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Hybridization Experiments among *Rana lessonae*, *Rana ridibunda* and *Rana esculenta*, with Special Reference to Hybridogenesis

By

Toshijiro KAWAMURA and Midori NISHIOKA

Laboratory for Amphibian Biology, Faculty of Science, Hiroshima University, Hiroshima 730, Japan

(With 35 Text-figures)

CONTENTS

INTRODUCTION

In a previous paper on isolating mechanisms among the green or water frog species in the Palearctic region, the present authors (1979) have reported on the results of hybridization experiments among *Rana nigromaculata* and *Rana brevipoda* from Japan, *Rana plancyi chosenica* from Korea, *Rana plancyi fukienensis* from Taiwan, *Rana esculenta* from West Germany, *Rana lessonae* from Luxembourg, *Rana esculenta* (correctly *Rana lessonae*) from Italy, *Rana esculenta* (correctly *Rana ridibunda*) from France, *Rana ridibunda* from Turkey and *Rana ridibunda* from Soviet Union and *Rana perezi* from France. It was found that the two species of Japanese green frogs are almost completely isolated from the four species of European green frogs by hybrid inviability or hybrid sterility. The results of crosses between *Rana plancyi chosenica* or *Rana plancyi fukienensis* and European green frogs are very similar to those of the crosses between Japanese and European frogs.

The results of crossings among European green frogs were only provisional, as stated in the paper. The number of frogs used for these crosses was very small, and, moreover, most of the hybrids were at the embryo, tadpole or immature frog stage. However, it was elucidated that *Rana esculenta* from West Germany more or less differ from *Rana lessonae* from Luxembourg and Italy and are very similar to *Rana ridibunda* from Turkey. *Rana lessonae* from Luxembourg and Italy are completely isolated from *Rana ridibunda* from Turkey and Soviet Union by hybrid sterility. Many triploids are produced from large eggs laid by several female hybrids between female *Rana lessonae* from Luxembourg and male *Rana ridibunda* from France.

The present authors, thereafter, have reared as far as possible the interspecific hybrids among the three species of European green frogs and the controls, and have made further experiments on crossings and backcrossings especially to elucidate the mechanisms of hybridogenesis in male *Rana esculenta*.

MATERIALS AND METHODS

The following six populations belonging to three species were used in the hybridization experiments of the present study.

1. *Rana lessonae* CAMERANO collected from Luxembourg (abbr. *les* L). One female (*les* L.W72♀, No. 1) and one male (*les* L.W72♂, No. 1) were sent in October, 1972 and two females (*les* L.W75♀, Nos. 2 and 3) and one male (*les* L.W75♂, No. 2) were sent in September, 1975 to our laboratory by Mr. R. THORN. These females and males and their offspring were used in

experiments.

2. *Rana lessonae* CAMERANO collected from Florence, Italy (abbr. *les* I). Seven females (*les* I.W77♀, Nos. 1～7) and eight males (*les* I.W77♂, Nos. 1～8) were sent to our laboratory by Prof. B. LANZA in March, 1977. These females and males and their offspring were used in experiments.

3. *Rana ridibunda* PALLAS collected from Rascoff, France (abbr. *rid* F). Of the frogs sent to Ueno Aquarium, Tokyo, by Dr. J. VASSEROT in November, 1974, two females (*rid* F.W74♀, Nos. 1 and 2) and four males (*rid* F.W74♂, Nos. 1～4) were used in experiments.

4. *Rana ridibunda* PALLAS collected from Adana, Turkey (abbr. *rid* T). Of the frogs sent to Dr. M. KURAMOTO in 1976 from Dr. L. J. BORKIN, two females (*rid* T.W76♀, Nos. 1 and 2) and six males (*rid* T.W76♂, Nos. 1～6) and their offspring were used in experiments.

5. *Rana ridibunda* PALLAS collected from Belgorod Region, near Village Borissouka, "Les na Vorscle" Nature-Reservation, USSR (abbr. *rid* S). Of the frogs sent to Dr. M. KURAMOTO in 1976 from Dr. L. J. BORKIN, a female (*rid* S.W76♀, No. 1) and a male (*rid* S.W76♂, No. 1) were used in experiments.

6. *Rana esculenta* L. collected from Hütenfeld near Heidelberg, West Germany (abbr. *esc* G). A female (*esc* G.W76♀, No. 1) and three males (*esc* G.W76♂, Nos. 1～3) sent to our laboratory by Prof. K. BACHMANN in September, 1976 were used in experiments.

Ovulation was accelerated by injecting suspension of bullfrog pituitaries into the abdominal cavity. Fertilization was always performed by the artificial method. Chromosomes were observed in the tail-tips of tadpoles by the squash method after water treatment. The gonads of metamorphosed frogs were fixed in NAVASHIN's fluid, sectioned at 10～12 μ and stained with HEIDENHAIN's iron hematoxylin. Tadpoles were fed on boiled spinach or chard, while metamorphosed frogs were fed on two-spotted crickets, *Gryllus bimaculatus* DE GEER.

Electrophoretic analyses of blood proteins and various enzymes extracted from the skeletal muscles and livers were made according to BREWER (1970) and NISHIOKA, OHTANI and SUMIDA (1980).

OBSERVATION

I. Developmental capacity of hybrids

1. Inter- and intraspecific matings between female *Rana lessonae* from Luxembourg and four kinds of males

a. Male *Rana lessonae* from Luxembourg (Control mating)

A mating between a female, *les* L.W72♀, No. 1, and a male, *les* L.W72♂, No. 1, collected from Luxembourg in 1972 was made in 1975. Two other matings between two females, *les* L.W75♀, Nos. 2 and 3, and a male, *les* L.W75♂, No. 2, collected in 1975 were made in 1976. In 1977, two more matings between two females, *les* L.75♀, Nos. 4 and 5, and two males, *les* L.75♂, Nos. 3 and 4, obtained

TABLE 1

Developmental capacity of the hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

Year	Parents		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	PMC
	Female	Male								
1975	*les* L.W72, No. 1	*les* L.W72, No. 1	110	93 (84.5%)	90 (81.8%)	89 (80.9%)	87 (79.1%)	82 (74.5%)	74 (67.3%)	79.6
		rid F.W74, No. 1	379	347 (91.6%)	307 (81.0%)	254 (67.0%)	254 (67.0%)	244 (64.4%)	244 (64.4%)	70.3
1976	*les* L.W75, No. 2	*les* L.W75, No. 2	144	128 (88.9%)	126 (87.5%)	119 (82.6%)	113 (78.5%)	64 (44.4%)	58 (40.3%)	45.3
		rid F.W74, No. 2	89	74 (83.1%)	73 (82.0%)	70 (78.7%)	68 (76.4%)	67 (75.3%)	62 (69.7%)	83.8
		rid T.W76, No. 1	159	107 (67.3%)	98 (61.6%)	95 (59.7%)	91 (57.2%)	73 (45.9%)	70 (44.0%)	65.4
	les L.W75, No. 3	*les* L.W75, No. 2	188	165 (87.8%)	158 (84.0%)	153 (81.4%)	151 (80.3%)	149 (79.3%)	141 (75.0%)	85.5
		rid F.W74, No. 2	58	47 (81.0%)	47 (81.0%)	46 (79.3%)	46 (79.3%)	46 (79.3%)	42 (72.4%)	89.4
		rid T.W76, No. 1	264	232 (87.9%)	212 (80.3%)	190 (72.0%)	188 (71.2%)	180 (68.2%)	179 (67.8%)	77.2
1977	*les* L. 75, No. 4	*les* L. 75, No. 3	164	76 (46.3%)	62 (37.8%)	59 (36.0%)	58 (35.4%)	58 (35.4%)	58 (35.4%)	76.3
		les I.W77, No. 1	125	85 (68.0%)	70 (56.0%)	63 (50.4%)	51 (40.8%)	46 (36.8%)	36 (28.8%)	42.4
		esc G.W76, No. 1	144	66 (45.8%)	61 (42.4%)	55 (38.2%)	46 (31.9%)	45 (31.3%)	41 (28.5%)	62.1
	les L. 75, No. 5	*les* L. 75, No. 4	268	217 (81.0%)	213 (79.5%)	213 (79.5%)	206 (76.9%)	155 (57.8%)	137 (51.1%)	63.1
		les I.W77, No. 2	263	234 (89.0%)	214 (81.4%)	193 (73.4%)	189 (71.9%)	178 (67.7%)	174 (66.2%)	74.4
Total	*les* L. (5)	*les* L. (4)	874	679 (77.7%)	649 (74.3%)	633 (72.4%)	615 (70.4%)	508 (58.1%)	468 (53.5%)	68.9
	les L. (2)	*les* I. (2)	388	319 (82.2%)	284 (73.2%)	256 (66.0%)	240 (61.9%)	224 (57.7%)	210 (54.1%)	65.8
	les L. (3)	*rid* F. (2)	526	468 (89.0%)	427 (81.2%)	370 (70.3%)	368 (70.0%)	357 (67.9%)	348 (66.2%)	74.4
	les L. (2)	*rid* T. (1)	423	339 (80.1%)	310 (73.3%)	285 (67.4%)	279 (66.0%)	253 (59.8%)	249 (58.9%)	73.5
	les L. (1)	*esc* G. (1)	144	66 (45.8%)	61 (42.4%)	55 (38.2%)	46 (31.9%)	45 (31.3%)	41 (28.5%)	62.1

