0.7-year-old male hybrids (Nos. 1～3) produced in 1981 were 38.0～41.5 mm, 40.0 mm on the average, in body length. The left and right testes of these males were 3.0 or 3.5 mm in length and 2.0 or 2.5 mm in width (Table 24).

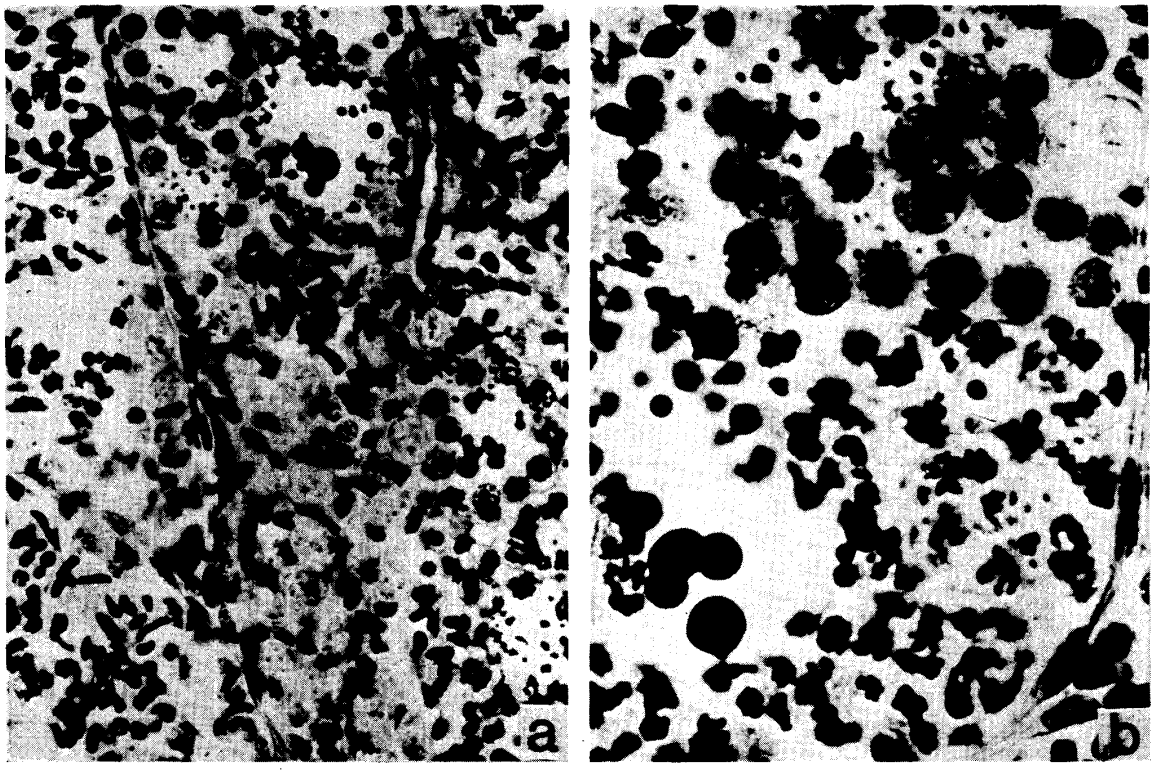


Fig. 30. Cross-section of the testis of a male hybrid between a female *Rana longicrus* and a male *Rana japonica*. This hybrid was 8 months old.

a. Hybrid ♂ No. 1, *Rana longicrus* ♀ No. 1 × *Rana japonica* ♂ No. 1, produced in 1981. ×400
b. The same as (a). ×700

The testes of these males were very abnormal in inner structure and contained no normal spermatozoa. In the seminiferous tubules, there were some abnormal spermatozoa, pycnotic nuclei and degenerating first spermatocytes at the metaphase or anaphase of reduction dividsion in addition to first spermatocytes at the prophase as well as spermatogonia situated along the inner wall (Fig. 30a, b).

3. Interspecific hybrids between female *Rana ornativentris* and males of two species

a. Controls

i) *Rana ornativentris* ♀ × *Rana ornativentris* ♂

Three 1-year-old males (Nos. 7～9) produced in 1975 were 47.0～51.5 mm in body length. The left and right testes of these males were 3.5～5.0 mm in length and 2.5～3.5 mm in width. Six 2-year-old males including two (Nos. 1 and

2) produced in 1962, one (No. 3) produced in 1964 and three (Nos. 4~6) produced in 1965 were 45.0~56.0 mm, 52.7 mm on the average, in body length. The left testes of these males were 4.0~5.0 mm, 4.4 mm on the average, in length and 3.0 or 3.5 mm, 3.3 mm on the average, in width, while the right testes were 3.5~5.0 mm, 4.3 mm on the average, in length and 3.0 or 3.5 mm, 3.3 mm on the average, in width (Table 25).

The testes of the above nine males were completely normal. The seminiferous tubules were filled with compact bundles of normal spermatozoa.

ii) *Rana temporaria*♀ × *Rana temporaria*♂

Five 2-year-old males (Nos. 1~5) produced in 1964 were 58.5~64.0 mm, 61.8 mm on the average, in body length. The left testes of these males were 8.0~11.0 mm, 9.9 mm on the average, in length and 6.5~8.0 mm, 7.4 mm on the average, in width, while the right testes were 8.0~11.0 mm, 10.0 mm on the average, in length and 7.0~8.0 mm, 7.4 mm on the average, in width. These

TABLE 25

Testes of mature male hybrids between female *Rana ornativentris* and males of two species, and the controls

Year	Parents		Individual no.	Age	Body length	Size of testes		Remarks
	Female	Male		year(s)	mm	Left mm	Right mm	
1962	*ornat.* No. 1	*ornat.* No. 1	1	2	45.0	4.0×3.0	3.5×3.0	Fert. test in 1964
			2	2	56.0	4.5×3.5	4.5×3.5	
1964	*ornat.* No. 1	*ornat.* No. 1	3	2	53.0	4.5×3.5	4.0×3.0	
1965	*ornat.* No. 1	*ornat.* No. 1	4	2	54.5	5.0×3.5	5.0×3.5	Fert. test in 1967
			5	2	55.0	4.5×3.0	4.5×3.0	Fert. test in 1967
			6	2	52.5	4.0×3.5	4.0×3.5	Fert. test in 1967
1975	*ornat.* No. 2	*ornat.* No. 2	7	1	51.5	5.0×3.5	5.0×3.5	
			8	1	49.5	4.5×3.0	4.5×3.0	
			9	1	47.0	3.5×2.5	3.5×2.5	
1964	*temp.* No. 1	*temp.* No. 1	1	2	64.0	10.5×8.0	10.5×7.5	
			2	2	60.5	9.5×7.0	10.0×7.0	
			3	2	58.5	8.0×6.5	8.0×7.0	
			4	2	62.0	10.5×7.5	10.5×7.5	Fert. test in 1967
			5	2	64.0	11.0×8.0	11.0×8.0	Fert. test in 1967
1962	*ornat.* No. 1	*chen.* No. 1	1	1	40.5	3.0×2.0	3.0×2.0	
			2	1	45.0	3.5×2.5	3.5×2.5	
			3	2	47.5	4.0×3.5	4.0×3.0	Fert. test in 1964
			4	2	47.0	3.5×3.0	4.0×3.0	Fert. test in 1964
			5	2	49.5	4.5×3.0	4.5×3.5	Fert. test in 1964
1962	*ornat.* No. 1	*temp.* No. 1 (♀)	1	2	52.5	3.5×2.5	2.0×1.5	Fert. test in 1964
			2	2	58.0	3.5×1.5	2.5×1.5	Fert. test in 1964
			3	2	43.5	2.0×1.5	2.0×1.5	
1964	*ornat.* No. 1	*temp.* No. 1	4	1	50.0	7.5×4.0	7.5×4.0	
			5	1	52.5	8.0×4.5	8.0×4.5	
1965	*ornat.* No. 1	*temp.* No. 1	6	2	54.0	7.5×4.5	7.0×4.0	Fert. test in 1967
			7	2	49.5	4.0×2.5	4.0×2.5	
			8	2	54.5	6.0×4.0	6.0×3.0	
			9	2	59.0	8.5×4.5	7.5×4.0	
			10	2	56.5	7.5×4.5	7.5×5.5	Fert. test in 1967

figures evidently showed that the testes of the control *Rana temporaria* were remarkably large just as those of the field-caught *Rana temporaria* used in the crossing experiments (Table 25).

The testes of the five males were completely normal in inner structure. The seminiferous tubules were filled with compact bundles of normal spermatozoa (Fig. 31a). The spermatozoa of this species were the most slender among those of the brown frog species used in the present study.

b. Hybrids, *Rana ornativentris*♀ × *Rana chensinensis*♂

Two 1-year-old male hybrids (Nos. 1 and 2) produced in 1962 were 40.5 mm and 45.0 mm in body length. The left and right testes of one of the two hybrids were 3.0 mm in length and 2.0 mm in width, while those of the other hybrid were 3.5 mm in length and 2.5 mm in width. Three 2-year-old male hybrids produced in 1962 were 47.0～49.5 mm in body length. The left testes of these hybrids were 3.5～4.5 mm in length and 3.0 or 3.5 mm in width, while the right testes were 4.0 or 4.5 mm in length and 3.0 or 3.5 mm in width (Table 25).

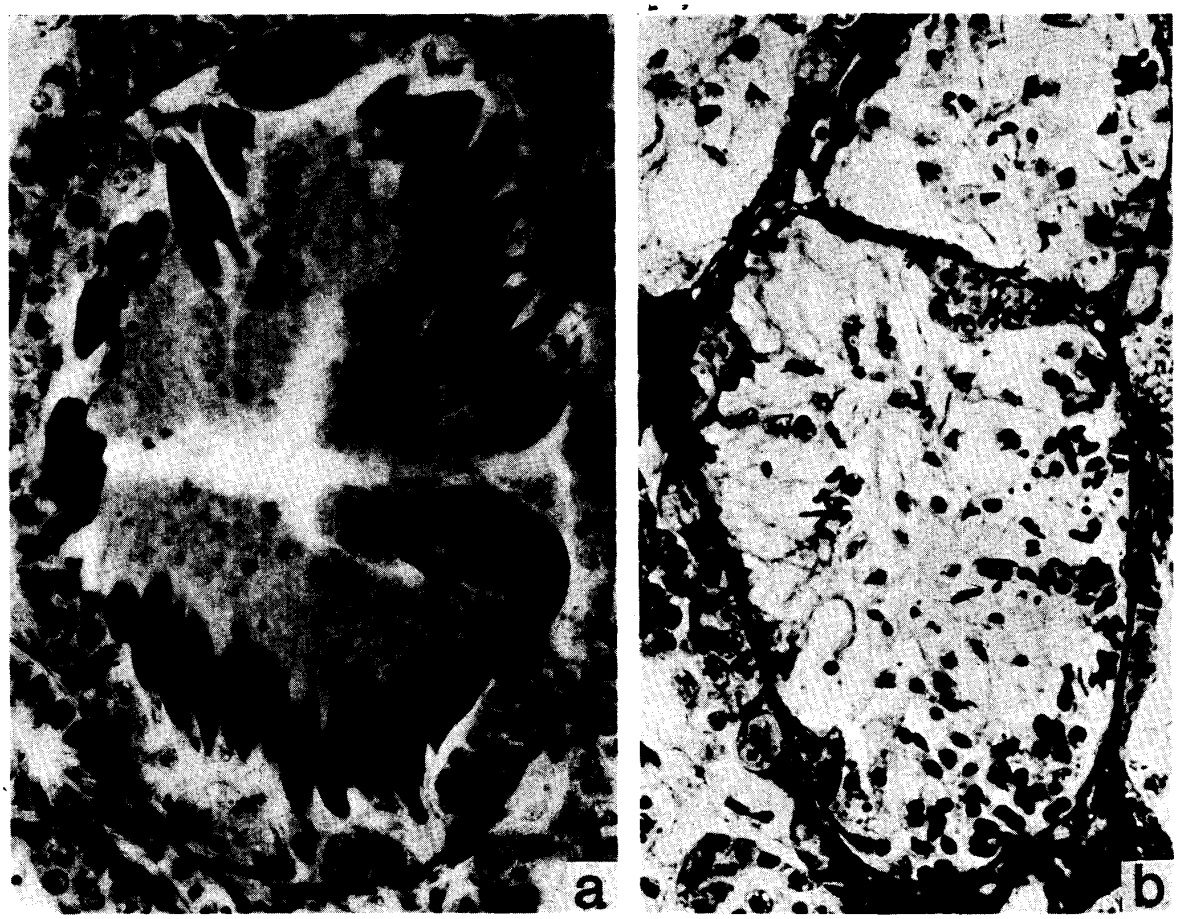


Fig. 31. Cross-sections of the testes of a male hybrid between a female *Rana ornativentris* and a male *Rana temporaria*, and the control male. All the males were two years old. ×350

a. Control *Rana temporaria*♂ No. 2, *Rana temporaria*♀ No. 1 × *Rana temporaria*♂ No. 1, produced in 1964.

b. Hybrid♂ No. 1, *Rana ornativentris*♀ No. 1 × *Rana temporaria*♂ No. 1, produced in 1962.

The testes of the above five hybrids were very abnormal in inner structure. The seminiferous tubules contained a few abnormal spermatozoa and some pycnotic nuclei. Besides, there were some spermatogonia and first spermatocytes along the inner wall of seminiferous tubules. Normal spermatozoa were never found.

c. Hybrids, *Rana ornativentris*♀ × *Rana temporaria*♂

Two 1-year-old male hybrids (Nos. 4 and 5) produced in 1964 were 50.0 mm and 52.5 mm in body length and had large testes. The left and right testes of one of these hybrids were 7.5 mm in length and 4.0 mm in width, while those of the other were 8.0 mm in length and 4.5 mm in width (Table 25).

Three 2-year-old male hybrids (Nos. 1～3) produced from mating with a hermaphrodite in 1962 were 43.5～58.0 mm in body length. The left testes of these hybrids were 2.0 or 3.5 mm in length and 1.5 or 2.5 mm in width, while the right testes were 2.0 or 2.5 mm in length and 1.5 mm in width. Five 2-year-old male hybrids (Nos. 6～10) produced in 1965 were 49.5～59.0 mm, 54.7 mm on the average, in body length. The smallest (No. 7) of these frogs had the smallest testes; the left and right testes were 4.0 mm in length and 2.5 mm in width. The left testes of the other four hybrids were 6.0～8.5 mm, 7.4 mm on the average, in length and 4.0 or 4.5 mm, 4.4 mm on the average, in width, while the right testes were 6.0～7.5 mm, 7.0 mm on the average, in length and 3.0～5.5 mm, 4.1 mm on the average, in width (Table 25).

The testes of the above 10 male hybrids were very abnormal in inner structure. The seminiferous tubules contained no normal spermatozoa, while they had some abnormal spermatozoa and pycnotic nuclei beside spermatogonia and first spermatocytes situated along the inner wall of seminiferous tubules (Fig. 31b).

4. Interspecific hybrids between female *Rana chensinensis* and males of three species

a. Controls, *Rana chensinensis*♀ × *Rana chensinensis*♂

Two 2-year-old male frogs (Nos. 1 and 2) produced in 1962 were 56.0 mm and 55.5 mm in body length. The left and right testes of these frogs were 4.0 mm in length and 2.0 mm in width (Table 26). Their testes were completely normal in inner structure. The seminiferous tubules were filled with compact bundles of normal spermatozoa.

b. Hybrids, *Rana chensinensis*♀ × *Rana japonica*♂

Two 2-year-old male hybrids (Nos. 1 and 2) produced in 1962 were 49.0 mm and 45.5 mm in body length. The left testes of these hybrids were 4.5 mm and 3.5 mm in length and 2.5 mm in width, while the right testes were 3.5 mm in length and 2.0 mm and 2.5 mm in width (Table 26).

The testes of these hybrids were very abnormal in inner structure and contained no normal spermatozoa. In the seminiferous tubules, there were some abnormal spermatozoa and pycnotic nuclei. Besides, some spermatogonia and first spermatocytes were found along the wall of seminiferus tubules.