PMC, Percentage of metamorphosed frogs to normally cleaved eggs

in 1975 from the control mating were made. It was found that 679 (77.7%) of 874 eggs used in these control matings cleaved normally, 649 (74.3%) became normal neurulae, and 633 (72.4%) developed into normal tail-bud embryos. Thereafter, 615 (70.4%) hatched normally, 508 (58.1%) became normally feeding tadpoles and 468 (53.5%) attained completion of metamorphosis. This number of metamorphosed frogs corresponds to 68.9% of the normally cleaved eggs (Table 1).

b. Male *Rana lessonae* from Italy

Two 2-year-old female *Rana lessonae* from Luxembourg (*les* L.75♀, Nos. 4 and 5) obtained in 1975 from the foregoing mating, *les* L.W72♀, No. 1 × *les* L.W72♂, No. 1, were mated in 1977 with two male *Rana lessonae* (*les* I.W77♂, Nos. 1 and 2) collected and sent to our laboratory from Italy in 1977. It was found that 319 (82.2%) of 388 eggs cleaved normally, 284 (73.2%) became normal neurulae and

256 (66.0%) developed into normal tail-bud embryos. Thereafter, 240 (61.9%) hatched normally, 224 (57.7%) became normally feeding tadpoles and eventually 210 (54.1%) attained completion of metamorphosis. This number of metamorphosed frogs corresponds to 65.8% of the normally cleaved eggs (Table 1).

c. Male *Rana ridibunda* from France

Three female *Rana lessonae* collected in 1972 and 1975 from Luxembourg (*les* L.W72♀, No. 1 and *les* L.W75♀, Nos. 2 and 3) were mated in the breeding seasons of 1975 and 1976 with two male *Rana ridibunda* (*rid* F.W74♂, Nos. 1 and 2) sent from France in 1974. From these three matings, 468 (89.0%) of 526 eggs cleaved normally, 427 (81.2%) became normal neurulae and 370 (70.3%) developed into normal tail-bud embryos. Thereafter, 368 (70.0%) hatched normally, 357 (67.9%) became normally feeding tadpoles and 348 (66.2%) attained completion of metamorphosis. This number of metamorphosed frogs corresponds to 74.4% of the normally cleaved eggs (Table 1).

d. A male *Rana ridibunda* from Turkey

Two female *Rana lessonae* collected from Luxembourg in 1975 (*les* L.W75♀, Nos. 2 and 3) were mated with a male *Rana ridibunda* collected and sent from Turkey in 1976 (*rid* T.W76♂, No. 1). The results of these two matings showed that 339 (80.1%) of 423 eggs cleaved normally, 310 (73.3%) became normal neurulae and 285 (67.4%) developed into normal tail-bud embryos. Thereafter, 279 (66.0%) hatched normally, 253 (59.8%) became normally feeding tadpoles and 249 (58.9%) attained completion of metamorphosis. This number of metamorphosed frogs corresponds to 73.5% of the normally cleaved eggs (Table 1).

e. A male *Rana esculenta* from West Germany

A 2-year-old female *Rana lessonae* from Luxembourg (*les* L.75♀, No. 4) obtained in 1975 from the foregoing mating, *les* L.W72♀, No. 1 × *les* L.W72♂, No. 1, was mated in the breeding season of 1977 with a male *Rana esculenta* (*esc* G.W76♂, No. 1) collected from West Germany in 1976. It was found that 66 (45.8%) of 144 eggs cleaved normally, 61 (42.4%) became normal neurulae and 55 (38.2%) developed into normal tail-bud embryos. Thereafter, 46 (31.9%) hatched normally, 45 (31.3%) became normally feeding tadpoles and 41 (28.5%) attained completion of metamorphosis. This number of metamorphosed frogs corresponds to 62.1% of the normally cleaved eggs (Table 1).

2. Inter- and intraspecific matings between female *Rana lessonae* from Italy and five kinds of males

a. Male *Rana lessonae* from Italy (Control mating)

In 1977, control matings were made between three female *Rana lessonae* from Italy (*les* I.W77♀, Nos. 1～3) and two male *Rana lessonae* from Italy (*les* I.W77♂, Nos. 1 and 2). It was found that 277 (60.6%) of 457 eggs cleaved normally, 261 (57.1%) became normal neurulae and 223 (48.8%) developed into normal

TABLE 2
Developmental capacity of the hybrids between female *Rana lessonae* from Italy and five kinds of males

Year	Parents		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	PMC
	Female	Male								
1977	*les* I.W77, No. 1	*les* I.W77, No. 1	160	82 (51.3%)	77 (48.1%)	48 (30.0%)	23 (14.4%)	20 (12.5%)	20 (12.5%)	24.4
		les L. 75, No. 3	226	116 (51.3%)	97 (42.9%)	86 (38.1%)	69 (30.5%)	67 (29.6%)	61 (27.0%)	52.6
		rid F.W74, No. 3	104	19 (18.3%)	11 (10.6%)	9 (8.7%)	8 (7.7%)	7 (6.7%)	7 (6.7%)	36.8
		rid T.W76, No. 2	222	55 (24.8%)	36 (16.2%)	29 (13.1%)	27 (12.2%)	24 (10.8%)	11 (5.0%)	20.0
		esc G.W76, No. 1	197	101 (51.3%)	78 (39.6%)	74 (37.6%)	66 (33.5%)	65 (33.0%)	51 (25.9%)	50.5
	les I.W77, No. 2	*les* I.W77, No. 1	165	105 (63.6%)	97 (58.8%)	91 (55.2%)	88 (53.3%)	73 (44.2%)	56 (33.9%)	53.3
		les L. 75, No. 3	183	144 (78.7%)	144 (78.7%)	136 (74.3%)	127 (69.4%)	119 (65.0%)	106 (57.9%)	73.6
		rid F.W74, No. 4	278	236 (84.9%)	155 (55.8%)	150 (54.0%)	143 (51.4%)	130 (46.8%)	117 (42.1%)	49.6
		rid T.W76, No. 3	237	192 (81.0%)	149 (62.9%)	129 (54.4%)	111 (46.8%)	106 (44.7%)	91 (38.4%)	47.4
		rid S.W76, No. 1	207	36 (17.4%)	26 (12.6%)	25 (12.1%)	21 (10.1%)	20 (9.7%)	19 (9.2%)	52.8
		esc G.W76, No. 1	219	188 (85.8%)	188 (85.8%)	186 (84.9%)	177 (80.8%)	168 (76.7%)	122 (55.7%)	64.9
	les I.W77, No. 3	*les* I.W77, No. 2	132	90 (68.2%)	87 (65.9%)	84 (63.6%)	76 (57.6%)	72 (54.5%)	67 (50.8%)	74.4
		esc G.W76, No. 1	240	196 (81.7%)	157 (65.4%)	131 (54.6%)	105 (43.8%)	101 (42.1%)	74 (30.8%)	37.8
Total	*les* I. (3)	*les* I. (2)	457	277 (60.6%)	261 (57.1%)	223 (48.8%)	187 (40.9%)	165 (36.1%)	143 (31.3%)	51.6
	les I. (2)	*les* L. (1)	409	260 (63.6%)	241 (58.9%)	222 (54.3%)	196 (47.9%)	186 (45.5%)	167 (40.8%)	64.2
	les I. (2)	*rid* F. (2)	382	255 (66.8%)	166 (43.5%)	159 (41.6%)	151 (39.5%)	137 (35.9%)	124 (32.5%)	48.6
	les I. (2)	*rid* T. (2)	459	247 (53.8%)	185 (40.3%)	158 (34.4%)	138 (30.1%)	130 (28.3%)	102 (22.2%)	41.3
	les I. (1)	*rid* S. (1)	207	36 (17.4%)	26 (12.6%)	25 (12.1%)	21 (10.1%)	20 (9.7%)	19 (9.2%)	52.8
	les I. (3)	*esc* G. (1)	656	485 (73.9%)	423 (64.5%)	391 (59.6%)	348 (53.0%)	334 (50.9%)	247 (37.7%)	50.9

PMC, Percentage of metamorphosed frogs to normally cleaved eggs

tail-bud embryos. Thereafter, 187 (40.9%) hatched normally, 165 (36.1%) became normally feeding tadpoles and 143 (31.3%) attained completion of metamorphosis. This number of metamorphosed frogs corresponds to 51.6% of the normally cleaved eggs (Table 2).

b. Male *Rana lessonae* from Luxembourg

Two (*les* I.W77♀, Nos. 1 and 2) of the above three female *Rana lessonae* from Italy were mated in 1977 with a male *Rana lessonae* from Luxembourg (*les* L. 75♂, No. 3) obtained in 1975 from the foregoing mating, *les* L.W72♀, No. 1 × *les* L.W72♂, No. 1. It was found that 260 (63.6%) of 409 eggs cleaved normally, 241 (58.9%) became normal neurulae and 222 (54.3%) developed into normal tail-bud embryos. Thereafter, 196 (47.9%) hatched normally, 186 (45.5%)

became normally feeding tadpoles and 167 (40.8%) attained completion of metamorphosis. This number of metamorphosed frogs corresponds to 64.2% of the normally cleaved eggs (Table 2).

c. Male *Rana ridibunda* from France

The foregoing two female *Rana lessonae* from Italy (*les* I.W77♀, Nos. 1 and 2) were mated in 1977 with two male *Rana ridibunda* from France (*rid* F.W74♂, Nos. 3 and 4). It was found that 255 (66.8%) of 382 eggs cleaved normally, 166 (43.5%) became normal neurulae and 159 (41.6%) developed into normal tail-bud embryos. Thereafter, 151 (39.5%) hatched normally, 137 (35.9%) began to eat normally and 124 (32.5%) completed metamorphosis. This number of metamorphosed frogs corresponds to 48.6% of the normally cleaved eggs (Table 2).

d. Male *Rana ridibunda* from Turkey

The foregoing two female *Rana lessonae* from Italy (*les* I.W77♀, Nos. 1 and 2) were mated in 1977 with two male *Rana ridibunda* from Turkey (*rid* T.W76♂, Nos. 2 and 3). It was found that 247 (53.8%) of 459 eggs cleaved normally, 185 (40.3%) became normal neurulae and 158 (34.4%) developed into normal tail-bud embryos. Thereafter, 138 (30.1%) hatched normally, 130 (28.3%) began to eat normally and 102 (22.2%) completed metamorphosis. This number of metamorphosed frogs corresponds to 41.3% of the normally cleaved eggs (Table 2).

e. A male *Rana ridibunda* from Soviet Union

A female *Rana lessonae* from Italy (*les* I.W77♀, No. 2) was mated in 1977 with a male *Rana ridibunda* from Soviet Union (*rid* S.W76♂, No. 1). It was found that 36 (17.4%) of 207 eggs cleaved normally, 26 (12.6%) became normal neurulae and 25 (12.1%) developed into normal tail-bud embryos. Thereafter, 21 (10.1%) hatched normally, 20 (9.7%) began to eat normally and 19 (9.2%) completed metamorphosis. This number of metamorphosed frogs corresponds to 52.8% of the normally cleaved eggs (Table 2).

f. A male *Rana esculenta* from West Germany

Three female *Rana lessonae* from Italy (*les* I.W77♀, Nos. 1～3) were mated in 1977 with a male *Rana esculenta* from West Germany (*esc* G.W76♂, No. 1). It was found that 485 (73.9%) of 656 eggs cleaved normally, 423 (64.5%) became normal neurulae and 391 (59.6%) developed into normal tail-bud embryos. Thereafter, 348 (53.0%) hatched normally, 334 (50.9%) began to eat normally and 247 (37.7%) completed metamorphosis. This number of metamorphosed frogs corresponds to 50.9% of the normally cleaved eggs (Table 2).

3. Inter- and intraspecific matings between female *Rana ridibunda* from Turkey and five kinds of males

In 1977, a female *Rana ridibunda* from Turkey (*rid* T.W76♀, No. 1) which was

TABLE 3

Developmental capacity of the hybrids between female *Rana ridibunda* from Turkey and five kinds of males

Year	Parents		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	PMC
	Female	Male								
1977	*rid* T.W76, No. 1	*rid* T.W76, No. 2	130	66 (50.8%)	14 (10.8%)	11 (8.5%)	7 (5.4%)	7 (5.4%)	5 (3.8%)	7.6
		rid F.W74, No. 3	132	55 (41.7%)	12 (9.1%)	9 (6.8%)	8 (6.1%)	6 (4.5%)	6 (4.5%)	10.9
		rid S.W76, No. 1	158	24 (15.2%)	14 (8.9%)	11 (7.0%)	9 (5.7%)	9 (5.7%)	9 (5.7%)	37.5
		les L. 75, No. 3	128	30 (23.4%)	15 (11.7%)	12 (9.4%)	11 (8.6%)	10 (7.8%)	10 (7.8%)	33.3
		les I.W77, No. 1	140	52 (37.1%)	26 (18.6%)	20 (14.3%)	17 (12.1%)	15 (10.7%)	11 (7.9%)	21.2
		esc G.W76, No. 1	162	76 (46.9%)	18 (11.1%)	13 (8.0%)	9 (5.6%)	9 (5.6%)	7 (4.3%)	9.2
1978	*rid* T.W76, No. 2	*rid* T. 77, No. 4	530	522 (98.5%)	508 (95.8%)	506 (95.5%)	503 (94.9%)	463 (87.4%)	418 (78.9%)	80.1
		rid S. 77, No. 2	264	235 (89.0%)	225 (85.2%)	221 (83.7%)	213 (80.7%)	210 (79.5%)	203 (76.9%)	86.4
		les L. 76, No. 5	273	242 (88.6%)	239 (87.5%)	234 (85.7%)	233 (85.3%)	215 (78.8%)	188 (68.9%)	77.7
		les I.W77, No. 3	242	226 (93.4%)	211 (87.2%)	208 (86.0%)	204 (84.3%)	204 (84.3%)	196 (81.0%)	86.7
		esc G.W76, No. 2	255	235 (92.2%)	234 (91.8%)	228 (89.4%)	228 (89.4%)	226 (88.6%)	217 (85.1%)	92.3