TABLE 26
Testes of mature male hybrids between female *Rana chensinensis* and males of three species, and the controls

Year	Parents		Individual no.	Age	Body length	Size of testes		Remarks
	Female	Male		year(s)	mm	Left mm	Right mm	
1962	*chen.* No. 1	*chen.* No. 1	1	2	56.0	4.0×2.0	4.0×2.0	Fert. test in 1964
			2	2	55.5	4.0×2.0	4.0×2.0	Fert. test in 1964
1962	*chen.* No. 1	*jap.* No. 1	1	2	49.0	4.5×2.5	3.5×2.0	Fert. test in 1964
			2	2	45.5	3.5×2.5	3.5×2.5	Fert. test in 1964
1962	*chen.* No. 1	*ornat.* No. 1	1	1	47.0	3.5×2.5	3.5×2.5	
			2	1	47.5	4.0×2.5	4.5×3.0	
			3	2	51.0	4.5×3.0	4.5×3.0	Fert. test in 1964
			4	2	53.0	4.0×2.5	4.0×2.5	Fert. test in 1964
			5	2	52.5	4.5×3.0	4.5×3.0	Fert. test in 1964
1962	*chen.* No. 1	*arv.* No. 1	1	1	43.5	2.5×2.0	2.5×2.0	
			2	1	44.0	3.0×2.5	3.0×2.5	
			3	1	46.0	3.5×3.0	3.5×2.5	
			4	2	52.5	4.0×3.0	4.0×3.0	Fert. test in 1964
			5	2	54.0	4.5×3.5	4.0×3.5	Fert. test in 1964
			6	2	54.5	5.0×3.5	4.5×3.5	Fert. test in 1964

c. Hybrids, *Rana chensinensis*♀ × *Rana ornativentris*♂

Two 1-year-old male hybrids (Nos. 1 and 2) produced in 1962 were 47.0 mm and 47.5 mm in body length. The left testes of these hybrids were 3.5 mm and 4.0 mm in length and 2.5 mm in width, while the right testes were 3.5 mm and 4.5 mm in length and 2.5 mm and 3.0 mm in width. Three 2-year-old male hybrids (Nos. 3～5) produced in 1962 were 51.0～53.0 mm in body length. The left and right testes of these hybrids were 4.0 or 4.5 mm in length and 2.5 or 3.0 mm in width (Table 26).

The testes of the above five hybrids were very abnormal in inner structure. The seminiferous tubules contained no normal spermatozoa. There were some abnormal spermatozoa and many pycnotic nuclei besides spermatogonia and first spermatocytes situated along the wall of seminiferous tubules.

d. Hybrids, *Rana chensinensis*♀ × *Rana arvalis*♂

Three 1-year-old male hybrids (Nos. 1～3) produced in 1962 were 43.5～46.0 mm in body length. The left testes of these hybrids were 2.5～3.5 mm in length and 2.0～3.0 mm in width, while the right testes were 2.5～3.0 mm in length and 2.0 or 2.5 mm in width. Three 2-year-old male hybrids (Nos. 4～6) produced in 1962 were 52.5～54.5 mm in body length. The left testes were 4.0～5.0 mm in length and 3.0 or 3.5 mm in width, while the right testes were 4.0 or 4.5 mm in length and 3.0 or 3.5 mm in width (Table 26).

The testes of the above six hybrids were very abnormal in inner structure. The seminiferous tubules contained some abnormal spermatozoa and pycnotic nuclei beside spermatogonia and first spermatocytes situated along the wall. Normal spermatozoa were never found.

5. Intraspecific hybrids of *Rana dybowskii* from Tsushima and Korea

a. Controls

i) *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Tsushima♂

Three 1-year-old males (Nos. 1~3) produced in 1970 were 32.5~36.5 mm in body length. The left testes of these frogs were 3.0 or 3.5 mm in length and 2.0~3.0 mm in width, while the right testes were 2.5~3.5 mm in length and 2.0~3.0 mm in width. Three 2-year-old males (Nos. 4~6) produced in the same year were 50.5~53.5 mm in body length. The left testes of these frogs were 4.5 or 5.0 mm in length and 3.0 or 3.5 mm in width, while the right testes were 4.5 or 5.0 mm in length and 2.5~3.5 mm in width (Table 27).

The testes of the above six male *Rana dybowskii* were completely normal in inner structure. The seminiferous tubules were filled with compact bunldes of

TABLE 27

Testes of mature male intraspecific hybrids between *Rana dybowskii* from Tsushima and *Rana dybowskii* from Korea, and the controls

Year	Parents		Indi-vidual	Age	Body length	Size of testes		Remarks
	Female	Male	no.	year(s)	mm	Left mm	Right mm	
1970	*dyb.* T. No. 2	*dyb.* T. No. 2	1	1	36.5	3.0×2.0	3.0×2.5	Fert. test in 1971
			2	1	32.5	3.5×3.0	3.5×3.0	Fert. test in 1971
1970	*dyb.* T. No. 6	*dyb.* T. No. 6	3	1	34.0	3.0×2.5	2.5×2.0	Fert. test in 1971
1970	*dyb.* T. No. 2	*dyb.* T. No. 2	4	2	50.5	4.5×3.0	4.5×3.0	Fert. test in 1972
			5	2	52.0	4.5×3.0	4.5×2.5	Fert. test in 1972
			6	2	53.5	5.0×3.5	5.0×3.5	Fert. test in 1972
1970	*dyb.* K. No. 1	*dyb.* K. No. 1	1	1	46.0	3.0×2.5	3.0×2.5	Fert. test in 1971
1970	*dyb.* K. No. 3	*dyb.* K. No. 3	2	1	45.5	2.5×1.5	3.0×2.0	Fert. test in 1971
1970	*dyb.* K. No. 4	*dyb.* K. No. 4	3	1	37.5	3.0×2.0	3.0×2.0	Fert. test in 1971
			4	2	54.0	5.5×3.5	5.5×3.5	Fert. test in 1972
			5	2	50.0	3.5×2.5	4.0×2.5	Fert. test in 1972
1970	*dyb.* T. No. 2	*dyb.* K. No. 2	1	1.5	44.0	4.0×2.5	4.0×2.5	
			2	1.5	43.5	4.5×2.5	4.5×2.5	
1970	*dyb.* T. No. 3	*dyb.* K. No. 3	3	1.5	45.0	4.0×2.0	4.5×2.0	
			4	1.5	46.5	4.5×2.5	4.5×2.5	
			5	1.5	47.0	4.5×2.5	4.5×2.5	
1970	*dyb.* T. No. 2	*dyb.* K. No. 2	6	2	48.0	5.0×2.5	5.0×2.5	Fert. test in 1972
			7	2	50.0	5.5×3.0	5.5×3.0	Fert. test in 1972
			8	2	48.5	6.0×2.5	6.0×2.5	Fert. test in 1972
			9	2	49.5	5.5×3.0	6.0×3.5	Fert. test in 1972
1970	*dyb.* K. No. 1	*dyb.* T. No. 1	1	1	41.5	3.0×2.5	3.0×2.5	Fert. test in 1971
1970	*dyb.* K. No. 3	*dyb.* T. No. 3	2	1	42.5	2.5×2 0	2.5×2.0	Fert. test in 1971
			3	1	42.0	2.5×2.0	2.5×2.0	Fert. test in 1971
1970	*dyb.* K. No. 1	*dyb.* T. No. 1	4	1.5	40.0	3.0×2.5	3.0×2.5	
1970	*dyb.* K. No. 3	*dyb.* T. No. 3	5	1.5	43.5	3.5×3.0	3.5×3.0	
			6	1.5	45.0	3.5×3.0	3.5×3.0	
1970	*dyb.* K. No. 4	*dyb.* T. No. 4	7	1.5	45.5	3.5×3.0	5.0×2.5	
			8	2	47.0	4.0×3.5	4.0×3.5	Fert. test in 1972
			9	2	42.5	2.0×1.5	2.0×1.5	Fert. test in 1972
			10	2	49.5	5.5×3.5	5.5×3.5	Fert. test in 1972
			11	2	49.0	4.0×3.5	4.0×3.5	Fert. test in 1972

normal spermatozoa (Fig. 32a).

ii) *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Korea♂

Three 1-year-old males (Nos. 1～3) produced in 1970 were 37.5～46.0 mm in body length. The left testes were 2.5 or 3.0 mm in length and 1.5～2.5 mm in width, while the right testes were 3.0 mm in length and 2.0 or 2.5 mm in width. Two 2-year-old males (Nos. 4 and 5) produced in 1970 were 50.0 mm and 54.0 mm in body length. The left testes of these males were 5.5 mm and 3.5 mm in length and 3.5 mm and 2.5 mm in width, while the right testes were 5.5 mm and 4.0 mm in length and 3.5 mm and 2.5 mm in width (Table 27).

The testes of the above five males were completely normal in inner structure. The seminiferous tubules were filled with compact bundles of normal spermatozoa (Fig. 34b).

b. Intraspecific hybrids, *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Korea♂

Five 1.5-year-old males (Nos. 1～5) produced in 1970 were 43.5～47.0 mm, 45.2 mm on the average, in body length. The left testes of these males were 4.0 or 4.5 mm, 4.3 mm on the average, in length and 2.0 or 2.5 mm, 2.4 mm on the average, in width, while the right testes were 4.0 or 4.5 mm, 4.4 mm on the average, in length and 2.0 or 2.5 mm, 2.4 mm on the average, in width. Four 2-year-old males (Nos. 6～9) produced in the same year were 48.0～50.0 mm, 49.0 mm on the average, in body length. The left testes of these males were 5.0～6.0 mm, 5.5 mm on the average, in length and 2.5 or 3.0 mm, 2.8 mm on the average, in width, while the right testes were 5.0～6.0 mm, 5.6 mm on the average, in length and 2.5～3.5 mm, 2.9 mm on the average, in width (Table 27).

The testes of the above nine males were completely normal. The seminiferous tubules were filled with compact bundles of normal spermatozoa (Fig. 34a).

c. Intraspecific hybrids, *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Tsushima

Three 1-year-old males (Nos. 1～3) produced in 1970 were 41.5～42.5 mm in body length. The left and right testes of these males were 2.5 or 3.0 mm in length and 2.0 or 2.5 mm in width. Four 1.5-year-old males (Nos. 4～7) produced in 1970 were 40.0～45.5 mm, 43.5 mm on the average, in body length. The left testes of these males were 3.0 or 3.5 mm, 3.4 mm on the average, in length and 2.5 or 3.0 mm, 2.9 mm on the average, in width, while the right testes were 3.0～5.0 mm, 3.8 mm on the average, in length and 2.5 or 3.0 mm, 2.8 mm on the average, in width. Four 2-year-old males (Nos. 8～11) produced in 1970 were 42.5～49.5 mm, 47.0 mm on the average, in body length. While the smallest male (No. 9) had small testes which were 2.0 mm in length and 1.5 mm in width, the left and right testes of the other three were 4.0 or 5.5 mm in length and 3.5 mm in width (Table 27).

The testes of the above 11 males were completely normal. The seminiferous tubules were filled with compact bundles of normal spermatozoa (Fig. 35d).

6. Interspecific hybrids between female *Rana dybowskii* from Tsushima and males of four species

a. Controls

i) *Rana japonica*♀ × *Rana japonica*♂

Two 1-year-old males (Nos. 1 and 2) produced in 1970 were 36.5 mm and 37.0 mm in body length. The left and right testes of these males were 2.5 or 3.0 mm in length and 1.5 or 2.0 mm in width. Two 2-year-old males (Nos. 3 and 4) produced in 1970 were 40.0 mm and 42.5 mm in body length. The left testes of these males were 3.5 or 4.0 mm in length and 2.5 mm in width, while the right testes were 3.5 mm in length and 2.5 or 3.0 mm in width (Table 28).

The testes of the above four males were completely normal in inner structure. The seminiferous tubules were filled with compact bundles of normal spermatozoa.

ii) *Rana ornativentris*♀ × *Rana ornativentris*♂

Two 1-year-old males (Nos. 1 and 2) produced in 1970 were 35.0 mm and 36.0 mm in body length. The left testes of these males were 3.0 or 3.5 mm in length and 1.5 or 2.0 mm in width, while the right testes were 3.0 or 3.5 mm in length and 2.0 mm in width. Two 2-year-old males (Nos. 3 and 4) produced in 1970 were 49.5 mm and 50.5 mm in body length. The left and right testes of these males were 4.0 or 4.5 mm in length and 2.5 or 3.0 mm in width (Table 28).

The testes of the above four males were completely normal. The seminiferous tubules were filled with compact bundles of normal spermatozoa (Fig. 35a).

iii) *Rana chensinensis*♀ × *Rana chensinensis*♂

One 1-year-old male (No. 1) produced in 1970 was 40.5 mm in body length. Both testes of this male were 3.5 mm in length and 2.0 mm in width. Two 2-year-old males (Nos. 2 and 3) produced in 1970 were 45.0 mm and 47.5 mm in body length. One of them had testes which were 4.0 mm in length and 2.5 mm in width, while the testes of the other male were 4.5 mm in length and 3.0 or 2.5 mm in width (Table 28).

The testes of these three males were completely normal in inner structure. The seminiferous tubules were filled with compact bundles of normal spermatozoa (Fig. 36d).

b. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana japonica*♂

Two 1-year-old male hybrids (Nos. 1 and 2) produced in 1970 were 42.0 mm and 43.0 mm in body length. The left testes of these males were 3.0 or 4.0 mm in length and 1.0 or 2.5 mm in width. The right testes were used in backcross experiments of 1971 without measuring their size. Three 1.5-year-old male hybrids (Nos. 3～5) produced in the same year were 37.5～42.5 mm in body length. The largest male had a very small testis on the left side, while the right testis was 3.0 mm in length and 2.5 mm in width. The left and right testes of the other two males were 2.5 or 3.0 mm in length and 1.5 or 2.0 mm in width. Two 2-year-old male hybrids (Nos. 6 and 7) produced in 1970 were 49.5 mm and 44.5 mm in body length. The testes of these males were 4.0 mm and 3.5 mm in length and

TABLE 28

Testes of mature male hybrids between female *Rana dybowskii* from Tsushima and males of four species, and the controls

Year	Parents		Individual no.	Age	Body length	Size of testes		Remarks
	Female	Male		year(s)	mm	Left mm	Right mm	
1970	*jap.* No. 1	*jap.* No. 1	1	1	36.5	2.5×1.5	2.5×2.0	Fert. test in 1971
			2	1	37.0	3.0×2.0	3.0×1.5	Fert. test in 1971
			3	2	40.0	3.5×2.5	3.5×2.5	Fert. test in 1972
			4	2	42.5	4.0×2.5	3.5×3.0	Fert. test in 1972
1970	*ornat.* No. 1	*ornat.* No. 1	1	1	35.0	3.0×1.5	3.5×2.0	Fert. test in 1971
			2	1	36.0	3.5×2.0	3.0×2.0	Fert. test in 1971
			3	2	49.5	4.0×3.0	4.0×2.5	Fert. test in 1972
			4	2	50.5	4.5×2.5	4.5×2.5	Fert. test in 1972
1970	*chen.* No. 1	*chen.* No. 1	1	1	40.5	3.5×2.0	3.5×2.0	Fert. test in 1971
			2	2	45.0	4.0×2.5	4.0×2.5	Fert. test in 1972
			3	2	47.5	4.5×3.0	4.5×2.5	Fert. test in 1972
1970	*dyb.* T.No. 1	*jap.* No. 1	1	1	42.0	3.0×1.0		Fert. test in 1971
			2	1	43.0	4.0×2.5		Fert. test in 1971
			3	1.5	39.0	2.5×2.0	2.5×2.0	
			4	1.5	37.5	3.0×1.5	3.0×1.5	
			5	1.5	42.5	Very small	3.0×2.5	
			6	2	49.5	4.0×2.5	6.0×2.5	Fert. test in 1972
			7	2	44.5	3.5×3.0	3.5×3.0	Fert. test in 1972
1970	*dyb.* T. No. 1	*ornat.* No. 1	1	1	43.5	4.0×2.5		Fert. test in 1971
			2	1	38.5	3.0×2.0		Fert. test in 1971
1970	*dyb.* T. No. 2	*ornat.* No. 2	3	1	43.0	3.5×2.5		Fert. test in 1971
			4	1	42.0	3.5×2.0		Fert. test in 1971
1970	*dyb.* T. No. 3	*ornat.* No. 3	5	1	41.5	3.0×2.0		Fert. test in 1971
1970	*dyb.* T. No. 1	*ornat.* No. 1	6	1.5	43.0	4.0×2.5	4.0×2.5	
			7	1.5	36.5	2.5×2.0	2.5×2.0	
1970	*dyb.* T. No. 2	*ornat.* No. 2	8	1.5	46.0	2.5×2.0	2.5×2.0	
			9	1.5	44.5	4.0×2.5	4.0×2.5	
1970	*dyb.* T. No. 3	*ornat.* No. 3	10	1.5	42.0	2.0×1.5	2.0×1.0	
1970	*dyb.* T. No. 2	*ornat.* No. 2	11	2	46.0	3.5×2.5	3.5×2.5	Fert. test in 1972
			12	2	45.5	3.0×2.0	3.5×2.0	Fert. test in 1972
			13	2	50.5	3.5×3.0	3.5×3.0	Fert. test in 1972
1970	*dyb.* T. No. 3	*ornat.* No. 3	14	2	48.0	3.5×3.0	0	Fert. test in 1972
			15	2	45.5	3.0×2.5	3.0×2.5	Fert. test in 1972
1970	*dyb.* T. No. 2	*chen.* No. 2	1	1	39.5	4.0×2.0		Fert. test in 1971
			2	1	40.0	1.5×1.0		Fert. test in 1971
1970	*dyb.* T. No. 1	*chen.* No. 1	3	1.5	38.0	2.5×2.5	2.5×2.5	
1970	*dyb.* T. No. 2	*chen.* No. 2	4	1.5	40.5	2.5×1.5	2.5×1.0	
			5	1.5	36.5	3.0×1.5	3.0×1.5	
			6	2	44.0	4.0×2.5	6.0×2.5	Fert. test in 1972
			7	2	38.5	3.5×2.0	3.5×2.0	Fert. test in 1972
1975	*dyb.* T. No. 1	*temp.* No. 1	1	2	50.5	3.5×2.5	4.0×2.5	
			2	2	56.0	4.0×3.0	3.5×2.5	

2.5 mm and 3.0 mm in width, while the right testes were 6.0 mm and 3.5 mm in length and 2.5 mm and 3.0 mm in width (Table 28).