PMC, Percentage of metamorphosed frogs to normally cleaved eggs

one of the two females reared in our laboratory was mated with six kinds of males, a male *Rana ridibunda* from Turkey (*rid* T.W76♂, No. 2), a male *Rana ridibunda* from France (*rid* F.W74♂, No. 3), a male *Rana ridibunda* from Soviet Union (*rid* S.W76♂, No. 1), a male *Rana lessonae* from Luxembourg (*les* L.75♂, No. 3) obtained in 1975 from a mating, *les* L.W72♀, No. 1 × *les* L.W72♂, No. 1, a male *Rana lessonae* from Italy (*les* I.W77♂, No. 1) and a male *Rana esculenta* from West Germany (*esc* G.W76♂, No. 1). The results showed that 66 (50.8%) of 130 eggs, 55 (41.7%) of 132 eggs, 24 (15.2%) of 158 eggs, 30 (23.4%) of 128 eggs, 52 (37.1%) of 140 eggs and 76 (46.9%) of 162 eggs cleaved normally, respectively. From these six kinds of matings, 14 (10.8%), 12 (9.1%), 14 (8.9%), 15 (11.7%), 26 (18.6%) and 18 (11.1%) became normal neurulae, respectively, and 11 (8.5%), 9 (6.8%), 11 (7.0%), 12 (9.4%), 20 (14.3%) and 13 (8.0%) developed into normal tail-bud embryos, respectively. Thereafter, 7 (5.4%), 8 (6.1%), 9 (5.7%), 11 (8.6%), 17 (12.1%) and 9 (5.6%) hatched normally, respectively, 7 (5.4%), 6 (4.5%), 9 (5.7%), 10 (7.8%), 15 (10.7%) and 9 (5.6%) began to eat normally, respectively, and 5 (3.8%), 6 (4.5%), 9 (5.7%), 10 (7.8%), 11 (7.9%) and 7 (4.3%) attained completion of metamorphosis, respectively. These numbers of metamorphosed frogs correspond to 7.6%, 10.9%, 37.5%, 33.3%, 21.2% and 9.2% of the normally cleaved eggs, respectively (Table 3).

In 1978, the other female *Rana ridibunda* from Turkey (*rid* T.W76♀, No. 2) was mated with a male *Rana ridibunda* from Turkey (*rid* T.77♂, No. 4) obtained in 1977 from a mating, *rid* T.W76♀, No. 1 × *rid* T.W76♂, No. 2, a male *Rana ridibunda* from Soviet Union (*rid* S.77♂, No. 2) obtained in 1977 from a mating,

rid S.W76♀, No. 1×*rid* S.W76♂, No. 1, a male *Rana lessonae* from Luxembourg (*les* L.76♂, No. 5) obtained in 1976 from a mating, *les* L.W75♀, No. 2×*les* L.W75♂, No. 2, a male *Rana lessonae* from Italy (*les* I.W77♂, No. 3) collected in 1977 from the field, and a male *Rana esculenta* from West Germany (*esc* G.W76♂, No. 2) collected in 1976 from the field. It was found that 522 (98.5%) of 530 eggs, 235 (89.0%) of 264 eggs, 242 (88.6%) of 273 eggs, 226 (93.4%) of 242 eggs and 235 (92.2%) of 255 eggs cleaved normally, respectively. From these five matings, 508 (95.8%), 225 (85.2%), 239 (87.5%), 211 (87.2%) and 234 (91.8%) became normal neurulae, respectively, and 506 (95.5%), 221 (83.7%), 234 (85.7%), 208 (86.0%) and 228 (89.4%) developed into normal tail-bud embryos, respectively. Thereafter, 503 (94.9%), 213 (80.7%), 233 (85.3%), 204 (84.3%) and 228 (89.4%) hatched normally, respectively, 463 (87.4%), 210 (79.5%), 215 (78.8%), 204 (84.3%) and 226 (88.6%) began to eat normally, respectively, and eventually 418 (78.9%), 203 (76.9%), 188 (68.9%), 196 (81.0%) and 217 (85.1%) attained completion of metamorphosis, respectively. These numbers of metamorphosed frogs correspond to 80.1%, 86.4%, 77.7%, 86.7% and 92.3% of the normally cleaved eggs, respectively (Table 3). These results of the mating experiments performed in 1978 showed that the eggs of the female (*rid* T.W76♀, No. 2) were remarkably superior in developmental capacity when compared with those of the female (*rid* T.W76♀, No. 1) used in 1977 (Table 3).

4. Inter- and intraspecific matings between a female *Rana ridibunda* from Soviet Union and five kinds of males

In 1977, a female *Rana ridibunda* from Soviet Union (*rid* S.W76♀, No. 1) was mated with a male *Rana ridibunda* from Soviet Union (*rid* S.W76♂, No. 1), a male *Rana ridibunda* from France (*rid* F.W74♂, No. 3), a male *Rana ridibunda* from Turkey (*rid* T.W76♂, No. 2), a 2-year-old male *Rana lessonae* from Luxembourg (*les* L.75♂, No. 3) obtained in 1975 from a mating, *les* L.W72♀, No. 1×*les* L.W72♂, No. 1, a male *Rana lessonae* from Italy (*les* I.W77♂, No. 1) and a male

TABLE 4

Developmental capacity of the hybrids between a female *Rana ridibunda* from Soviet Union and five kinds of males

Year	Parents		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	PMC
	Female	Male								
1977	*rid* S.W76, No. 1	*rid* S.W76, No. 1	274	80 (29.2%)	20 (7.3%)	20 (7.3%)	16 (5.8%)	14 (5.1%)	12 (4.4%)	15.0
		rid F.W74, No. 3	169	65 (38.5%)	45 (26.6%)	38 (22.5%)	28 (16.6%)	26 (15.4%)	18 (10.7%)	27.7
		rid T.W76, No. 2	195	97 (49.7%)	75 (38.5%)	63 (32.3%)	41 (21.0%)	33 (16.9%)	30 (15.4%)	30.9
		les L. 75, No. 3	169	66 (39.1%)	47 (27.8%)	32 (18.9%)	25 (14.8%)	23 (13.6%)	14 (8.3%)	21.2
		les I.W77, No. 1	196	69 (35.2%)	50 (25.5%)	32 (16.3%)	30 (15.3%)	27 (13.8%)	20 (10.2%)	29.0
		esc G.W76, No. 1	170	62 (36.5%)	43 (25.3%)	31 (18.2%)	26 (15.3%)	22 (12.9%)	17 (10.0%)	27.4

PMC, Percentage of metamorphosed frogs to normally cleaved eggs

Rana esculenta (*esc* G.W76♂, No. 1). The results showed that 80 (29.2%) of 274 eggs, 65 (38.5%) of 169 eggs, 97 (49.7%) of 195 eggs, 66 (39.1%) of 169 eggs, 69 (35.2%) of 196 eggs and 62 (36.5%) of 170 eggs cleaved normally, respectively. From these six matings, 20 (7.3%), 45 (26.6%), 75 (38.5%), 47 (27.8%), 50 (25.5%) and 43 (25.3%) became normal neurulae, and 20 (7.3%), 38 (22.5%), 63 (32.3%), 32 (18.9%), 32 (16.3%) and 31 (18.2%) developed into normal tail-bud embryos, respectively. Thereafter, 16 (5.8%), 28 (16.6%), 41 (21.0%), 25 (14.8%), 30 (15.3%) and 26 (15.3%) hatched normally, respectively, 14 (5.1%), 26 (15.4%), 33 (16.9%), 23 (13.6%), 27 (13.8%) and 22 (12.9%) began to eat normally, respectively, and 12 (4.4%), 18 (10.7%), 30 (15.4%), 14 (8.3%), 20 (10.2%) and 17 (10.0%) attained completion of metamorphosis, respectively. These numbers of metamorphosed frogs correspond to 15.0%, 27.7%, 30.9%, 21.2%, 29.0% and 27.4% of the normally cleaved eggs, respectively (Table 4).

II. Sex of hybrids

1. Inter- and intraspecific hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

a. Controls, *les* L♀ × *les* L♂

In 1975, 1976 and 1977, five mating experiments were made between five females and four males of *Rana lessonae* from Luxembourg. From these five

TABLE 5

Sex and external appearance of the hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

Year	Parents		No. of mature frogs	Female	Male (%)	External appearance (Type)
	Female	Male				
1975	*les* L.W72, No. 1	*les* L.W72, No. 1	59 (74)	30	29 (49.2)	LL
		rid F.W74, No. 1	148 (244)	75	73 (49.3)	LR
1976	*les* L.W75, No. 2	*les* L.W75, No. 2	58 (58)	24	34 (58.6)	LL
		rid F.W74, No. 2	54 (62)	25	29 (53.7)	LR
		rid T.W76, No. 1	61 (70)	26	35 (57.4)	LR
	les L.W75, No. 3	*les* L.W75, No. 2	112 (141)	58	54 (48.2)	LL
		rid F.W74, No. 2	42 (42)	20	22 (52.4)	LR
		rid T.W76, No. 1	149 (179)	55	94 (63.1)	LR
1977	*les* L. 75, No. 4	*les* L. 75, No. 3	47 (58)	22	25 (53.2)	LL
		les I.W77, No. 1	27 (36)	9	18 (66.7)	LL
		esc G.W76, No. 1	17	12	5	LR
			15 (41)	0	15 (62.5)	LL
	les L. 75, No. 5	*les* L. 75, No. 4	88 (137)	43	45 (51.1)	LL
		les I.W77, No. 2	106 (174)	46	60 (56.6)	LL
Total	*les* L. (5)	*les* L. (4)	364 (468)	177	187 (51.4)	LL
	les L. (2)	*les* I. (2)	133 (210)	55	78 (58.6)	LL
	les L. (3)	*rid* F. (2)	244 (348)	120	124 (50.8)	LR
	les L. (2)	*rid* T. (1)	210 (249)	81	129 (61.4)	LR
	les L. (1)	*esc* G. (1)	32 (41)	12	20 (62.5)	LR or LL

Values in parentheses in the columns of parents and mature frogs show the numbers of parents and normally metamorphosed frogs, respectively.

matings, 74, 58, 141, 58 and 137, 468 in total, normally metamorphosed frogs were produced. Of these frogs, 59, 58, 112, 47 and 88, 364 in total, attained sexual maturity, respectively. When the sex of mature frogs produced from the five matings was examined, 30, 24, 58, 22 and 43, 177 in total, of these frogs were females, while the remaining 29 (49.2%), 34 (58.6%), 54 (48.2%), 25 (53.2%) and 45 (51.1%), 187 (51.4%) in total, were males (Table 5).

b. Intraspecific hybrids, *les* L♀ × *les* I♂

In 1977, two mating experiments were made between two female *Rana lessonae* from Luxembourg and two male *Rana lessonae* from Italy. Although these two matings produced 36 and 174, 210 in total, normally metamorphosed frogs, 27 and 106, 133 in total, of these juvenile frogs attained sexual maturity. Of the mature frogs, 9 and 46, 55 in total, were females, while the remaining 18 (66.7%) and 60 (56.6%), 78 (58.6%) in total, were males (Table 5). The percentages of males in these matings were somewhat higher than those in the control matings.

c. Interspecific hybrids, *les* L♀ × *rid* F♂

In 1975 and 1976, three mating experiments were made between three female *Rana lessonae* from Luxembourg and two male *Rana ridibunda* from France. From these matings, 244, 62 and 42, 348 in total, normally metamorphosed frogs were produced. Of these juvenile frogs, 148, 54 and 42, 244 in total, attained sexual maturity. When the sex of these mature frogs was examined, 75, 25 and 20 of them, 120 in total, were females, while the other 73 (49.3%), 29 (53.7%) and 22 (52.4%), 124 (50.8%) in total, were males (Table 5).

d. Interspecific hybrids, *les* L♀ × *rid* T♂

In 1976, two mating experiments were made between two female *Rana lessonae* from Luxembourg and a male *Rana ridibunda* from Turkey. From these matings, 70 and 179, 249 in total, normally metamorphosed frogs were produced. Of these frogs, 61 and 149, 210 in total, attained sexual maturity. When the sex of these mature frogs was examined, it was found that 26 and 55, 81 in total, were females, while 35 (57.4%) and 94 (63.1%), 129 (61.4%) in total, were males. It was remarkable that males were fairly more numerous than females in the hybrids produced from these matings (Table 5).

e. Interspecific hybrids, *les* L♀ × *esc* G♂

In 1977, a mating experiment was made between a female *Rana lessonae* from Luxembourg and a male *Rana esculenta* from West Germany. From this mating, 41 normally metamorphosed frogs were produced. Of these juvenile frogs, 32 attained sexual maturity. Twelve of the mature frogs were females which were all of the LR-type and very similar to the paternal *Rana esculenta* in external characters. The other 20 (62.5%) were males, 15 of which were small in size and very similar to *Rana lessonae* in external appearance, while the remaining five were of the LR-type like the females (Table 5).

2. Inter- and intraspecific hybrids between female *Rana lessonae* from Italy and five kinds of males

a. Controls, *les* I♀ × *les* I♂

In 1977, three control matings were made between three (Nos. 1～3) female and two (Nos. 1 and 2) male *Rana lessonae* from Italy. The results showed that 20, 56 and 67 tadpoles, 143 in total, completed metamorphosis, and 19, 49 and 61, 129 in total, of the juvenile frogs attained sexual maturity. Of these mature frogs, 9, 23 and 30, 62 in total, were females, while the remaining 10 (52.6%), 26 (53.1%) and 31 (50.8%), 67 (51.9%) in total, were males (Table 6).

TABLE 6

Sex and external appearance of the hybrids between female *Rana lessonae* from Italy and five kinds of males

Year	Parents		No. of mature frogs	Female	Male (%)	External appearance (Type)
	Female	Male				
1977	*les* I.W77, No. 1	*les* I.W77, No. 1	19 (20)	9	10 (52.6)	LL
		les L. 75, No. 3	58 (61)	16	42 (72.4)	LL
		rid F.W74, No. 3	5 (7)	0	5	LR
		rid T.W76, No. 2	8 (11)	1	7 (87.5)	LR
		esc G.W76, No. 1	29	24	5	LR
			20 (51)	0	20 (51.0)	LL
	les I.W77, No. 2	*les* I.W77, No. 1	49 (56)	23	26 (53.1)	LL
		les L. 75, No. 3	83 (106)	35	48 (57.8)	LL
		rid F.W74, No. 4	99 (117)	42	57 (57.6)	LR
		rid T.W76, No. 3	81 (91)	23	58 (71.6)	LR
		rid S.W76, No. 1	12 (19)	0	12	LR
		esc G.W76, No. 1	51	36	15	LR
			54 (122)	0	54 (65.7)	LL
	les I.W77, No. 3	*les* I.W77, No. 2	61 (67)	30	31 (50.8)	LL
		esc G.W76, No. 1	31	26	5	LR
			29 (74)	0	29 (56.7)	LL
Total	*les* I. (3)	*les* I. (2)	129 (143)	62	67 (51.9)	LL
	les I. (2)	*les* L. (1)	141 (167)	51	90 (63.8)	LL
	les I. (2)	*rid* F. (2)	104 (124)	42	62 (59.6)	LR
	les I. (2)	*rid* T. (2)	89 (102)	24	65 (73.0)	LR
	les I. (1)	*rid* S. (1)	12 (19)	0	12	LR
	les I. (3)	*esc* G. (1)	214 (247)	86	128 (59.8)	LR or LL