The testes of the above seven male hybrids were very abnormal in inner structure. In two hybrids (Nos. 1 and 4), the left testes scarcely contained any germ cells and were filled with hypertrophied stromatic cells. The other five

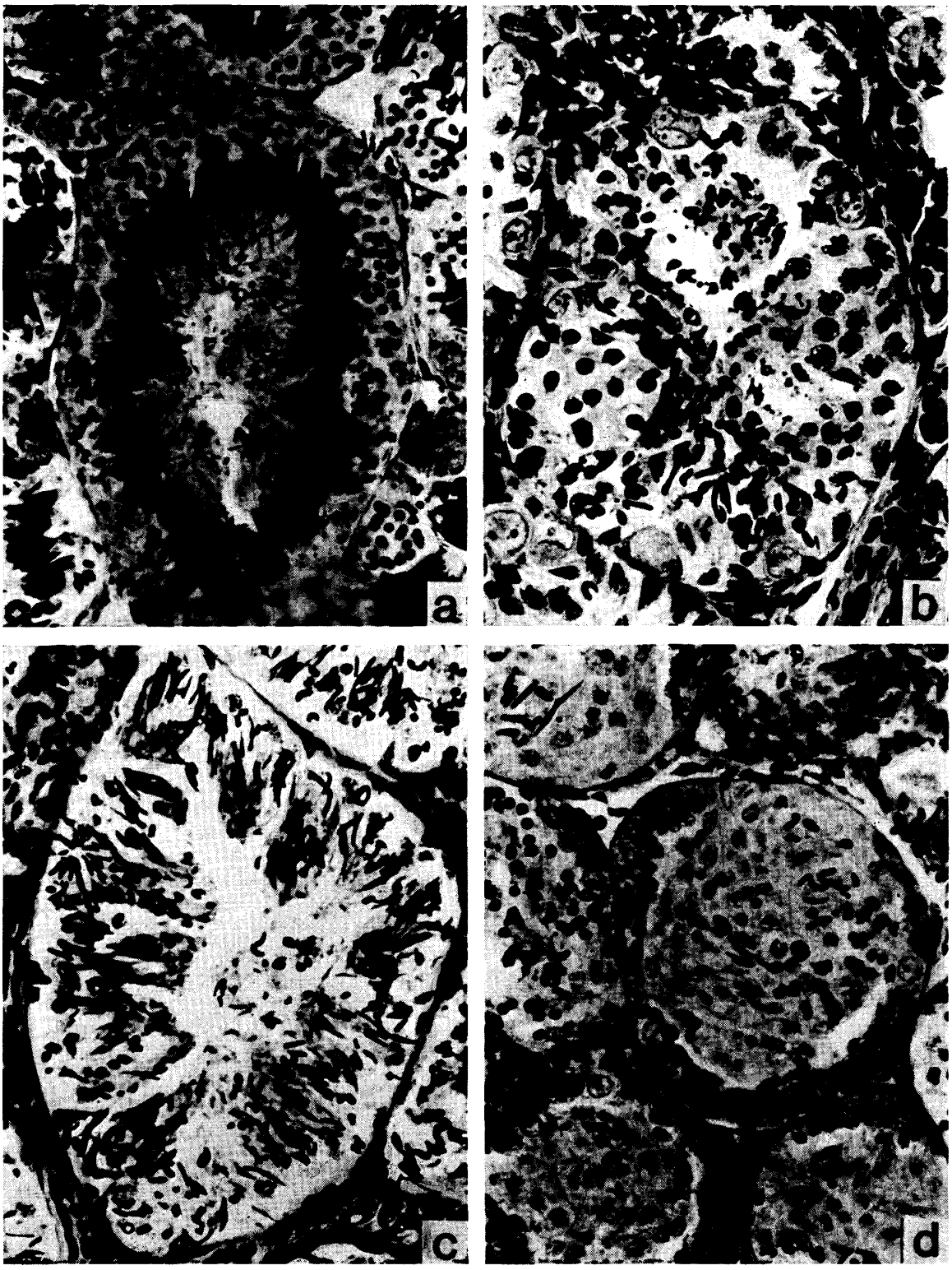


Fig. 32. Cross-sections of the testes of male hybrids between female *Rana dybowskii* from Tsushima and males of three species, and the control male. All the hybrids were one year old. ×350

a. Control *Rana dybowskii* from Tsushima ♂ No. 1, *Rana dybowskii* from Tsushima ♀ No. 2 × *Rana dybowskii* from Tsushima ♂ No. 2, produced in 1970.
b. Hybrid ♂ No. 2, *Rana dybowskii* from Tsushima ♀ No. 1 × *Rana japonica* ♂ No. 1, produced in 1970.
c. Hybrid ♂ No. 1, *Rana dybowskii* from Tsushima ♀ No. 1 × *Rana ornativentris* ♂ No. 1, produced in 1970.
d. Hybrid ♂ No. 1, *Rana dybowskii* from Tsushima ♀ No. 2 × *Rana chensinensis* ♂ No. 2, produced in 1970.

hybrids had no normal spermatozoa in their testes. The seminiferous tubules contained some abnormal spermatozoa and pycnotic cells in addition to spermatogonia and first spermatocytes (Fig. 32b).

c. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana ornativentris*♂

Five 1-year-old male hybrids (Nos. 1～5) produced in 1970 were 38.5～43.5 mm, 41.7 mm on the average, in body length. The left testes of these males were 3.0～4.0 mm, 3.4 mm on the average, in length and 2.0 or 2.5 mm, 2.2 mm on the average, in width. The right testes were used in backcross experiments of 1971 without measuring of their size. Five 1.5-year-old male hybrids (Nos. 6～10) produced in the same year were 36.5～46.0 mm, 42.4 mm on the average, in body length. The left testes of these males were 2.0～4.0 mm, 3.0 mm on the average, in length and 1.5～2.5 mm, 2.1 mm on the average, in width, while the right testes were 2.0～4.0 mm, 3.0 mm on the average, in length and 1.0～2.5 mm, 2.0 mm on the average, in width. Five 2-year-old male hybrids (Nos. 11～15) produced in 1970 were 45.5～50.5 mm, 47.1 mm on the average, in body length. The left testes of these males were 3.0 or 3.5 mm, 3.3 mm on the average, in length and 2.0～3.0 mm, 2.6 mm on the average, in width. The right testes were 3.0 or 3.5 mm, 3.4 mm on the average, in length and 2.0～3.0 mm, 2.5 mm on the average, in width, although one male (No. 14) had no right testis (Table 28).

The testes of the five 1-year-old and five 2-year-old male hybrids were examined and it was found that all of them were very abnormal in inner structure. The seminiferous tubules contained no normal spermatozoa. In place of the latter, there were some abnormal spermatozoa and pycnotic nuclei. Besides, there were spermatogonia and first spermatocytes (Fig. 32c).

d. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana chensinensis*♂

Two 1-year-old male hybrids (Nos. 1 and 2) produced in 1970 were 39.5 mm and 40.0 mm in body length. The left testes of these males were 4.0 mm and 1.5 mm in length and 2.0 mm and 1.0 mm in width. The right testes were used in backcross experiments without measuring of their size. Three 1.5-year-old male hybrids (Nos. 3～5) produced in the same year were 36.5～40.5 mm in body length. The left testes of these males were 2.5 or 3.0 mm in length and 1.5 or 2.5 mm in width, while the right testes were 2.5 or 3.0 mm in length and 1.0～2.5 mm in width. Two 2-year-old male hybrids (Nos. 6 and 7) produced in 1970 were 44.0 mm and 38.5 mm in body length. The left testes of these males were 4.0 and 3.5 mm in length and 2.5 and 2.0 mm in width, while the right testes were 6.0 and 3.5 mm in length and 2.5 and 2.0 mm in width (Table 28).

The testes of the above seven male hybrids were very abnormal in inner structure. Normal spermatozoa were never found in the seminiferous tubules. There were some abnormal spermatozoa and pycnotic nuclei beside spermatogonia and first spermatocytes (Fig. 32d).

e. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana temporaria*♂

Two 2-year-old male hybrids (Nos. 1 and 2) produced in 1975 were 50.5 mm and 56.0 mm in body length. The left testes of these males were 3.5 mm and 4.0 mm in length and 2.5 mm and 3.0 mm in width, while the right testes were 4.0 mm and 3.5 mm in length and 2.5 mm in width (Table 28).

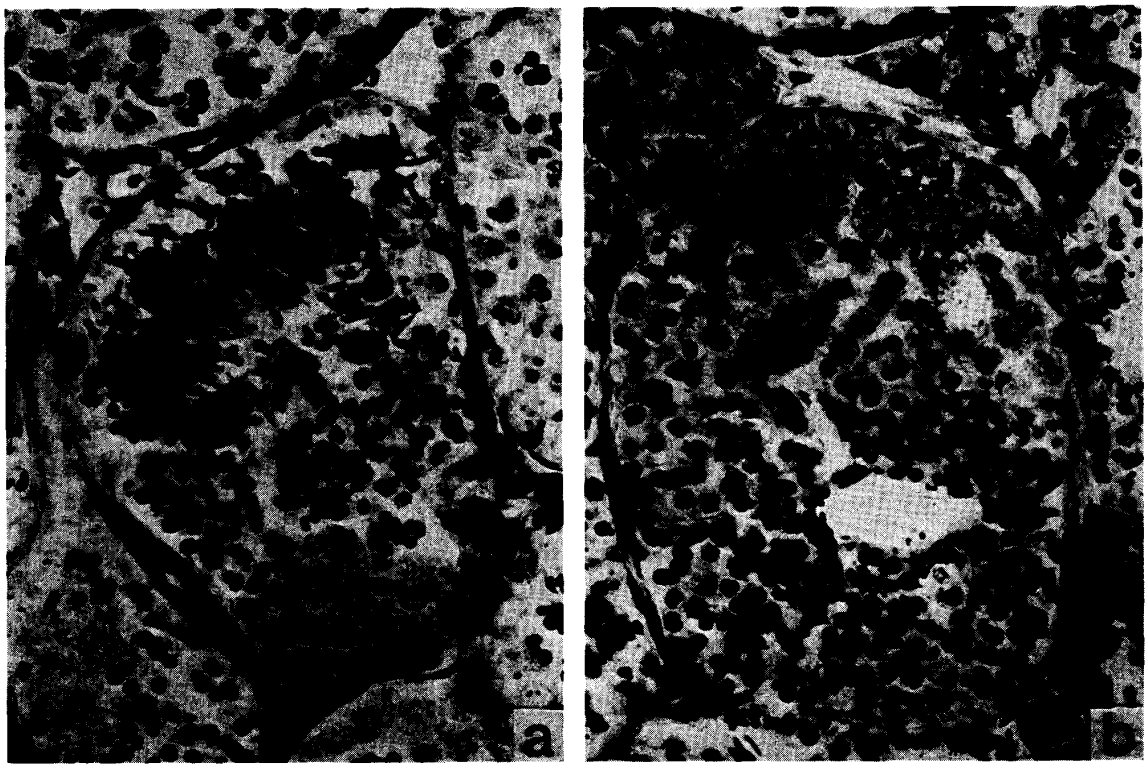


Fig. 33. Cross-sections of the testes of male hybrids between a female *Rana dybowskii* from Tsushima and a male *Rana temporaria*. All the hybrids were two years old. ×350

a. Hybrid ♂ No. 1, *Rana dybowskii* from Tsushima ♀ No. 1 × *Rana temporaria* ♂ No. 1, produced in 1975.

b. Hybrid ♂ No. 2, *Rana dybowskii* from Tsushima ♀ No. 1 × *Rana temporaria* ♂ No. 1, produced in 1975.

The testes of these two male hybrids were very abnormal in inner structure and contained no normal spermatozoa. One male (No. 1) had loose bundles of large abnormally shaped spermatozoa in a part of the seminiferous tubules (Fig. 33a). In the most parts of the latter, there were many abnormal spermatozoa distributed sparsely as well as many pycnotic nuclei. Along the inner wall of seminiferous tubules, there were spermatogonia and first spermatocytes. The other male hybrid (No. 2) had a few abnormal spermatozoa and many pycnotic cells in addition to spermatogonia and first spermatocytes (Fig. 33b).

7. Interspecific hybrids between female *Rana dybowskii* from Korea and males of four species

a. Hybrids, *Rana dybowskii* from Korea ♀ × *Rana japonica* ♂

Three 1.5-year-old male hybrids (Nos. 1~3) produced in 1970 were 33.5 or 39.0 mm in body length. The left and right testes of these males were 2.5 or

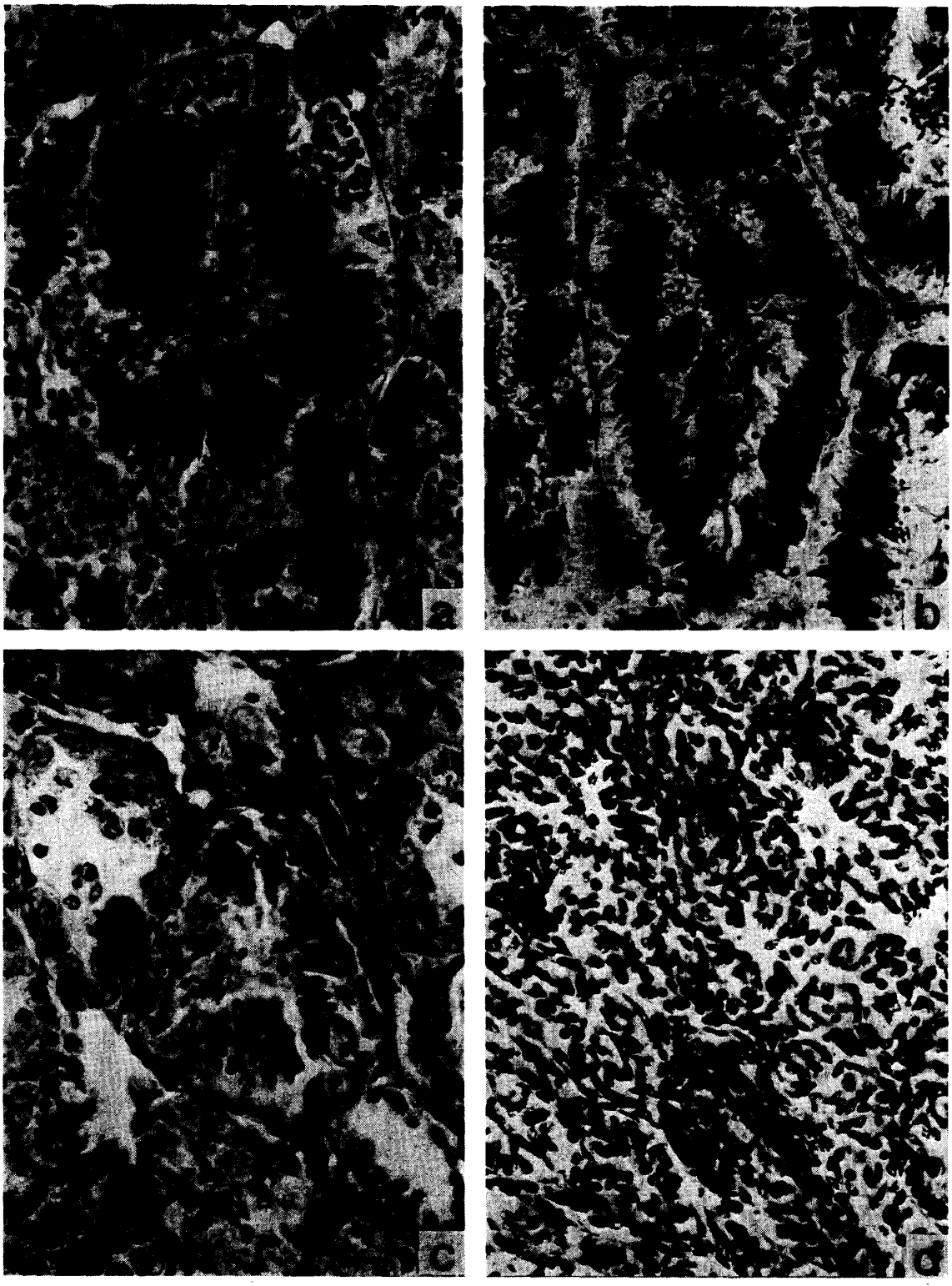


Fig. 34. Cross-sections of the testes of male hybrids between female *Rana dybowskii* and males of three species, and the control male. ×350

a. Intraspecific hybrid ♂ No. 5, *Rana dybowskii* from Tsushima ♀ No. 3 × *Rana dybowskii* from Korea ♂ No. 3, produced in 1970. One and a half years old.
b. Control *Rana dybowskii* from Korea ♂ No. 2, *Rana dybowskii* from Korea ♀ No. 3 × *Rana dybowskii* from Korea ♂ No. 3, produced in 1970. One year old.
c. Interspecific hybrid ♂ No. 1, *Rana dybowskii* from Korea ♀ No. 3 × *Rana japonica* ♂ No. 3, produced in 1970. One and a half years old.
d. Interspecific hybrid ♂ No. 3, *Rana dybowskii* from Korea ♀ No. 3 × *Rana japonica* ♂ No. 3, produced in 1970. One and a half years old.