Values in parentheses in the columns of parents and mature frogs show the numbers of parents and normally metamorphosed frogs, respectively.

b. Intraspecific hybrids, *les* I♀ × *les* L♂

In 1977, two mating experiments were made between two (Nos. 1 and 2) of the above three female *Rana lessonae* from Italy and a male *Rana lessonae* from Luxembourg. The results showed that 61 and 106 tadpoles, 167 in total, completed metamorphosis, and 58 and 83, 141 in total, of the juvenile frogs attained sexual maturity. Of these mature frogs, 16 and 35, 51 in total, were females, while the other 42 (72.4%) and 48 (57.8%), 90 (63.8%) in total, were males. It was

found that males were fairly numerous, when compared with those in the control matings (Table 6).

c. Interspecific hybrids, *les* I♀ × *rid* F♂

In 1977, two mating experiments were made between the above two female *Rana lessonae* from Italy and two male *Rana ridibunda* from France. It was found that seven and 117 tadpoles, 124 in total, completed metamorphosis, and five and 99 of them, 104 in total, attained sexual maturity. Of these mature frogs, 42 from mating with female No. 2 were females, while five (100%) from mating with female No. 1 and the remaining 57 (57.6%) from mating with female No. 2, 62 (59.6%) in total, were males. In these matings, males were fairly more numerous than females (Table 6).

d. Interspecific hybrids, *les* I♀ × *rid* T♂

In 1977, two mating experiments were made between the above two female *Rana lessonae* from Italy and two male *Rana ridibunda* from Turkey. The results showed that 11 and 91 tadpoles, 102 in total, completed metamorphosis, and eight and 81 of them, 89 in total, attained sexual maturity. Of these mature frogs, one and 23, 24 in total, were females, while the other seven (87.5%) and 58 (71.6%), 65 (73.0%) in total, were males. It was remarkable that the males were very numerous, when compared with the females (Table 6).

e. Interspecific hybrids, *les* I♀ × *rid* S♂

In 1977, a mating experiment between one (No. 2) of the above two female *Rana lessonae* from Italy and a male *Rana ridibunda* from Soviet Union was made. From this mating, 19 normally metamorphosed frogs were produced. Of these juvenile frogs, 12 attained sexual maturity and all became males (Table 6).

f. Interspecific hybrids, *les* I♀ × *esc* G♂

In 1977, three mating experiments were made between three (Nos. 1~3) female *Rana lessonae* from Italy and one male *Rana esculenta* from West Germany. The results showed that 51, 122 and 74 tadpoles, 247 in total, completed metamorphosis, and 49, 105 and 60 of them, 214 in total, attained sexual maturity. Of these mature frogs, 24, 36 and 26, 86 in total, were females which were all of the LR-type in external characters. The remaining 25 (51.0%), 69 (65.7%) and 34 (56.7%), 128 (59.8%) in total, were males. Of these males, five of 25 from mating with female No. 1, 15 of 69 from mating with female No. 2 and five of 34 from mating with female No. 3, 25 in total, were of the LR-type, while the other 103 were all of the LL-type (Table 6).

3. Inter- and intraspecific hybrids between female *Rana ridibunda* from Turkey and five kinds of males

a. Controls, *rid* T♀ × *rid* T♂

In 1977, a mating experiment was made between a female (*rid* T.W76♀,

TABLE 7
Sex and external appearance of the hybrids between female *Rana ridibunda* from Turkey and five kinds of males

Year	Parents		No. of mature frogs	Female	Male (%)	External appearance (Type)
	Female	Male				
1977	*rid* T.W76, No. 1	*rid* T.W76, No. 2	5 (5)	0	5	RR
		rid F.W74, No. 3	5 (6)	0	5	RR
		rid S.W76, No. 1	6 (9)	6	0	RR
		les L. 75, No. 3	8 (10)	2	6 (75.0)	RL
		les I.W77, No. 1	9 (11)	2	7 (77.8)	RL
		esc G.W76, No. 1	5	2	3	RR
			2 (7)	0	2 (71.4)	RL
1978	*rid* T.W76, No. 2	*rid* T. 77, No. 4	314 (418)	312	2 (0.6)	RR
		rid S. 77, No. 2	122 (203)	103	19 (15.6)	RR
		les L. 76, No. 5	82 (188)	42	40 (48.8)	RL
		les I.W77, No. 3	114 (196)	60	54 (47.4)	RL
		esc G.W76, No. 2	154 (217)	152	2 (1.3)	RR

Values in parentheses in the column of mature frogs show the numbers of normally metamorphosed frogs.

No. 1) and a male (*rid* T.W76♂, No. 2) *Rana ridibunda* from Turkey. From this control mating, five metamorphosed frogs were produced. All these frogs attained sexual maturity and became males. One (*rid* T.77♂, No. 4) of these males was mated in 1978 with another female (*rid* T.W76♀, No. 2). Of the tadpoles produced from this mating, 418 completed metamorphosis and 314 attained sexual maturity. Of the latter, 312 were females and only two (0.6%) were males. Thus, it is believed that the male (*rid* T.77♂, No. 4) was a sex-reversed genetic female (Table 7).

b. Intraspecific hybrids, *rid* T♀ × *rid* F♂

In 1977, the foregoing female parent was mated with a male *Rana ridibunda* from France (*rid* F. W74♂, No. 3). From this mating, six normally metamorphosed frogs were produced. Five of them attained sexual maturity and became males (Table 7).

c. Intraspecific hybrids, *rid* T♀ × *rid* S♂

In 1977, the foregoing female was mated with a male *Rana ridibunda* from Soviet Union (*rid* S.W76♂, No. 1). From this mating, nine metamorphosed frogs were produced. Six of them attained sexual maturity and all became females. In 1978, the other female (No. 2) was mated with a male *Rana ridibunda* (*rid* S.77♂, No. 2) obtained in 1977 from a mating between a female (*rid* S.W76♀, No. 1) and a male (*rid* S.W76♂, No. 1) *Rana ridibunda* from Soviet Union. Of 203 metamorphosed frogs produced from this mating, 122 attained sexual maturity. Of these mature frogs, 103 were females and 19 (15.6%) were males (Table 7). Thus, it is believed that the male (*rid* S.77♂, No. 2) was a sex-reversed genetic female (Table 7).

d. Interspecific hybrids, *rid* T♀ × *les* L♂

In 1977, the foregoing female (No. 1) parent was mated with a male *Rana lessonae* from Luxembourg (*les* L.75♂, No. 3). From this mating, 10 metamorphosed frogs were produced. Eight of them attained sexual maturity. Two of the eight were females and six (75.0%) were males. In 1978, the other female (No. 2) parent was mated with a male *Rana lessonae* from Luxembourg (*les* L.76♂, No. 5) and produced 188 metamorphosed frogs. When half the number of these juvenile frogs were continuously reared, 82 of them attained sexual maturity. Of these frogs, 42 were females and 40 (48.8%) were males (Table 7).

e. Interspecific hybrids, *rid* T♀ × *les* I♂

In 1977, the foregoing female (No. 1) parent was mated with a male *Rana lessonae* from Italy (*les* I.W77♂, No. 1). From this mating, 11 metamorphosed frogs were produced. Nine of them attained sexual maturity; two were females and seven (77.8%) were males. In 1978, the other female (No. 2) parent was mated with a male *Rana lessonae* from Italy (*les* I.W77♂, No. 3). From this mating, 196 normally metamorphosed frogs and 114 sexually mature ones were produced. Of these mature frogs, 60 were females and 54 (47.4%) were males (Table 7).

f. Interspecific hybrids, *rid* T♀ × *esc* G♂

In 1977, the foregoing female (No. 1) parent was mated with a male *Rana esculenta* from West Germany (*esc* G.W76♂, No. 1). From this mating, seven normally metamorphosed frogs were obtained. All of them attained sexual maturity. Two were females and were of the RR-type in external characters, while the other five (71.4%) were males, of which three were of the RR-type and two were of the RL-type. In 1978, the other female (No. 2) parent was mated with a male *Rana esculenta* from West Germany (*esc* G.W76♂, No. 2). From this mating, 217 normally metamorphosed frogs were produced. Of these juvenile frogs, 154 attained sexual maturity. All these mature frogs were of the RR-type in external characters and consisted of 152 females and two (1.3%) males (Table 7).

4. Inter- and intraspecific hybrids between a female *Rana ridibunda* from Soviet Union and five kinds of males

a. Controls, *rid* S♀ × *rid* S♂

In 1977, a mating experiment was made between a female (*rid* S.W76♀, No. 1) and a male (*rid* S.W76♂, No. 1) *Rana ridibunda* from Soviet Union. From this mating, 12 normally metamorphosed frogs were produced. Of these juvenile frogs, six attained sexual maturity and became males (Table 8).

b. Intraspecific hybrids, *rid* S♀ × *rid* F♂

In 1977, a mating experiment was made between the foregoing female and a male *Rana ridibunda* from France (*rid* F.W74♂, No. 3). From this mating, 18

TABLE 8
Sex and external appearance of the hybrids between a female *Rana ridibunda* from Soviet Union and five kinds of males

Year	Parents		No. of mature frogs	Female	Male (%)	External appearance (Type)
	Female	Male				
1977	*rid* S.W76, No. 1	*rid* S.W76, No. 1	6 (12)	0	6	RR
		rid F.W74, No. 3	7 (18)	1	6 (85.7)	RR
		rid T.W76, No. 2	29 (30)	8	21 (72.4)	RR
		les L. 75, No. 3	7 (14)	1	6 (85.7)	RL
		les I.W77, No. 1	12 (20)	2	10 (83.3)	RL
		esc G.W76, No. 1	6 (17)	4	2 (60.0)	RR
			4	0	4	RL

Values in parentheses in the column of mature frogs show the numbers of normally metamorphosed frogs.

normally metamorphosed frogs were produced, but only seven of them attained sexual maturity. While one of the mature frogs was a female, the other six (85.7%) were males (Table 8).

c. Intraspecific hybrids, *rid* S♀ × *rid* T♂

In 1977, a mating experiment was made between the foregoing female and a male *Rana ridibunda* from Turkey (*rid* T.W76♂, No. 2). Of 30 normally metamorphosed frogs obtained from this mating, 29 attained sexual maturity. Of these mature frogs, eight were females and 21 (72.4%) were males (Table 8).

d. Interspecific hybrids, *rid* S♀ × *les* L♂

In 1977, a mating experiment was made between the foregoing female and a male *Rana lessonae* from Luxembourg (*les* L.75♂, No. 3). Of 14 normally metamorphosed frogs, seven attained sexual maturity. One of them was a female and six (85. 7%) were males (Table 8).

e. Interspecific hybrids, *rid* S♀ × *les* I♂

In 1977, 20 normally metamorphosed frogs were produced from a mating between the foregoing female and a male *Rana lessonae* from Italy (*les* I.W77♂, No. 1). Of these juvenile frogs, 12 attained sexual maturity. Two of the mature frogs were females and 10 (83.3%) were males (Table 8).

f. Interspecific hybrids, *rid* S♀ × *esc* G♂

In 1977, 17 normally metamorphosed frogs were produced from a mating between the foregoing female and a male *Rana esculenta* from West Germany (*esc* G.W76♂, No. 1). Of these frogs, 10 attained sexual maturity. Four of the mature frogs were females and the other six (60.0%) were males. The four females and two of the males were of the RR-type in external characters, while the other four males were of the RL-type (Table 8).

III. External characters of mature frogs

1. Field-caught frogs used in the present study

a. *Rana lessonae* from Luxembourg

The external characters of *Rana lessonae* from Luxembourg were observed in three females, *les* L.W72♀, No. 1 and *les* L.W75♀, Nos. 2 and 3, and two males, *les* L.W72♂, No. 1 and *les* L.W75♂, No. 2, collected in 1972 and 1975. These frogs were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type).

They were 50.0~58.5 mm, 55.3 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, their distal ends did not come into contact with each other (LL-type). The inner metatarsal tubercle was comparatively large (Figs. 1 and 2). The ratio (b/c) of tibia length (b) to the length of the inner metatarsal tubercle (c) was 6.6~7.9, 7.3 on the average, and the ratio (d/c) of first-toe length (d) to the length of the inner metatarsal tubercle (c) was 7.5~8.6, 8.0 on the average. The height of the inner metatarsal tubercle (e) was also comparatively large. The ratio (b/e) of tibia length (b) to the height of the inner metatarsal tubercle (e) was 10.9~14.7, 12.6 on the average (Table 9; Fig. 3a~d).

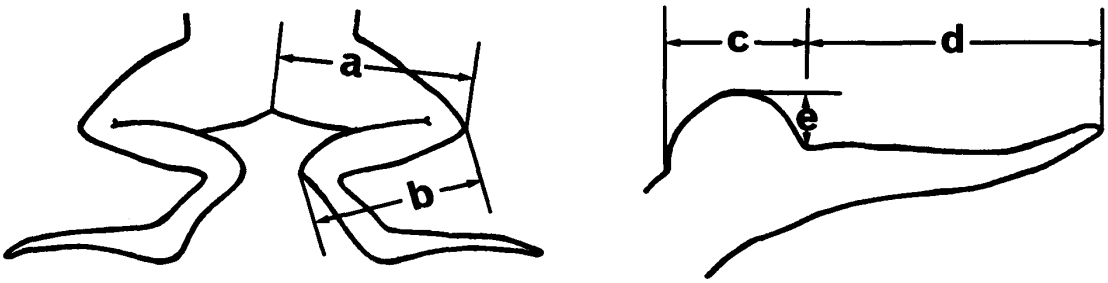


Fig. 1. Sites of measurements in hind legs.

a. Femur length. b. Tibia length.
c. Length of inner metatarsal tubercle.
d. First-toe length.
e. Height of inner metatarsal tubercle.

b. *Rana lessonae* from Italy

The external characters of *Rana lessonae* from Italy were observed in three females, *les* I.W77♀, Nos. 1~3 and two males, *les* I.W77♂, Nos. 1 and 2. Of these five frogs, one female, *les* I.W77♀, No. 1, and the two males were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). These three frogs could scarcely be distinguished from the above *Rana lessonae* from Luxembourg in external characters. In contrast to them, the other two females, *les* I.W77♀, Nos. 2 and 3, were yellowish brown in dorsal ground color and had a light

yellowish-green dorso-median stripe and some irregularly shaped brown-black spots on the back (LL-type).