3.0 mm in length and 2.0 or 2.5 mm in width. Two 2-year-old male hybrids were 42.5 mm and 43.0 mm in body length. The left testes of these males were 4.5 mm in length and 3.0 or 3.5 mm in width, while the right testes were 3.0 and 4.5 mm in length and 2.5 and 3.5 mm in width (Table 29).

The testes of the above five male hybrids were very abnormal in inner structure. All the testes had no normal spermatozoa. Especially, germ cells had almost completely degenerated in the testes of one male (No. 3). The seminiferous tubules were filled with hypertrophied stromatic cells (Fig. 34d). The other four male hybrids had some abnormal spermatozoa and pycnotic nuclei in addition to spermatogonia and first spermatocytes in the seminiferous tubules (Fig. 34c).

TABLE 29

Testes of mature male hybrids between female *Rana dybowskii* from Korea and males of four species

Year	Parents		Individual no.	Age	Body length	Size of testes		Remarks
	Female	Male		year(s)	mm	Left mm	Right mm	
1970	*dyb.* K. No. 3	*jap.* No. 3	1	1.5	39.0	3.0×2.5	2.5×2.0	
			2	1.5	33.5	3.0×2.0	3.0×2.5	
			3	1.5	39.0	2.5×2.0	2.5×2.0	
			4	2	42.5	4.5×3.5	4.5×3.5	Fert. test in 1972
			5	2	43.0	4.5×3.0	3.0×2.5	Fert. test in 1972
1970	*dyb.* K. No. 2	*ornat.* No. 2	1	1	42.5	4.0×2.5		Fert. test in 1971
1970	*dyb.* K. No. 3	*ornat.* No. 3	2	1	46.5	3.5×2.5		Fert. test in 1971
			3	1	44.0	3.0×2.0		Fert. test in 1971
			4	1	40.5	2.0×1.0		Fert. test in 1971
			5	1	46.0	2.5×2.0		Fert. test in 1971
1970	*dyb.* K. No. 2	*ornat.* No. 2	6	1.5	42.5	3.5×2.0	3.5×2.0	
1970	*dyb.* K. No. 3	*ornat.* No. 3	7	1.5	43.5	1.0×0.5	3.0×2.0	
			8	1.5	45.5	0.5×0.5	2.5×2.0	
			9	1.5	45.0	1.0×0.5	2.0×1.5	
			10	1.5	41.5	1.0×0.5	2.0×1.5	
			11	1.5	44.5	4.5×2.0	3.0×2.5	
			12	1.5	40.0	2.5×1.5	1.5×1.5	
			13	1.5	47.0	3.0×2.5	2.5×2.5	
			14	1.5	46.5	2.0×1.5	2.5×2.0	
1970	*dyb.* K. No. 2	*ornat.* No. 2	15	2	46.0	4.5×3.5	4.0×3.0	Fert. test in 1972
1970	*dyb.* K. No. 3	*ornat.* No. 3	16	2	48.5	4.5×3.5	4.5×3.5	Fert. test in 1972
1970	*dyb.* K. No. 4	*ornat.* No. 4	17	2	49.0	5.0×3.5	5.0×3.5	Fert. test in 1972
			18	2	48.0	0.5×0.5	5.0×3.5	Fert. test in 1972
			19	2	45.5	2.5×2.0	2.5×2.0	
1970	*dyb.* K. No. 6	*tsu.* No. 6	1	2	37.5	Very small	4.0×3.0	Fert. test in 1972
1970	*dyb.* K. No. 3	*chen.* No. 3	1	1	43.0	4.0×2.5		Fert. test in 1971
1970	*dyb.* K. No. 4	*chen.* No. 4	2	1	42.5	4.0×2.5		Fert. test in 1971
1970	*dyb.* K. No. 3	*chen.* No. 3	3	1.5	45.0	3.5×2.5	3.5×2.0	
			4	1.5	38.0	3.0×1.0	3.0×1.5	
1970	*dyb.* K. No. 4	*chen.* No. 4	5	1.5	42.5	3.0×2.0	3.0×2.0	
			6	1.5	45.5	2.5×1.5	2.5×1.5	
1970	*dyb.* K. No. 3	*chen.* No. 3	7	2	47.0	Very small	4.0×3.0	Fert. test in 1972
			8	2	51.5	4.5×3.5	4.5×3.5	Fert. test in 1972
1970	*dyb.* K. No. 4	*chen.* No. 4	9	2	48.5	2.5×1.5	2.5×1.5	Fert. test in 1972
			10	2	50.0	4.0×2.5	4.0×2.5	Fert. test in 1972

b. Hybrids, *Rana dybowskii* from Korea♀ × *Rana ornativentris*♂

Five 1-year-old male hybrids (Nos. 1～5) produced in 1970 were 40.5～46.5 mm, 43.9 mm on the average, in body length. The left testes of these males were 2.0～4.0 mm, 3.0 mm on the average, in length and 1.0～2.5 mm, 2.0 mm on the average, in width. The right testes were used in backcross experiments in 1971 without measuring of their size. Nine 1.5-year-old male hybrids (Nos. 6～14) produced in the same year were 40.0～47.0 mm, 44.0 mm on the average, in body length. While the left testes of four males (Nos. 7～10) were very small, that is, 0.5 or 1.0 mm in length and 0.5 mm in width, those of the other five males were 2.0～4.5 mm, 3.1 mm on the average, in length and 1.5～2.5 mm, 1.9 mm on the average, in width. The right testes of the nine 1.5-year-old males were 1.5～3.5 mm, 2.5 mm on the average, in length and 1.5～2.5 mm, 1.9 mm on the average, in width. Five 2-year-old male hybrids (Nos. 15～19) produced in 1970 were 45.5～49.0 mm, 47.4 mm on the average, in body length. While the left testis of one male (No. 18) was very small, that is, 0.5 mm in both length and width, those of the other four males were 2.5～5.0 mm, 4.1 mm on the average, in length and 2.0 or 3.5 mm, 3.1 mm on the average, in width. The right testes of the five males were 2.5～5.0 mm, 4.2 mm on the average, in length and 2.0～3.5 mm, 3.1 mm on the average, in width (Table 29).

The testes of the above 19 male hybrids were very abnormal in inner structure. Normal spermatozoa were scarce in the seminiferous tubules. The latter contained abnormal spermatozoa, pycnotic nuclei in addition to spermatogonia and first spermatocytes at various stages of reduction division (Fig. 35b). The testis of male No. 18 was very degenerative in inner structure.

c. Hybrid, *Rana dybowskii* from Korea♀ × *Rana tsushimensis*♂

A 2-year-old hybrid (No. 1) produced in 1970 was 37.5 mm in body length. While the left testis was very small, the right one was 4.0 mm in length and 3.0 mm in width (Table 29). These testes were very abnormal in inner structure and contained no normal spermatozoa. There were some abnormal spermatozoa and pycnotic nuclei in addition to spermatogonia and first spermatocytes in the seminiferous tubules.

d. Hybrids, *Rana dybowskii* from Korea♀ × *Rana chensinensis*♂

Two 1-year-old male hybrids (Nos. 1 and 2) produced in 1970 were 43.0 mm and 42.5 mm in body length. The left testes of these males were 4.0 mm in length and 2.5 mm in width. The right testes were used in backcross experiments of 1971 without measuring of their size. Four 1.5-year-old male hybrids (Nos. 3～6) produced in the same year were 38.0～45.5 mm, 42.8 mm on the average, in body length. The left and right testes of these males were 2.5～3.5 mm, 3.0 mm on the average, in length and 1.0～2.5 mm, 1.8 mm on the average, in width. Four 2-year-old male hybrids (Nos. 7～10) produced in 1970 were 47.0～51.5 mm, 49.3 mm on the average, in body length. While the left testis of one male (No. 7) was very small, those of the other three males were 2.5～

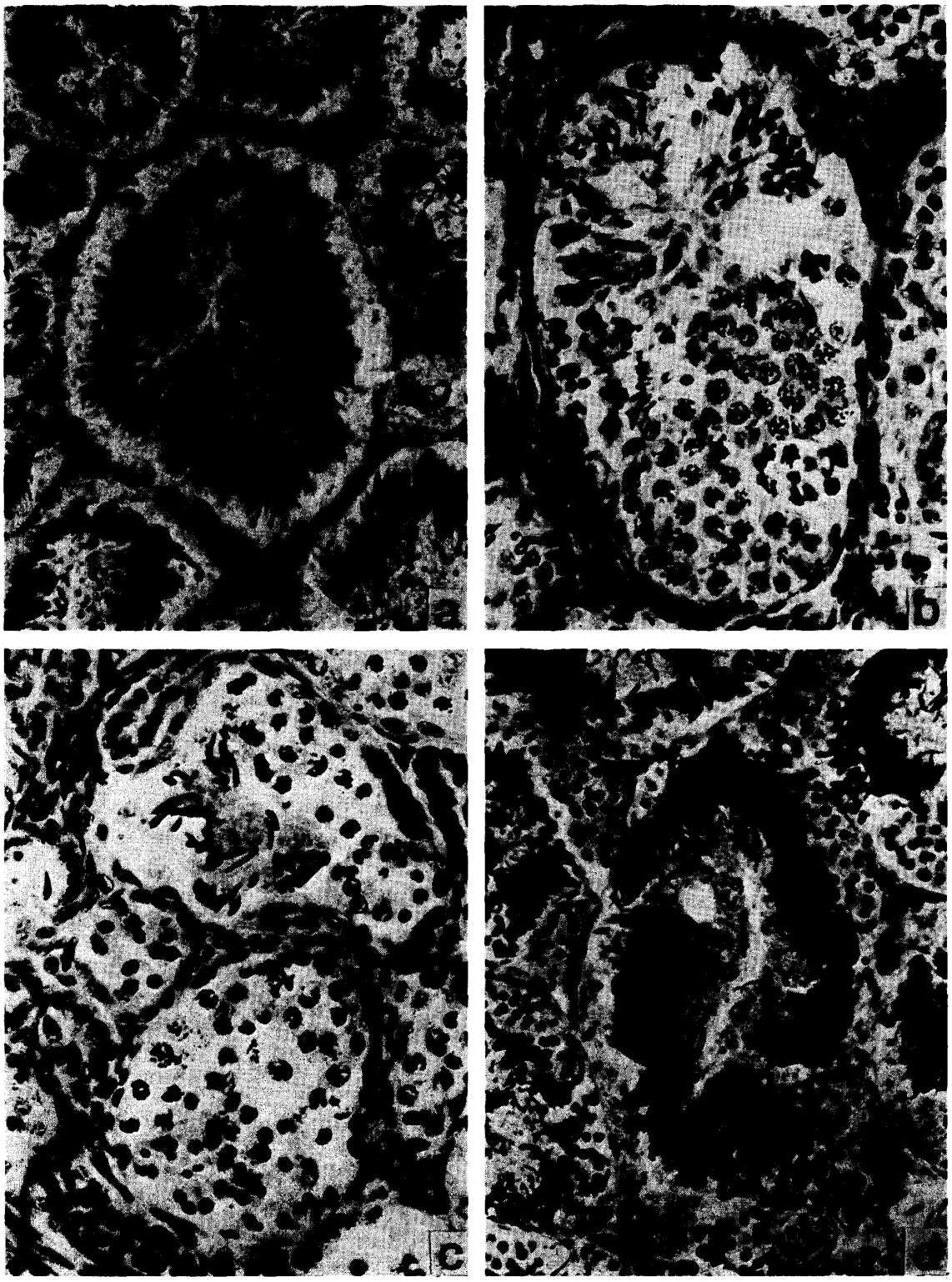


Fig. 35. Cross-sections of the testes of male hybrids between female *Rana dybowskii* from Korea and males of two species, and the control male. All the hybrids were one year old. ×350

a. Control *Rana ornativentris* ♂ No. 2, *Rana ornativentris* ♀ No. 1 × *Rana ornativentris* ♂ No. 1, produced in 1970.
b. Interspecific hybrid ♂ No. 1, *Rana dybowskii* from Korea ♀ No. 2 × *Rana ornativentris* ♂ No. 2, produced in 1970.
c. Interspecific hybrid ♂ No. 1, *Rana dybowskii* from Korea ♀ No. 3 × *Rana chensinensis* ♂ No. 3, produced in 1970.
d. Intraspecific hybrid ♂ No. 2, *Rana dybowskii* from Korea ♀ No. 3 × *Rana dybowskii* from Tsushima ♂ No. 3, produced in 1970.

4.5 mm, 3.7 mm on the average, in length and 1.5~3.5 mm, 2.5 mm on the average, in width. The right testes of the four males were 2.5~4.5 mm, 3.8 mm on the average, in length and 1.5~3.5 mm, 2.6 mm on the average, in width (Table 29).

The testes of the above 10 male hybrids were very abnormal in inner structure and contained no normal spermatozoa. In the seminiferous tubules, there were some abnormal spermatozoa and pycnotic nuclei in addition to spermatogonia and first spermatocytes at various stages of reduction division (Fig. 35c).

8. Interspecific hybrids between female *Rana arvalis* and males of four species

a. Controls, *Rana arvalis*♀ × *Rana arvalis*♂

Two 2-year-old males (Nos. 1 and 2) produced in 1962 were 55.5 mm and 54.0 mm in body length. The left testes of these males were 4.5 mm in length and 3.0 or 3.5 mm in width, while the right testes were 4.0 or 4.5 mm in length and 3.0 mm in width. Another 1-year-old male (No. 3) produced in 1976 was 40.5 mm in body length and had testes which were 3.0 mm in length and 2.0 mm in width (Table 30).

The testes of these males were completely normal in inner structure. The seminiferous tubules were filled with compact bundles of normal spermatozoa, although the testes of the 1-year-old male (No. 3) were slightly immature.

TABLE 30

Testes of mature male hybrids between *Rana arvalis* and males of four species, and the controls

Year	Parents		Individual no.	Age year(s)	Body length mm	Size of testes Left mm	Size of testes Right mm	Remarks
	Female	Male						
1962	*arv.* No. 1	*arv.* No. 1	1	2	55.5	4.5×3.5	4.5×3.0	Fert. test in 1964
			2	2	54.0	4.5×3.0	4.0×3.0	Fert. test in 1964
1976	*arv.* No. 1	*arv.* No. 1	3	1	40.5	3.0×2.0	3.0×2.0	
1962	*arv.* No. 2	*jap.* No. 2	1	2	43.5	3.5×3.0	3.5×2.5	Fert. test in 1964
			2	2	48.5	4.0×3.0	4.0×3.0	Fert. test in 1964
			3	2	44.5	3.5×2.5	3.5×2.5	
1962	*arv.* No. 3	*jap.* No. 3	4	2	47.0	4.5×3.5	4.5×3.0	Fert. test in 1964
			5	2	46.0	4.0×3.5	4.0×3.5	
1962	*arv.* No. 2	*ornat.* No. 1	1	2	43.0	3.5×2.5	3.5×2.5	Fert. test in 1964
			2	2	46.0	4.0×3.0	4.0×3.0	Fert. test in 1964
			3	2	45.5	4.5×3.5	3.5×2.0	Fert. test in 1964
			4	2	39.5	3.5×2.0	3.0×2.5	
			5	2	47.5	5.0×3.5	4.5×2.5	
1976	*arv.* No. 1	*ornat.* No. 1	6	1	46.0	1.5×1.0	1.5×1.0	
1976	*arv.* No. 1	*chen.* No. 1	1	1	50.0	2.0×1.5	2.0×1.0	
			2	1	53.0	2.5×2.0	2.5×1.5	
			3	1	50.5	2.5×1.5	2.5×1.5	
			4	1	53.5	3.0×2.0	2.5×2.0	
			5	1	49.0	2.0×1.5	2.0×1.0	
			6	1	52.5	3.0×1.0	3.0×1.0	
1977	*arv.* No. 1	*tsu.* No. 1	1	1	42.0	1.5×1.0	2.5×1.0	

b. Hybrids, *Rana arvalis*♀ × *Rana japonica*♂

Five 2-year-old male hybrids produced in 1962 were 43.5～48.5 mm, 45.9 mm on the average, in body length. The left testes of these males were 3.5～4.5 mm, 3.9 mm on the average, in length and 2.5～3.5 mm, 3.1 mm on the average, in width, while the right testes were 3.5～4.5 mm, 3.9 mm on the average, in length and 2.5～3.5 mm, 2.9 mm on the average, in width (Table 30).

The testes of these male hybrids were very abnormal in inner structure and had no normal spermatozoa. In the seminiferous tubules, there were some abnormal spermatozoa, pycnotic nuclei and first spermatocytes degenerating at the metaphase or anaphase of reduction division. Besides, there were first spermatocytes and spermatogonia situated along the inner wall of seminiferous tubules.

c. *Rana arvalis*♀ × *Rana ornativentris*♂

Five 2-year-old male hybrids (Nos. 1～5) produced in 1962 were 39.5～47.5 mm, 44.3 mm on the average, in body length. The left testes of these males were 3.5～5.0 mm, 4.1 mm on the average, in length and 2.0～3.5 mm, 2.9 mm on the average, in width, while the right testes were 3.0～4.5 mm, 3.7 mm on the average, in length and 2.0～3.0 mm, 2.5 mm on the average, in width (Table 30). One 1-year-old male hybrid produced in 1976 was 46.0 mm in body length and had small testes which were 1.5 mm in length and 1.0 mm in width.

The testes of the above six male hybrids were very abnormal in inner structure. There were no normal spermatozoa in the seminiferous tubules. The latter contained some abnormal spermatozoa and pycnotic nuclei in addition to spermatogonia and first spermatocytes (Fig. 36a).

d. Hybrids, *Rana arvalis*♀ × *Rana chensinensis*♂

Six 1-year-old male hybrids (Nos. 1～6) produced in 1976 were 49.0～53.5 mm, 51.4 mm on the average, in body length. The left testes were 2.0～3.0 mm, 2.5 mm on the average, in length and 1.0～2.0 mm, 1.6 mm on the average, in width, while the right testes were 2.0～3.0 mm, 2.4 mm on the average, in length and 1.0～2.0 mm, 1.3 mm on the average, in width (Table 30).

The testes of these male hybrids were very abnormal in inner structure and had no normal spermatozoa. In the seminiferous tubules, there were some abnormal spermatozoa, pycnotic nuclei and small or large masses of pycnotic nuclei in addition to spermatogonia and first spermatocytes situated along the inner wall (Fig. 36c).

e. Hybrid, *Rana arvalis*♀ × *Rana tsushimensis*♂

A 1-year-old male hybrid (No. 1) produced in 1977 was 42.0 mm in body length. The left testis was 1.5 mm in length and 1.0 mm in width, while the right testis was 2.5 mm in length and 1.0 mm in width (Table 30).

The testes were very abnormal in inner structure and had no normal spermatozoa. The seminiferous tubules contained some abnormal spermatozoa and pycnotic nuclei in addition to spermatogonia and first spermatocytes situated

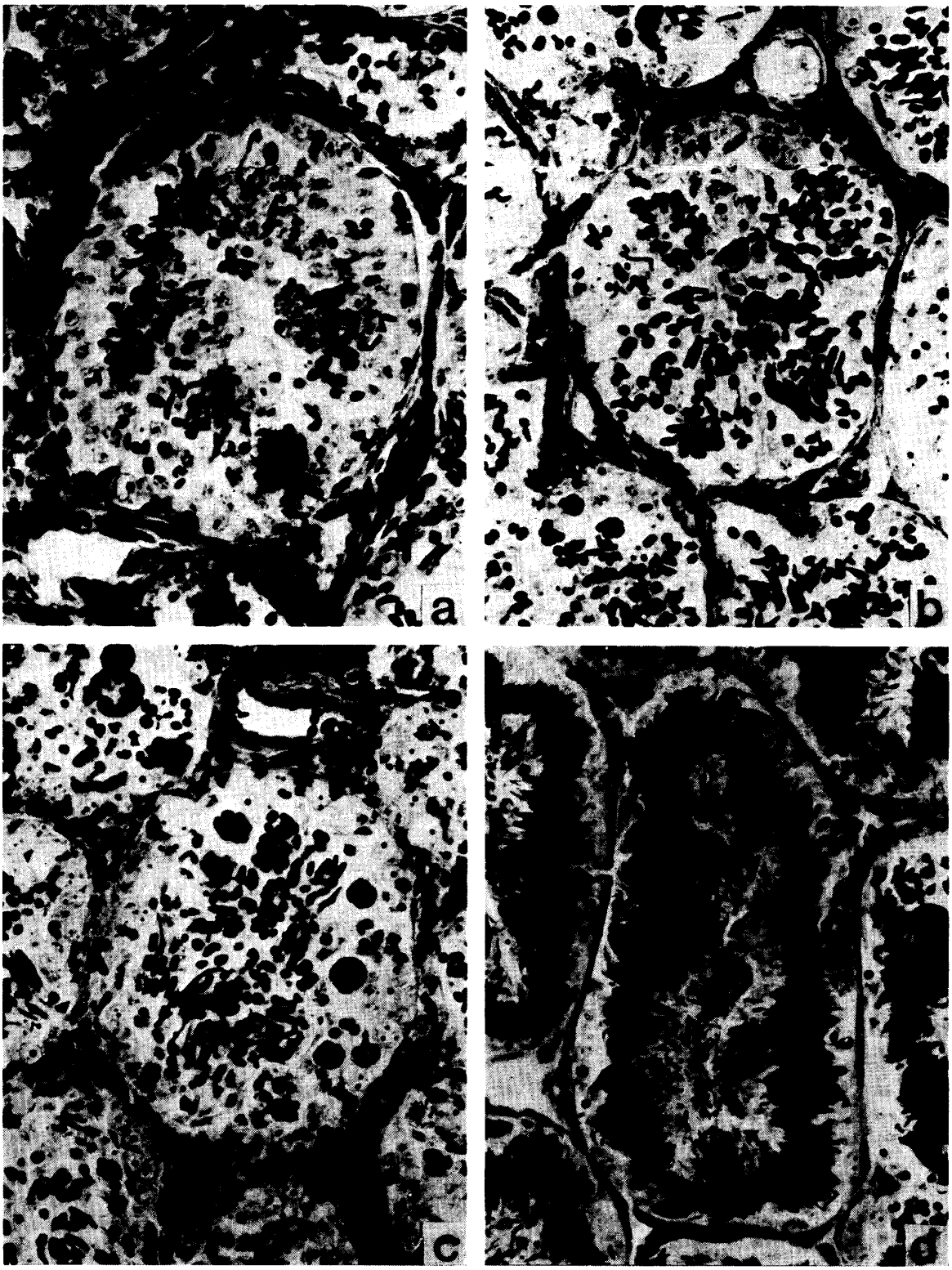


Fig. 36. Cross-sections of the testes of male hybrids between female *Rana arvalis* and males of three species, and the control male. All the hybrids were one year old. ×350

a. Hybrid ♂ No. 6, *Rana arvalis* ♀ No. 1 × *Rana ornativentris* ♂ No. 1, produced in 1976.
b. Hybrid ♂ No. 1, *Rana arvalis* ♀ No. 1 × *Rana tsushimensis* ♂ No. 1, produced in 1977.
c. Hybrid ♂ No. 4, *Rana arvalis* ♀ No. 1 × *Rana chensinensis* ♂ No. 1, produced in 1976.
d. Control *Rana chensinensis* ♂ No. 1, *Rana chensinensis* ♀ No. 1 × *Rana chensinensis* ♂ No. 1, produced in 1970.

along the inner wall (Fig. 36b).

VI. Reproductive capacity

1. Interspecific hybrids between female *Rana japonica* and males of four species

a. Controls, *Rana japonica*♀ × *Rana japonica*♂

Two 2-year-old males (Nos. 3 and 4) produced in 1962 from female *jap.* No. 1 and male *jap.* No. 1 (Table 24) and one 2-year-old male (No. 7) produced in 1962 from female *jap.* No. 3 and male *jap.* No. 3 (Table 24) were mated in the breeding season of 1964 with three 2-year-old females (Nos. 1～3) which had been produced in 1962 from female *jap.* No. 1 and male *jap.* No. 1. It was found that 294 (92.7%) of 317 eggs in total cleaved normally, 276 (87.1%) hatched normally and 272 (85.8%) became normally feeding tadpoles.

b. Hybrids, *Rana japonica*♀ × *Rana ornativentris*♂

Three 2-year-old male hybrids (Nos. 3～5) produced in 1962 from female *jap.* No. 1 and male *ornat.* No. 1 (Table 24) were backcrossed in 1964 with the same three female *Rana japonica* as those used in the control matings. The results showed that none of 523 eggs cleaved.

c. Hybrids, *Rana japonica*♀ × *Rana chensinensis*♂

Three 2-year-old male hybrids (Nos. 3～5) produced in 1962 from female *jap.* No. 3 and male *chen.* No. 3 (Table 24) were backcrossed in 1964 with the same three female *Rana japonica* as those used in the control matings. It was found that none of 642 eggs cleaved.

d. Hybrids, *Rana japonica*♀ × *Rana temporaria*♂

A 2-year-old male hybrid (No. 3) produced in 1962 from female *jap.* No. 1 and male *temp.* No. 1 (Table 24) and three 2-year-old male hybrids (Nos. 9～11) produced in 1962 from female *jap.* No. 3 and male *temp.* No. 2 (Table 24) were backcrossed in 1964 with the same three female *Rana japonica* as those used in the control matings. It was found that none of 895 eggs cleaved.

e. Hybrids, *Rana japonica*♀ × *Rana arvalis*♂

Three 2-year-old male hybrids (Nos. 1～3) produced in 1962 from female *jap.* No. 1 and male *arv.* No. 1 (Table 24) were backcrossed in 1964 with the same three female *Rana japonica* as those used in the control matings. It was found that none of 544 eggs cleaved.

2. Interspecific hybrids between female *Rana ornativentris* and males of two species

a. Controls, *Rana ornativentris*♀ × *Rana ornativentris*♂

One 2-year-old male (No. 1) and two 2-year-old females (Nos. 1 and 2) produced in 1962 from female *ornat.* No. 1 and male *ornat.* No. 1 were mated in 1964 (Table 25). The results showed that 147 (96.1%) of 153 eggs cleaved normally, 145 (94.8%) hatched normally and 141 (92.2%) became normally feeding tadpoles.

Three 2-year-old males (Nos. 4~6) and three 2-year-old females (Nos. 1~3) produced in 1965 from female *ornat.* No. 1 and male *ornat.* No. 1 were mated in 1967 (Table 25). It was found that 191 (94.1%) of 203 eggs cleaved normally, 186 (91.6%) hatched normally and 184 (90.6%) became normally feeding tadpoles.

b. Hybrids, *Rana ornativentris*♀ × *Rana chensinensis*♂

Three 2-year-old male hybrids (Nos. 3~5) produced in 1962 from female *ornat.* No. 1 and male *chen.* No. 1 (Table 25) were backcrossed in 1964 with the same two females as those used in the control matings of 1964. The results showed that none of 421 eggs cleaved.

c. Hybrids, *Rana ornativentris*♀ × *Rana temporaria*♂

Two 2-year-old male hybrids (Nos. 1 and 2) produced in 1962 from female *ornat.* No. 1 and male *temp.* No. 1 (Table 25) were backcrossed in 1964 with the same two females (Nos. 1 and 2) as those used in the control matings of 1964. It was found that none of 370 eggs cleaved.

Two 2-year-old male hybrids (Nos. 6 and 10) produced in 1965 from female *ornat.* No. 1 and male *temp.* No. 1 (Table 25) were backcrossed in 1967 with the same three females (Nos. 1~3) as those used in the control matings of 1967. The results showed that none of 364 eggs cleaved.

3. Interspecific hybrids between female *Rana chensinensis* and males of three species

a. Controls, *Rana chensinensis*♀ × *Rana chensinensis*♂

Two 2-year-old females (Nos. 1 and 2) and two 2-year-old males (Nos. 1 and 2) produced in 1962 from female *chen.* No. 1 and male *chen.* No. 1 (Table 26) were mated in 1964. It was found that 132 (94.3%) of 140 eggs cleaved normally, 93 (66.4%) hatched normally and 76 (54.3%) became normally feeding tadpoles.

b. Hybrids, *Rana chensinensis*♀ × *Rana japonica*♂

Two 2-year-old male hybrids (Nos. 1 and 2) produced in 1962 from female *chen.* No. 1 and male *jap.* No. 1 (Table 26) were backcrossed in 1964 with the same two females as those used in the control matings. The results showed that none of 403 eggs in total cleaved.

c. Hybrids, *Rana chensinensis*♀ × *Rana ornativentris*♂

Three 2-year-old male hybrids (Nos. 3~5) produced in 1962 from female

chen. No. 1 and male *ornat.* No. 1 (Table 26) were backcrossed in 1964 with the same two females as those used in the control matings of 1964. None of 526 eggs cleaved.

d. Hybrids, *Rana chensinensis*♀ × *Rana arvalis*♂

Three 2-year-old male hybrids (Nos. 4~6) produced in 1962 from female *chen.* No. 1 and male *arv.* No. 1 (Table 26) were backcrossed in 1964 with the same two females as those used in the control matings of 1964. It was found that none of 597 eggs cleaved.

4. Intraspecific hybrids of *Rana dybowskii* from Tsushima and Korea

a. Controls

i) *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Tsushima♂

In 1971, two 1-year-old males (Nos. 1 and 2) produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* T. No. 2 (Table 27) and one 1-year-old male (No. 3) produced in the same year from female *dyb.* T. No. 6 and male *dyb.* T. No. 6 (Table 27) were mated with a field-caught female from Tsushima (70.dyb.T.W♀ No. 1) which had been used in the crossing experiments of 1970. The results showed that 154 (60.9%) of 253 eggs cleaved normally. Nearly half of the normally cleaved eggs attained completion of metamorphosis. This low developmental capacity of eggs as well as the low cleavage rate may be attributable to incomplete sexual maturity of the males, as the latter were one year old.

Three 2-year-old males (Nos. 4~6) and three 2-year-old females (Nos. 1~3) produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* T. No. 2 (Table 27) were mated in 1972 (Table 31). The results showed that 93.7~99.0% of the respective number of eggs in three control series, 327 (96.7%) of 338 eggs in total, cleaved normally, 81.0~99.0%, 306 (90.5%) in total, hatched normally and 77.5~91.3%, 287 (84.9%) in total, attained completion of metamorphosis.

Of the metamorphosed frogs, the sex of 137 was examined at the juvenile stage. Of these frogs, 68 were females, 3 were hermaphrodites and 66 were males. When the hermaphrodites were counted as males, 46.2~52.2%, 50.4% on the average, were males.

ii) *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Korea♂

In 1971, three 1-year-old males produced in 1970, including one from female *dyb.* K. No. 1 and male *dyb.* K. No. 1, one from female *dyb.* K. No. 3 and male *dyb.* K. No. 3 and one from female *dyb.* K. No. 4 and male *dyb.* K. No. 4 (Table 27) were mated with a field-caught female (70 *dyb.* T.W♀No. 1). The results showed that only 14 of 304 eggs cleaved normally. The normally cleaved eggs developed almost normally and completed metamorphosis. The paucity of normally cleaved eggs may be attributable to incomplete sexual maturity of the 1-year-old males.

In 1972, two 2-year-old males (Nos. 4 and 5) and two 2-year-old females (Nos. 1 and 2) produced in 1970 from female *dyb.* K. No. 4 and male *dyb.* K. No. 4 (Table 27) were mated. Of the respective number of eggs in two control matings,

78.4% and 84.7%, 112 (82.4%) of 136 eggs in total, cleaved normally, 54.9% and 25.9%, 50 (36.8%) in total, hatched normally and 31.4% and 21.2%, 34 (25.0%) in total, attained completion of metamorphosis (Table 32).

The sex of 30 of the 34 metamorphosed frogs was examined at the juvenile stage. It was found that 14 were females and 16 (53.3%) were males.

b. Intraspecific hybrids, *Rana dybowskii* from Tsushima♀ × *Rana dybowskii* from Korea♂

i) Matings with female *Rana dybowskii* from Tsushima

Four 2-year-old males (Nos. 6~9) produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* K. No. 2 were mated in 1972 with three 2-year-old females (Nos. 1~3) produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* T. No. 2 (Table 27). The results showed that 97.5~100% of the respective number of eggs in four mating series, 499 (99.0%) of 504 eggs, cleaved normally, 90.7~99.2%, 483 (95.8%) in total, hatched normally and 79.6~87.9%, 421 (83.5%) in total, attained completion of metamorphosis (Table 31).

TABLE 31

Developmental capacity and the sex of the offspring of intraspecific hybrids between a female *Rana dybowskii* from Tsushima and a male *Rana dybowskii* from Korea

Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of metamorphosed frogs	Sex of juvenile frogs			
Female	Male						Number	♀	⚥	♂(%)
(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 1	(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 4	104	103 (99.0%)	103 (99.0%)	103 (99.0%)	95 (91.3%)	65	32	3	30(50.8)
(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 2	(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 5	92	91 (98.9%)	88 (95.7%)	88 (95.7%)	82 (89.1%)	26	14	0	12(46.2)
(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 3	(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 6	142	133 (93.7%)	116 (81.7%)	115 (81.0%)	110 (77.5%)	46	22	0	24(52.2)
Total		338	327 (96.7%)	307 (90.8%)	306 (90.5%)	287 (84.9%)	137	68	3	66(50.4)
(*dyb.* T♀ × *dyb.* T♂)$_2$ Nos. 1~3	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 6	161	157 (97.5%)	146 (90.7%)	146 (90.7%)	135 (83.9%)	110	54	4	52(50.9)
	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 7	124	123 (99.2%)	123 (99.2%)	123 (99.2%)	109 (87.9%)	87	41	1	45(92.9)
	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 8	116	116 (100 %)	113 (97.4%)	113 (97.4%)	95 (81.9%)	57	25	7	25(56.1)
	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 9	103	103 (100 %)	102 (99.0%)	101 (98.1%)	82 (79.6%)	57	29	5	23(49.1)
Total		504	499 (99.0%)	484 (96.0%)	483 (95.8%)	421 (83.5%)	311	149	17	145(52.1)
(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 1	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 6	62	55 (88.7%)	54 (87.1%)	49 (79.0%)	42 (67.7%)	36	17	0	19(52.8)
(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 2	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 7	73	70 (95.9%)	65 (89.0%)	61 (83.6%)	52 (71.2%)	44	16	1	27(63.6)
(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 3	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 8	87	81 (93.1%)	69 (79.3%)	58 (66.7%)	42 (48.3%)	25	13	0	12(48.0)
(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 4	(*dyb.* T♀ × *dyb.* K♂)$_2$ No. 9	208	194 (93.3%)	176 (84.6%)	176 (84.6%)	161 (77.4%)	91	48	0	43(47.3)
Total		430	400 (93.0%)	364 (84.7%)	344 (80.0%)	297 (69.1%)	196	94	1	101(52.0)

dyb. T, *Rana dybowskii* from Tsushima *dyb.* K, *Rana dybowskii* from Korea

(*dyb.* T♀ × *dyb.* T♂)$_2$, *dyb.* T♀ No. 2 × *dyb.* T♂ No. 2

(*dyb.* T♀ × *dyb.* K♂)$_2$, *dyb.* T♀ No. 2 × *dyb.* K♂ No. 2

The sex of 311 of the metamorphosed frogs was examined at the juvenile stage. It was found that 149 were females, 17 were hermaphrodites and 145 were males. When the hermaphrodites were counted as males, 49.1～56.1% in the four mating series, 52.1% on the average, were males.

ii) Brother and sister matings

Four 2-year-old females (Nos. 1～4) and four 2-year-old males (Nos. 6～9) produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* K. No. 2 (Table 27) were mated in 1972 (Table 31). In four mating series, 88.7～95.9% of the respective number of eggs, 400 (93.0%) of 430 eggs in total, cleaved normally, 66.7～84.6%, 344 (80.0%) in total, hatched normally and 48.3～77.4%, 297 (69.1%) in total, attained completion of metamorphosis (Table 31).

The sex of 196 of the metamorphosed frogs was examined at the juvenile stage. It was found that 94 were females, one was a hermaphrodite and 101 were males. When the hermaphrodite was counted as a male, 47.3～63.6% in the four mating series, 52.0% on the average, were males.

c. Intraspecific hybrids, *Rana dybowskii* from Korea♀ × *Rana dybowskii* from Tsushima♂

i) Matings with female *Rana dybowskii* from Tsushima

In 1971, three 1-year-old males including one male produced in 1970 from female *dyb.* K. No. 1 and male *dyb.* T. No. 1 and two males produced in 1970 from female *dyb.* K. No. 3 and male dyb. T. No. 3 (Table 27) were mated with a field-caught female *Rana dybowskii* from Tsushima (70 *dyb.* T.W♀No. 1).

The results showed that only 39 of 242 eggs cleaved and hatched normally. The paucity of the normally cleaved eggs may be attributable to incomplete sexual maturity of the 1-year-old males.

In 1972, four 2-year-old male intraspecific hybrids (Nos. 8～11) produced in 1970 from female *dyb.* K. No. 4 and male *dyb.* T. No. 4 (Table 27) were mated with a 2-year-old female *Rana dybowskii* produced from female *dyb.* T. No. 2 and male *dyb.* T. No. 2 (No. 4).

As a control series of matings using female *Rana dybowskii* No. 4 from Tsushima, a 2-year-old male (No. 4) and a 2-year-old female (No. 4) produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* T. No. 2 were mated in 1972 (Table 32). It was found that all of 54 eggs cleaved normally, 53 (98.2%) hatched normally and 50 (92.6%) attained completion of metamorphosis. Of 48 metamorphosed frogs whose sex was examined at the juvenile stage, 21 were females, two were hermaphrodites and 25 were males. When hermaphrodites were counted as males, 56.3% were males.

Of the respective number of eggs of female *Rana dybowskii* No. 4 from Tsushima in three of four mating series which were mated with male intraspecific hybrids Nos. 8～11, 92.3～100%, 269 (96.1%) of 280 in total, cleaved normally, 85.7～96.8%, 255 (91.1%) in total, hatched normally and 69.2～86.0%, 222 (79.3%) in total, attained completion of metamorphosis (Table 32). In the remaining

TABLE 32

Developmental capacity and the sex of the offspring of intraspecific hybrids between a female *Rana dybowskii* from Korea and a male *Rana dybowskii* from Tsushima

Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of metamorphosed frogs	Sex of juvenile frogs			
Female	Male						Number	♀	♀♂	♂(%)
(*dyb.* K♀ × *dyb.* K♂)$_4$ No. 1	(*dyb.* K♀ × *dyb.* K♂)$_4$ No. 4	51	40 (78.4%)	28 (54.9%)	28 (54.9%)	16 (31.4%)	16	7	0	9(56.3)
(*dyb.* K♀ × *dyb.* K♂)$_4$ No. 2	(*dyb.* K♀ × *dyb.* K♂)$_4$ No. 5	85	72 (84.7%)	27 (31.8%)	22 (25.9%)	18 (21.2%)	14	7	0	7(50.0)
Total		136	112 (82.4%)	55 (40.4%)	50 (36.8%)	34 (25.0%)	30	14	0	16(53.3)
(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 4	(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 4	54	54 (100 %)	54 (100 %)	53 (98.2%)	50 (92.6%)	48	21	2	25(56.3)
(*dyb.* K♀ × *dyb.* K♂)$_4$ Nos. 1, 2	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 8	159	63 (39.6%)	24 (15.1%)	23 (14.5%)	13 (8.2%)	13	7	0	6(46.2)
	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 9	92	2 (2.2%)	2 (2.2%)	1 (1.1%)	1 (1.1%)	—	—	—	—
	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 10	164	144 (87.8%)	68 (41.5%)	64 (39.0%)	54 (32.9%)	46	24	0	22(47.8)
	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 11	42	40 (95.2%)	15 (35.7%)	15 (35.7%)	10 (23.8%)	7	3	0	4(57.1)
Total		457	249 (54.5%)	109 (23.9%)	103 (22.5%)	78 (17.1%)	66	34	0	32(48.5)
(*dyb.* T♀ × *dyb.* T♂)$_2$ No. 4	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 8	91	84 (92.3%)	81 (89.0%)	78 (85.7%)	63 (69.2%)	54	23	1	30(57.4)
	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 9	91	2 (2.2%)	2 (2.2%)	2 (2.2%)	2 (2.2%)	—	—	—	—
	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 10	96	92 (95.8%)	89 (92.7%)	87 (90.6%)	79 (82.3%)	65	33	0	32(49.2)
	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 11	93	93 (100 %)	92 (98.9%)	90 (96.8%)	80 (86.0%)	64	27	0	37(57.8)
Total		371	271 (73.0%)	264 (71.2%)	257 (69.3%)	224 (60.4%)	183	83	1	99(54.6)
(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 1	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 8	79	18 (22.8%)	18 (22.8%)	17 (21.5%)	15 (19.0%)	15	8	0	7(46.7)
(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 2	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 9	50	0	0	0	0	—	—	—	—
(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 3	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 10	76	70 (92.1%)	69 (90.8%)	65 (85.5%)	58 (76.3%)	55	25	3	27(54.5)
(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 4	(*dyb.* K♀ × *dyb.* T♂)$_4$ No. 11	119	117 (98.3%)	115 (96.6%)	111 (93.3%)	106 (89.1%)	88	45	2	41(48.9)
Total		324	205 (63.3%)	202 (62.3%)	193 (59.6%)	179 (55.2%)	158	78	5	75(50.6)

dyb. K, *Rana dybowskii* from Korea *dyb.* T, *Rana dybowskii* from Tsushima

(*dyb.* K♀ × *dyb.* K♂)$_4$, *dyb.* K♀ No. 4 × *dyb.* K♂ No. 4

(*dyb.* K♀ × *dyb.* T♂)$_4$, *dyb.* K♀ No. 4 × *dyb.* T♂ No. 4

series mated with male No. 9 only two (2.2%) of 91 eggs cleaved, hatched and metamorphosed normally. Male No. 9 had testes which were the smallest among those of the 11 males produced from female *Rana dybowskii* from Korea and male *Rana dybowskii* from Tsushima (Table 27). Thus, this male was considered to be incomplete in sexual maturity.

Of the 224 normally metamorphosed frogs in total, the sex of 183 was examined. It was found that 83 were females, one was a hermaphrodite and 99 were males. When the hermaphrodite was counted as a male, 49.2~57.8%, 54.6% on the average, were males in three mating series (Table 32).

ii) Matings with female *Rana dybowskii* from Korea

In 1972, four 2-year-old males (Nos. 8~11) produced in 1970 from female *dyb*. K. No. 4 and male *dyb*. T. No. 4 (Table 27) were mated with two 2-year-old females (Nos. 1 and 2) produced in 1970 from female *dyb*. K. No. 4 and male *dyb*. K. No. 4. Of the respective number of eggs of female *Rana dybowskii* from Korea Nos. 1 and 2 in three of four mating series, 39.6~95.2%, 247 (67.7%) of 365 eggs in total, cleaved normally, 14.5~39.0%, 102 (27.9%) in total, hatched normally and 8.2~32.9%, 77 (21.1%) in total, attained completion of metamorphosis (Table 32). In the remaining series mated with male No. 9, only two (2.2%) of 92 eggs cleaved and eventually one (1.1%) egg hatched and attained completion of metamorphosis. As stated above, this male had testes which were the smallest among those of the same kind of males (Table 27).

The sex of 66 of the 78 metamorphosed frogs in total was examined at the juvenile stage. It was found that 34 were females and 32 (48.5%) were males (Table 32).

iii) Brother and sister matings

In 1972, four 2-year-old males (Nos. 8~11) and four 2-year-old females (Nos. 1~4) produced in 1970 from female *dyb*. K. No. 4 and male *dyb*. T. No. 4 were mated (Table 32). The results showed that 22.8~98.3%, 205 (74.8%) of 274 eggs in total, of the respective number of eggs in three of four mating series cleaved normally, 21.5~93.3%, 193 (70.4%) in total, hatched normally and 19.0~89.1%, 179 (65.3%) in total, attained completion of metamorphosis. In the remaining series mated with male No. 9, none of 50 eggs cleaved normally, probably due to incomplete sexual maturity of male No. 9 (Table 32).

5. Interspecific hybrids between female *Rana dybowskii* from Tsushima and males of three species

a. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana japonica*♂

Two 1-year-old male hybrids (Nos. 1 and 2) produced in 1970 from female *dyb*. T. No. 1 and male *jap*. No. 1 (Table 28) were backcrossed with a female *Rana dybowskii* from Tsushima (70 *dyb*. T. W♀No. 1) in 1971. No cleaved eggs were obtained from this kind of backcrosses. On the other hand, the same two male hybrids (Nos. 1 and 2) were backcrossed in 1971 with two 1-year-old female *Rana japonica* (Nos. 1 and 2) produced in 1970 from female *jap*. No. 1 and male *jap*. No. 1. The results showed that four of 172 eggs and two of 184 eggs cleaved normally and became normal neurulae by insemination with sperm of male hybrid No. 1 and No. 2, respectively. However, these six neurulae in total became abnormal at the tail-bud stage and died before the hatching stage.

The two female *Rana japonica* used in the backcross experiments were completely normal, as 102 of 117 eggs of the females cleaved normally by insemination with sperm of two males produced in 1970 from female *jap*. No. 1 and male *jap*. No. 1 (Table 28). All the normally cleaved eggs developed and hatched almost normally.

In 1972, two 2-year-old male hybrids (Nos. 6 and 7) produced in 1970 from

female *dyb.* T. No. 1 and male *jap.* No. 1 (Table 28) were backcrossed with three female *Rana dybowskii* from Tsushima (Nos. 1~3) produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* T. No. 2. However, none of 261 eggs of these females cleaved. In the same year, the same two male hybrids (Nos. 6 and 7) were backcrossed with three 2-year-old female *Rana japonica* (Nos. 3~5) produced in 1970 from female *jap.* No. 1 and male *jap.* No. 1. The results showed that only 11 of 898 eggs obtained from the three females cleaved abnormally, although these abnormally cleaved eggs did not develop further.

It was confirmed by mating with two 2-year-old males (Nos. 1 and 4) produced in 1970 from the same parents that the three female *Rana japonica* were normal in reproductive capacity (Table 28). Of 495 eggs obtained from the three females, 476 (96.2%) cleaved normally and 458 (92.5%) hatched normally.

b. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana ornativentris*♂

Five 1-year-old male hybrids (Nos. 1~5) produced in 1970 including two from female *dyb.* T. No. 1 and male *ornat.* No. 1, two from female *dyb.* T. No. 2 and male *ornat.* No. 2 and one from female *dyb.* T. No. 3 and male *ornat.* No. 3 (Table 28) were backcrossed in 1971 with a field-caught female *Rana dybowskii* from Tsushima (70 *dyb.* T. W. No. 1) and a field-caught female *Rana ornativentris* (70 *ornat.* W. No. 1). However, no cleaved eggs were obtained from these backcross experiments.

It was confirmed that the field-caught female *Rana ornativentris* used in the backcross experiments was normal in reproductive capacity by mating with two male *Rana ornativentris* (Nos. 1 and 2) produced in 1970 from female *ornat.* No. 1 and male *ornat.* No. 1 (Table 28). In this case, 119 of 126 eggs cleaved normally and almost all the normally cleaved eggs hatched normally.

In 1972, five 2-year-old male hybrids produced in 1970 including three (Nos. 11~13) from female *dyb.* T. No. 2 and male *ornat.* No. 2 and two (Nos. 14 and 15) from female *dyb.* T. No. 3 and male *ornat.* No. 3 (Table 28) were backcrossed with three 2-year-old female *Rana dybowskii* from Tsushima produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* T. No. 2 and two 2-year-old female *Rana ornativentris* produced in 1970 from female *ornat.* No. 1 and male *ornat.* No. 1. In these experiments, no cleaved eggs were obtained.

The two 2-year-old female *Rana ornativentris* used in the experiments were confirmed to be normal in reproductive capacity by mating with three 2-year-old males produced from the same parents (Table 28). In this case, 151 of 164 eggs cleaved normally, 142 hatched normally and 133 attained completion of metamorphosis.

c. Hybrids, *Rana dybowskii* from Tsushima♀ × *Rana chensinensis*♂

In 1971, two 1-year-old male hybrids (Nos. 1 and 2) produced in 1970 from female *dyb.* T. No. 2 and male *chen.* No. 2 (Table 28) were backcrossed with a field-caught female *Rana dybowskii* from Tsushima (70 *dyb.* T. W♀No. 1). However, no cleaved eggs were obtained.

In 1972, two 2-year-old male hybrids (Nos. 6 and 7) produced in 1970 from the above cross (Table 28) were backcrossed with three 2-year-old female *Rana dybowskii* (Nos. 1～3) from Tsushima produced in 1970 from female *dyb.* T. No. 2 and male *dyb.* T. No. 2 as well as with two 2-year-old female *Rana chensinensis* (Nos. 1 and 2) produced in 1970 from female *chen.* No. 1 and male *chen.* No. 1. In these backcross experiments, no cleaved eggs were obtained.

6. Interspecific hybrids between female *Rana dybowskii* from Korea and males of four species

a. Hybrids, *Rana dybowskii* from Korea♀ × *Rana japonica*♂

In 1972, two 2-year-old male hybrids (Nos. 4 and 5) produced in 1970 from female *dyb.* K. No. 3 and male *jap.* No. 3 (Table 29) were backcrossed with two 2-year-old female *Rana dybowskii* from Korea produced in 1970 from female *dyb.* K. No. 4 and male *dyb.* K. No. 4 as well as with two 2-year-old female *Rana japonica* (Nos. 3 and 4) produced in 1970 from female *jap.* No. 1 and male *jap.* No. 1. However, none of 144 *Rana dybowskii* and 387 *Rana japonica* eggs cleaved in these backcross experiments.

b. Hybrids, *Rana dybowskii* from Korea♀ × *Rana ornativentris*♂

In 1971, five 1-year-old male hybrids including one (No. 1) produced in 1970 from female *dyb.* K. No. 2 and male *ornat.* No. 2 and four (Nos. 2～5) produced in 1970 from female *dyb.* K. No. 3 and male *ornat.* No. 3 (Table 29) were backcrossed with a field-caught female *Rana dybowskii* from Korea (70 *dyb.* K. W♀ No. 1) as well as with a field-caught female *Rana ornativentris* (70 *ornat.*♀No. 1). However, no cleaved eggs were obtained.

In 1972, four 2-year-old male hybrids including one (No. 15) produced in 1970 from female *dyb.* K. No. 2 and male *ornat.* No. 2, one (No. 16) produced in 1970 from female *dyb.* K. No. 3 and male *ornat.* No. 3 and two (Nos. 17 and 18) produced in 1970 from female *dyb.* K. No. 4 and male *ornat.* No. 4 (Table 29) were backcrossed with two 2-year-old female *Rana dybowskii* from Korea (Nos. 1 and 2) produced from female *dyb.* K. No. 4 and male *dyb.* K. No. 4 as well as with two 2-year-old female *Rana ornativentris* (Nos. 1 and 2) produced from female *ornat.* No. 1 and male *ornat.* No. 1. However, none of 481 *Rana dybowskii* and 226 *Rana ornativentris* eggs cleaved in these backcross experiments.

c. Hybrids, *Rana dybowskii* from Korea♀ × *Rana tsushimensis*♂

In 1972, one 2-year-old male hybrid (No. 1) produced in 1970 from female *dyb.* K. No. 6 and male *tsu.* No. 6 (Table 29) was backcrossed with two 2-year-old female *Rana dybowskii* from Korea (Nos. 1 and 2) produced from female *dyb.* K No. 4 and male *dyb.* K. No. 4 as well as with two 2-year-old female *Rana tsushimensis* (Nos. 1 and 2) produced from female *tsu.* No. 1 and male *tsu.* No. 1. None of 261 *Rana dybowskii* and 223 *Rana tsushimensis* eggs cleaved in these backcross experiments.

d. Hybrids, *Rana dybowskii* from Korea♀ × *Rana chensinensis*♂

In 1971, two 1-year-old male hybrids including one (No. 1) produced from female *dyb.* K. No. 3 and male *chen.* No. 3 and one (No. 2) produced from female *dyb.* K. No. 4 and male *chen.* No. 4 (Table 29) were backcrossed with a field-caught female *Rana dybowskii* from Korea (70 *dyb.* K. W♀No. 1). No cleaved eggs were obtained in these experiments.

In 1972, four 2-year-old male hybrids including two (Nos. 7 and 8) produced from female *dyb.* K. No. 3 and male *chen.* No. 3 and two (Nos. 9 and 10) produced from female *dyb.* K. No. 4 and male *chen.* No. 4 (Table 29) were backcrossed with two 2-year-old female *Rana dybowskii* from Korea (Nos. 1 and 2) produced from female *dyb.* K. No. 4 and male *dyb.* K. No. 4 as well as with two 2-year-old female *Rana chensinensis* (Nos. 1 and 2) produced in 1970 from female *chen.* No. 1 and male *chen.* No. 1. It was found that none of 371 *Rana dybowskii* and 200 *Rana chensinensis* eggs cleaved.

7. Interspecific hybrids between female *Rana arvalis* and males of two species

a. Controls, *Rana arvalis*♀ × *Rana arvalis*♂

Two 2-year-old males (Nos. 1 and 2) and two 2-year-old females (Nos. 1 and 2) produced in 1962 from female *arv.* No. 1 and male *arv.* No. 1 (Table 30) were mated in 1964. Of 175 eggs in total, 132 (75.4%) cleaved normally, 120 (68.6%) hatched normally and 114 (65.1%) became normally feeding tadpoles.

b. Hybrids, *Rana arvalis*♀ × *Rana japonica*♂

Three 2-year-old male hybrids including two (Nos. 1 and 2) produced in 1962 from female *arv.* No. 2 and male *jap.* No. 2 (Table 30) and one (No. 4) produced in 1962 from female *arv.* No. 3 and male *jap.* No. 3 (Table 30) were backcrossed in 1964 with two 2-year-old female *Rana arvalis* (Nos. 1 and 2) produced in 1962 from female *arv.* No. 1 and male *arv.* No. 1. However, none of 557 eggs cleaved in these backcross experiments.

c. Hybrids, *Rana arvalis*♀ × *Rana ornativentris*♂

Three 2-year-old male hybrids (Nos. 1~3) produced in 1962 from female *arv.* No. 2 and *ornat.* No. 1 (Table 30) were mated in 1964 with two 2-year-old female *Rana arvalis* (Nos. 1 and 2) produced in 1962 from female *arv.* No. 1 and male *arv.* No. 1. None of 609 eggs obtained from the females cleaved.

DISCUSSION

1. Reproductive isolation between sympatric species

Two sympatric species of brown frogs are found Honshu (the main island of Japan), Tsushima Island, Korea, Formosa and Europe. The diploid chromosome number of one of the two sympartric species is 26, while that of the other is 24,

although the chromosome number of the two sympartric species in Formosa is 26. The species having 26 chromosomes is *Rana japonica* in Honshu (KAWAMURA, 1940; KOBAYASHI, 1962; SETO, 1965), *Rana tsushimensis* in Tsushima (KAWAMURA and NISHIOKA, 1973), *Rana amurensis coreana* in Korea (KAWAMURA and NISHIOKA, 1973), *Rana longicrus* and *Rana latouchii* in Formosa (KURAMOTO et al., 1973; KURAMOTO, 1980), and *Rana temporaria* in Europe (WITSCHI, 1922a, b, 1924, 1933; WICKBOM, 1945; GUILLEMIN, 1967; MORESCALCHI, 1967; ULLERICH, 1967; NISHIOKA et al, 1972), while the species having 24 chromosomes is *Rana ornativentris* in Honshu (KOBAYASHI, 1962; SETO, 1965; NISHIOKA et al., 1972), *Rana dybowskii* in Tsushima and Korea (KAWAMURA and NISHIOKA, 1973) and *Rana arvalis* in Europe (WITSCHI, 1933; WICKBOM, 1945; KOBAYASHI, 1962; MORESCALCHI, 1962, 1967; ULLERICH, 1967; NISHIOKA et al., 1972). In Honshu, Tsushima and Korea, the brown frogs having 26 chromosomes are generally smaller and more slender than those having 24 chromosomes. They are comparatively warm-adapted and fond of grassy plain, while those having 24 chromosomes are cold-adapted and select rather mountainous areas covered with forest as their habitat. The two sympatric species in Europe are inverse in this respect. *Rana temporaria* is generally larger, stouter and more cold-adapted than *Rana arvalis*. *Rana longicrus* distributed in Formosa is much more slender than the sympatric *Rana latouchii*. These two species are nearly the same in body length. The present authors have so far no convincing information on the differences between them in ecology.

In Honshu, female *Rana ornativentris* were completely isolated from male *Rana japonica* by gametic isolation, while female *Rana japonica* were completely isolated from male *Rana ornativentris* by hybrid sterility, although either gametic isolation or hybrid inviability was scarcely found between female *Rana japonica* and male *Rana ornativentris*. *Rana japonica* and *Rana ornativentris* are also sympatric in Shikoku and Kyushu. In Tsushima Island, *Rana tsushimensis* and *Rana dybowskii* were completely isolated from each other in reciprocal combinations by hybrid inviability, while the cleavage percentage of the two combinations was nearly half or somewhat higher than half of that in the controls. In Korea, *Rana amurensis coreana* and *Rana dybowskii* were also completely isolated from each other by hybrid inviability, although the cleavage percentage in the combination of female *Rana amurensis coreana* and male *Rana dybowskii* was rather higher than that in the controls. The cleavage percentage in the reciprocal combination was somewhat higher than half of that in the controls. In Formosa, the eggs of female *Rana longicrus* were barely fertilized with sperm of a male *Rana latouchii*. Normally cleaved eggs were very few and all died before metamorphosis. Although the reciprocal hybridization experiments have not yet been made, it is very probable that female *Rana latouchii* are completely isolated from male *Rana longicrus* by hybrid inviability, because various number of eggs of a female *Rana latouchii* cleaved normally by inseminating with sperm of a male *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis* or *Rana dybowskii*, and all the normally cleaved eggs died before beginning of gastrulation. In Europe, *Rana temporaria* and *Rana*

arvalis were almost completely isolated from each other by gametic isolation except that a few *Rana arvalis* eggs were fertilized with sperm of *Rana temporaria* and grew into juvenile males which would invariably become sterile.

Brown frogs distinctly differ from pond frogs in that two sympatric species are completely isolated from each other by various physiological isolating mechanisms. The two sympatric pond frogs in Japan, that is, *Rana nigromaculata* and *Rana brevipoda* as well as *Rana ridibunda* and *Rana lessonae* in Europe produce hybrids which are not always completely sterile (KAWAMURA and NISHIOKA, 1979).

As the two sympatric brown frog species in Honshu, Tsushima, Korea or Europe differ from each other in size and shape of the body, temperature adaptation and chromosome number, it is no doubt that they immigrated into each area after their speciation had been completed in their own habitats.

2. Gametic isolation

Brown frogs are remarkably different from pond frogs and toads in that they are often completely isolated from one another by gametic isolation (KAWAMURA and NISHIOKA, 1979; KAWAMURA, NISHIOKA and UEDA, 1980). Brown frog species can be arranged in order of difficulty with which their eggs are inseminated with foreign sperm. The eggs of *Rana temporaria* were the most difficult to be inseminated, since none of them cleaved by inseminating with sperm of *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis* and *Rana arvalis*. Thus, there was complete gametic isolation between female *Rana temporaria* and males of the other five species. The eggs of *Rana ornativentris* seemed to be the second in difficulty of insemination. No cleaved eggs were produced by inseminating with sperm of *Rana japonica, Rana okinavana, Rana tsushimensis, Rana longicrus, Rana latouchii, Rana arvalis, Rana dalmatina, Rana macrocnemis* and *Rana sylvatica*. Only a few eggs cleaved by inseminating with sperm of *Rana dybowskii* and *Rana amurensis coreana*. However, in contrast with the *Rana temporaria* eggs, about 26% and 60% of *Rana ornativentris* eggs cleaved normally by inseminating with sperm of *Rana chensinensis* and *Rana temporaria*, respectively.

The eggs of *Rana chensinensis* and *Rana dybowskii* seemed to be the third in difficulty of insemination. No cleaved eggs were obtained from female *Rana chensinensis* by inseminating with sperm of *Rana amurensis coreana* and *Rana latouchii*, and from female *Rana dybowskii* by inseminating with sperm of a *Rana sylvatica*, while about 9% of *Rana dybowskii* eggs cleaved normally by inseminating with sperm of *Rana amurensis coreana*. No cleaved eggs were produced by sperm of *Rana latouchii* and *Rana macrocnemis*. While about 82% and 95% of *Rana chensinensis* eggs cleaved normally by inseminating with sperm of *Rana dybowskii* from Tsushima and Korea, respectively, about 18% of the eggs of *Rana dybowskii* from Tsushima and about 81% of the eggs of *Rana dybowskii* from Korea cleaved normally by inseminating with sperm of *Rana chensinensis*. About 47~79% of *Rana chensinensis* and about 58~95% of *Rana dybowskii* eggs also cleaved normally by inseminating with sperm of *Rana japonica, Rana ornativentris, Rana tsushimensis* and *Rana temporaria*. By inseminating with sperm of *Rana longicrus*, about 19% of *Rana chensinensis* eggs and

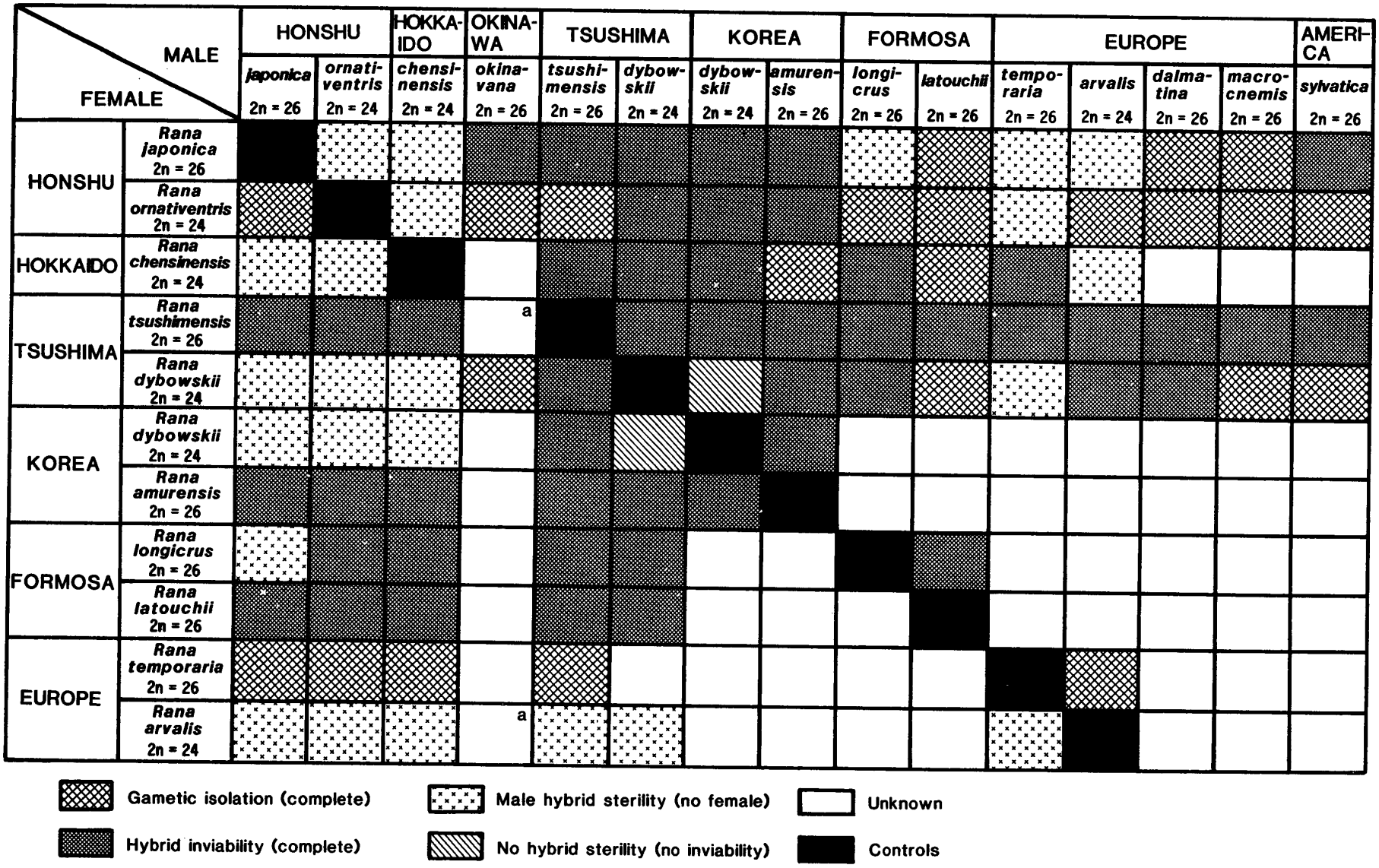


Fig. 37. Isolating mechanisms found in various combinations among 14 brown frog species. The mark of each section shows the isolating mechanism by which two species are completely isolated from each other.

a, All hybrids perished in an accident immediately after metamorphosis

about 8% of *Rana dybowskii* eggs cleaved normally, while about 28% of *Rana chensinensis* eggs and about 19% of *Rana dybowskii* eggs did so by inseminating with sperm of *Rana arvalis*. It is noteworthy that *Rana temporaria, Rana ornativentris, Rana chensinensis* and *Rana dybowskii* are larger and more cold-adapted than the others.

In contrast with *Rana chensinensis* eggs, about 26% of *Rana japonica* eggs and 77% of *Rana tsushimensis* eggs cleaved normally by inseminating with sperm of *Rana amurensis coreana*. While no cleavage occurred in *Rana ornativentris* and *Rana dybowskii* eggs by inseminating with sperm of *Rana okinavana*, only 1% of *Rana japonica* eggs and 44% of *Rana tsushimensis* eggs cleaved normally in 1977 and 1978. These percentages of normally cleaved eggs were remarkably lower than those obtained by KURAMOTO (1974). The results of crossing experiments repeated by the present authors late in 1981 showed that 91.4% of *Rana japonica* eggs and 97.1% of *Rana tsushimensis* eggs cleaved normally by inseminating with sperm of a male *Rana okinavana*. The lower percentages of normally cleaved eggs in 1977 and 1978 were probably attributable to captivity of warm-adapted males in a colder condition for about three months. The eggs of *Rana japonica* somewhat differed from those of *Rana tsushimensis* in reaction to sperm of *Rana latouchii, Rana dalmatina* and *Rana macrocnemis*. While *Rana japonica* eggs did not cleave by inseminating with sperm of these three species, about 5~19% of *Rana tsushimensis* eggs cleaved normally (Fig. 37).

The eggs of *Rana amurensis coreana* and *Rana longicrus* were very similar to those of *Rana japonica* and *Rana tsushimensis* in reaction to sperm of *Rana ornativentris, Rana chensinensis* and *Rana dybowskii*. The eggs of *Rana longicrus* were fairly similar to those of *Rana tsushimensis* in reaction to sperm of *Rana latouchii*, as about 2% of the eggs cleaved normally. The eggs of *Rana arvalis* were somewhat similar to those of *Rana japonica*, as about 72%, 59%, and 40% of eggs cleaved normally with sperm of *Rana japonica, Rana ornativentris* and *Rana tsushimensis*, respectively. About 10~16% of *Rana arvalis* eggs cleaved normally by inseminating with sperm of *Rana chensinensis, Rana okinavana* and *Rana dybowskii*. However, *Rana arvalis* eggs differed from the other species examined in that normal cleavage occurred in only 0.4% of eggs by inseminating with sperm of *Rana temporaria*. The sperm of *Rana latouchii, Rana dalmatina* and *Rana macrocnemis* were very similar to one another in that they could not fertilize the eggs of *Rana japonica* and *Rana ornativentris*. Moreover, they could not fertilize more than about 19% of *Rana tsushimensis* or *Rana dybowskii* eggs.

The species of larger and more cold-adapted frogs lay larger eggs which are enveloped with harder and thicker jelly. The eggs of *Rana ornativentris, Rana chensinensis, Rana dybowskii* and *Rana temporaria* were 2.0 mm, 2.2 mm, 2.0 or 2.1 mm, and 2.2 mm in mean diameter, respectively. The jelly envelopes of eggs were always hard in quality and kept each egg from the others at intervals of about 5.0~14.5 mm about 5 hours after the eggs were laid in water. In contrast, the eggs of *Rana japonica, Rana tsushimensis, Rana amurensis coreana, Rana longicrus* and *Rana arvalis* were 1.6 mm, 1.9 mm, 1.7 mm, 1.6 mm and 1.7 mm in mean diameter, respectively. All these eggs were enveloped with soft jelly and separated

from one another at intervals of about 2.5～7.5 mm about 5 hours after they were laid in water. Thus, it is very probable that spermatozoa of the species having harder and thicker jelly envelopes can easily penetrate softer and thinner jelly envelopes, whereas spermatozoa of the species having softer and thinner jelly envelopes are difficult to penetrate harder and thicker envelopes. As the size of eggs as well as the hardness and thickness of jelly envelopes in brown frogs is considered to be a genetic character acquired by temperature adaptation of each species, the gametic isolation seems to be a by-product of such temperature adaptation.

3. Hybrid inviability

When the two brown frogs of each mating were not completely isolated by gametic isolation, they were completely isolated from each other by hybrid inviability, hybrid sterility or combination of these two isolating mechanisms. All the hybrids between female *Rana tsushimensis* and males of *Rana japonica, Rana ornativentris, Rana chensinensis, Rana dybowskii, Rana amurensis coreana, Rana longicrus, Rana latouchii, Rana temporaria, Rana arvalis, Rana dalmatina, Rana macrocnemis* and *Rana sylvatica* died during embryonic or tadpole stage. All the hybrids between female *Rana amurensis coreana* and males of *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis, Rana dybowskii* also died during the embryonic or tadpole stage. In this respect, *Rana tsushimensis* seems to be closely allied to *Rana amurensis coreana* which is geographically isolated from *Rana tsushimensis* by a channel. These two species are very similar to each other in external characters as well as in developmental velocity during the embryonic stage at 12°C and 18°C (unpublished data). It was noteworthy that all the normally cleaved eggs produced from mating between female *Rana tsushimensis* and male *Rana amurensis coreana* or *Rana latouchii* became abnormal gastrulae and died without growing into normal neurulae. Although it is evident that the hybrid inviability is attributable to incompatibility of the two genomes, the genetic characters taking part in the incompatibility have not yet been examined.

Female *Rana japonica* produced fairly many metamorphosed hybrids by inseminating with sperm of *Rana ornativentris, Rana chensinensis, Rana longicrus, Rana temporaria* and *Rana arvalis,* while there was distinct hybrid inviability during the embryonic or tadpole stage in most of the combinations. The metamorphosed hybrids were obtained from about 12～74% of the respective number of eggs. Female *Rana japonica* were completely isolated by hybrid inviability from male *Rana okinavana, Rana tsushimensis, Rana dybowskii, Rana amurensis coreana* and *Rana sylvatica,* although a few inviable metamorphosed hybrids were produced by mating with male *Rana okinavana* and *Rana tsushimensis.* From female *Rana ornativentris,* a small number of metamorphosed hybrids were produced by mating with male *Rana chensinensis* and *Rana temporaria,* while an overwhelming majority of fertilized eggs died during embryonic or tadpole stage. Female *Rana ornativentris* were completely isolated by hybrid inviability from male *Rana dybowskii* and *Rana amurensis coreana.* Female *Rana chensinensis* produced a small number of

metamorphosed hybrids which corresponded to about 4~8% of the respective number of eggs by mating with male *Rana japonica, Rana ornativentris* and *Rana arvalis,* while an overwhelming majority of fertilized eggs died during the embryonic or tadpole stage. Female *Rana chensinensis* were completely isolated by hybrid inviability from *Rana tsushimensis, Rana dybowskii, Rana longicrus* and *Rana temporaria* (Fig. 37).

From female *Rana dybowskii,* about 5~61% of the respective number of eggs became metamorphosed hybrids by mating with male *Rana japonica, Rana ornativentris, Rana chensinensis* and *Rana temporaria,* while an overwhelming majority of fertilized eggs died during embryonic or tadpole stage in most cases. Female *Rana dybowskii* were completely isolated by hybrid inviability from male *Rana tsushimensis, Rana amurensis coreana, Rana longicrus, Rana arvalis* and *Rana dalmatina.* The inviable hybrids produced from these combinations usually became abnormal at the gastrula stage and scarcely attained the neurula stage except those derived from male *Rana tsushimensis.*

Female *Rana arvalis* distinctly differed from the females of the other species in that there were no combinations isolated completely by hybrid inviability. By mating with male *Rana japonica, Rana ornativentris, Rana chensinensis, Rana okinavana, Rana tsushimensis, Rana dybowskii* and *Rana temporaria,* 0.2~8% of the respective number of eggs became metamorphosed hybrids, although an overwhelming majority of the fertilized eggs died during embryonic or tadpole stage. The relationship between *Rana japonica* and *Rana longicrus* was also peculiar in that these two species were scarcely isolated by gametic isolation or hybrid inviability. In reciprocal crosses, about 92% and 88% of the respective number of eggs cleaved normally and 70% and 52% attained completion of metamorphosis. This finding agrees with that by KURAMOTO (1974) and suggests that the two species are most closely related to each other.

Formosan *Rana latouchii* appeared to be a particular brown frog species in that all the eggs fertilized with sperm of *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis* and *Rana dybowskii* from Tsushima died before beginning of gastrulation, although a few of the reciprocal hybrids became feeding tadpoles. This finding indicates that *Rana latouchii* is remarkably different in reproductive physiology from the other brown frog species distributed in Far East. It is also evident that North American *Rana sylvatica* is most distantly related to Japanese brown frog species, as the eggs of a female *Rana japonica* or *Rana tsushimensis* fertilized with sperm of a male *Rana sylvatica* all died at the late blastula stage, while *Rana ornativentris* or *Rana dybowskii* eggs were not fertilized with sperm of this male. MOORE (1951) has reported that the hybrids between female *Rana sylvatica* and male *Rana temporaria* die at the late blastula stage, while no cleavage occurs in the reciprocal combination. Thus, the affinity between North American and Palaearctic brown frogs seems to be more conclusively distant than that between Far Eastern and European brown frogs.

4. Hybrid sterility

The present study has clarified that all viable interspecific hybrids become males which are completely sterile as repeatedly reported by DÜRKEN (1935, 1938), KAWAMURA (1940, 1943, 1950), KAWAMURA and KOBAYASHI (1959, 1960), KAWAMURA and NISHIOKA (1962, 1973, 1977), KAWAMURA, NISHIOKA and UEDA (1972). Immediately after metamorphosis, a small number of hermaphrodites were always found among interspecific hybrids. The remaining hybrids usually had normal testes in appearance except a small number of males with rudimentary testes. The existence of such juvenile hermaphrodites and males with rudimentary testes indicates that sex reversal occurs from females to males in interspecific hybrids. All the mature hybrids produced by present authors were males with a single exception. The fact that they were completely sterile was confirmed by observing the inner structure of testes as well as by backcross experiments. The single exception was a female hybrid produced from crossing between a female *Rana dybowskii* from Tsushima and a male *Rana japonica*. Although she was a mature female in appearance, she had no gonads. It is probable that sex reversal did not occur due to nonexistence of gonads which had been brought about by degeneration of all germ cells at an early developmental stage.

From the present study it is evident that different brown frog species are first of all completely or incompletely isolated from each other by gametic isolation. When the gametic isolation is incomplete, the two species are completely or incompletely isolated by hybrid inviability. When the hybrid inviability is incomplete, the two species are completely isolated by hybrid sterility. These findings distinctly differ from those in both pond frogs (KAWAMURA and NISHIOKA, 1975, 1979) and toads (KAWAMURA, NISHIOKA and UEDA, 1980). The fact that hybrid sterility is always complete in contrast with hybrid inviability or gametic isolation seems to indicate that this is the most ubiquitous and most fundamental among the three innate reproductive isolating mechanisms in brown frogs. The gametic isolation and hybrid inviability are probably those which were superadded to the existence of hybrid sterility. As the hybrid sterility in anurans is considered to be attributable to structural differences in chromosome between the parental species, each of the brown frog species used in the present study seems to have been evolved in an far older geological age than those of pond frogs and toads.

5. *Rana dybowskii* from Tsushima and Korea

In order to examine the existence of differences between *Rana dybowskii* from Tsushima and those from Korea, reciprocal intraspecific hybrids were produced by using six female and four male specimens collected from Tsushima and eight female and four male specimens from Korea. In the crossing experiments, about 99% of the total number of Tsushima eggs cleaved normally by inseminating with Korean sperm, while about 98% of the total number of Korean eggs did so by inseminating with Tsushima sperm. Thereafter, about 86% and 64%

of the Tsushima eggs hatched normally and attained completion of metamorphosis, respectively, while 77% and 66% of the Korean eggs normally hatched and metamorphosed, respectively. All these percentages are not inferior to those of the controls. On the other hand, about 56% and 51% of reciprocal hybrids were males, while 53% and 52% of the control frogs were males. These percentages also indicate that the intraspecific hybrids are nearly the same as the controls in sex ratio. Thus, it is evident that the Tsushima population of *Rana dybowskii* scarcely differs from the Korean population of this species in reproductive physiology as well as in external characters.

However, a strange phenomenon was observed in all the interspecific hybrids between female *Rana dybowskii* from Korea and males of *Rana japonica, Rana ornativentris, Rana chensinensis* and *Rana tsushimensis*. Many roundish spots and blotches of faded color appeared on the uppersurfaces of the body and four legs. These spots and blotches were found in both juvenile and mature hybrids and scarcely changed in shape and number with age of the hybrids. It was curious that such spots and blotches were not found in reciprocal intraspecific hybrids between *Rana dybowskii* from Tsushima and those from Korea as well as in interspecific hybrids between female *Rana dybowskii* from Tsushima and males of *Rana japonica, Rana ornativentris, Rana chensinensis* and *Rana temporaria*. The mechanism forming spots or blotches of faded color in the skin of interspecific hybrids produced from females of Korean population of *Rana dybowskii* remains to be elucidated.

SUMMARY

1. In 20 years from 1962 to 1981, a total of 99 kinds of crossing experiments were made among 14 brown frog species distributed in Japan, Korea, Formosa, Europe and North America. It was found that all these species were completely isolated from one another by gametic isolation, hybrid inviability, hybrid sterility or cooperation of two or three of these reproductive isolating mechanisms.

2. Female *Rana japonica* were completely isolated from male *Rana latouchii, Rana dalmatina* and *Rana macrocnemis* by gametic isolation. They were completely isolated from male *Rana okinavana, Rana tsushimensis, Rana dybowskii, Rana amurensis coreana* and *Rana sylvatica* by hybrid inviability, while they were either scarcely or to some extent isolated from these males by gametic isolation. They were completely isolated from male *Rana ornativentris, Rana chensinensis, Rana longicrus, Rana temporaria* and *Rana arvalis* by hybrid sterility, while they were either scarcely or to some extent isolated from these males by gametic isolation or hybrid sterility.

3. Female *Rana ornativentris* were completely isolated from male *Rana japonica, Rana okinavana, Rana tsushimensis, Rana longicrus, Rana latouchii, Rana arvalis, Rana dalmatina, Rana macrocnemis* and *Rana sylvatica* by gametic isolation. They were completely isolated from male *Rana dybowskii* and *Rana amurensis coreana* by hybrid inviability, while they were isolated to a great extent from these males by gametic

isolation. They were completely isolated from male *Rana chensinensis* and *Rana temporaria* by hybrid sterility, while they were isolated to some extent from these males by gametic isolation and hybrid inviability.

4. Female *Rana chensinensis* were completely isolated from male *Rana amurensis coreana* and *Rana latouchii* by gametic isolation. They were completely isolated from male *Rana tsushimensis, Rana dybowskii, Rana longicrus* and *Rana temporaria* by hybrid inviability, while they were either scarcely or to some extent isolated from these males by gametic isolation. They were completely isolated from male *Rana japonica, Rana ornativentris* and *Rana arvalis* by hybrid sterility, while they were isolated to some extent from these males by gametic isolation and hybrid inviability.

5. Female *Rana tsushimensis* were completely isolated from male *Rana japonica, Rana ornativentris, Rana chensinensis, Rana dybowskii, Rana amurensis coreana, Rana longicrus, Rana latouchii, Rana temporaria, Rana arvalis, Rana dalmatina, Rana macrocnemis* and *Rana sylvatica* by hybrid inviability, while they were either scarcely or to some extent isolated from these males by gametic isolation.

6. Female *Rana dybowskii* were completely isolated from male *Rana okinavana, Rana latouchii, Rana macrocnemis* and *Rana sylvatica* by gametic isolation. They were completely isolated from male *Rana tsushimensis, Rana amurensis coreana, Rana longicrus, Rana arvalis* and *Rana dalmatina* by hybrid inviability, while they were either scarcely or to some extent isolated from these males by gametic isolation. They were completely isolated from male *Rana japonica, Rana ornativentris, Rana chensinensis* and *Rana temporaria* by hybrid sterility, while they were either scarcely or to some extent isolated from these males by gametic isolation and hybrid inviability.

7. Female *Rana amurensis coreana* were completely isolated from male *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis* and *Rana dybowskii* by hybrid inviability, while they were scarcely isolated from these males by gametic isolation.

8. Female *Rana longicrus* were completely isolated from male *Rana ornativentris, Rana chensinensis, Rana tsushimensis, Rana dybowskii* and *Rana latouchii* by hybrid inviability, while they were either scarcely or to some extent isolated from these males by gametic isolation. They were completely isolated from male *Rana japonica* by hybrid sterility, while they were scarcely isolated from these males by gametic isolation and hybrid inviability.

9. A female *Rana latouchii* was completely isolated from male *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis* and *Rana dybowskii* by hybrid inviability, while she was either scarcely or to some extent isolated from these males by gametic isolation.

10. Female *Rana temporaria* were completely isolated from male *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis* and *Rana arvalis* by gametic isolation.

11. Female *Rana arvalis* were completely isolated from male *Rana japonica, Rana ornativentris, Rana chensinensis, Rana tsushimensis* and *Rana dybowskii* by hybrid

sterility, while they were isolated to some extent by gametic isolation and hybrid inviability. Only a few eggs cleaved by inseminating with sperm of male *Rana temporaria,* and half of the normally cleaved eggs became male juvenile frogs.

12. Immediately after metamorphosis, a small number of hermaphrodites were always found among interspecific hybrids. The remaining hybrids usually had normal testes in appearance except a small number of males with rudimentary testes. All the mature hybrids were sterile males with a single exception. Sterility was confirmed by examining the inner structure of testes as well as by backcross experiments. The single exception was apparently a female whose gonads had completely degenerated.

13. Interspecific hybrids were intermediate as a whole between the two parental species in external characters.

14. Tsushima population of *Rana dybowskii* did not differ from Korean population of this species in reproductive physiology as well as in external characters. However, many roundish spots and blotches of faded color appeared on the upper-surfaces of the body and four legs in all the interspecific hybrids between female *Rana dybowskii* from Korea and male *Rana japonica, Rana ornativentris, Rana chensinensis* and *Rana tsushimensis.*

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