These five frogs were 55.5～62.5 mm, 60.6 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends of

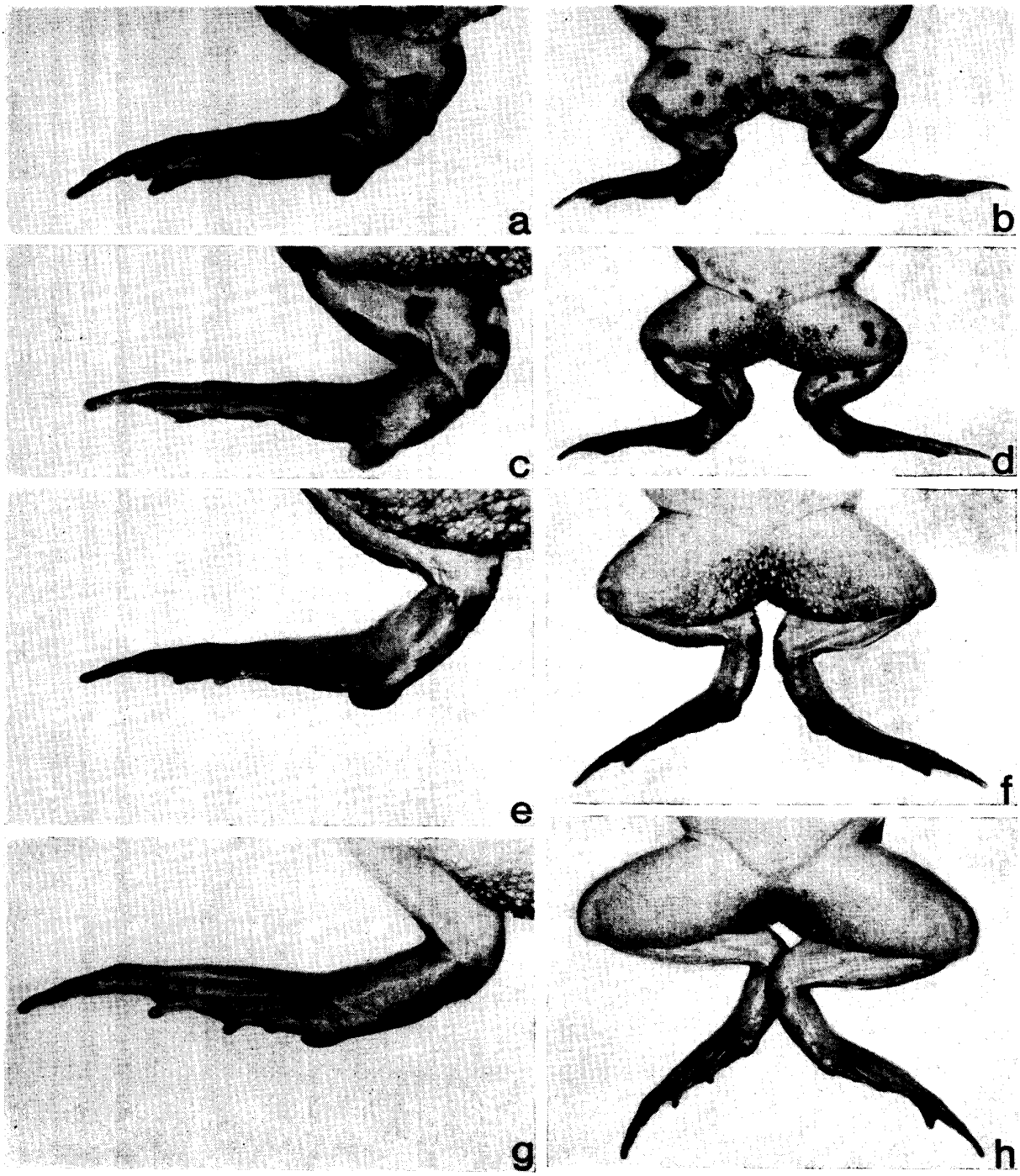


Fig. 2. Aspects of hind legs in four kinds of mature European green frogs.

a, b. LL-type in *Rana lessonae* from Luxembourg.
c, d. LL-type in *Rana lessonae* from Italy.
e, f. RL-type in *Rana esculenta* from West Germany.
g, h. RR-type in *Rana ridibunda* from Turkey.

TABLE 9

External characters of the mature field-caught frogs used in the present study

Kinds	External appearance (Type)	Body lengths (mm)	Femur lengths (mm)	Tibia lengths (mm)	Type of hind legs	b/c	d/c	b/e
les L.W72♀, No. 1	LL	58.5	28.0	25.5	LL	7.7	8.4	12.1
les L.W75♀, No. 2	LL	58.0	29.0	27.0	LL	7.9	8.6	12.3
les L.W75♀, No. 3	LL	58.5	28.0	25.0	LL	6.9	7.5	10.9
les L.W72♂, No. 1	LL	50.0	23.0	22.0	LL	7.4	8.0	14.7
les L.W75♂, No. 2	LL	51.5	26.0	23.5	LL	6.6	7.5	12.8
les I.W77♀, No. 1	LL	61.0	29.0	27.0	LL	6.1	5.8	12.3
les I.W77♀, No. 2	LL	62.0	29.0	28.0	LL	6.0	5.9	12.2
les I.W77♀, No. 3	LL	62.5	29.5	27.0	LL	7.1	7.0	12.3
les I.W77♂, No. 1	LL	62.0	29.5	28.0	LL	7.6	7.6	13.3
les I.W77♂, No. 2	LL	55.5	27.5	26.5	LL	7.6	7.3	13.3
rid F.W74♂, No. 1	RR	76.5	36.0	38.0	RR	8.6	8.0	27.7
rid F.W74♂, No. 2	RR	72.5	33.5	36.0	RR	8.5	8.9	27.9
rid F.W74♂, No. 3	RR	70.0	31.0	32.0	RL	8.9	9.1	25.7
rid F.W74♂, No. 4	RR	62.0	30.0	31.5	RR	10.5	9.8	31.5
rid T.W76♀, No. 1	RR	86.0	38.0	41.5	RR	10.4	10.4	20.8
rid T.W76♀, No. 2	RR	85.0	37.0	40.0	RR	10.0	9.8	20.0
rid T.W76♂, No. 1	RR	86.0	38.0	40.0	RR	11.1	10.8	22.2
rid T.W76♂, No. 2	RR	61.0	30.0	32.5	RR	9.8	8.9	27.3
rid T.W76♂, No. 3	RR	81.0	35.0	37.5	RR	9.3	8.2	26.6
rid S.W76♀, No. 1	RR	85.0	41.0	44.0	RR	10.5	9.8	27.6
rid S.W76♂, No. 1	RR	75.0	37.5	40.0	RR	10.9	9.9	39.8
esc G.W76♂, No. 1	RL	64.5	30.0	32.5	RR	7.9	7.6	19.8
esc G.W76♂, No. 2	RL	58.5	32.0	32.0	RL	10.3	10.2	17.1

b/c, the ratio of tibia length to the length of the inner metatarsal tubercle

d/c, the ratio of first-toe length to the length of the inner metatarsal tubercle

b/e, the ratio of tibia length to the height of the inner metatarsal tubercle

the tibias did not come into contact with each other (LL-type), as observed in *Rana lessonae* from Luxembourg (Figs. 1 and 2). The inner metatarsal tubercle was comparatively large. The ratio b/c was 6.0～7.6, 6.9 on the average, and the ratio d/c was 5.8～7.6, 6.7 on the average. The ratio b/e was 12.2～13.3, 12.7 on the average (Table 9; Fig. 3e～l).

c. *Rana ridibunda* from France

The external characters of *Rana ridibunda* from France were observed in four males, *rid* F.W74♂, Nos. 1～4, collected in 1974. These males were grayish brown in dorsal ground color and had a light green or light olive dorso-median

Fig. 3. Dorsal and ventral views of *Rana lessonae* from Luxembourg and Italy.

a, b. Female from Luxembourg, *les* L.W75♀, No. 2.

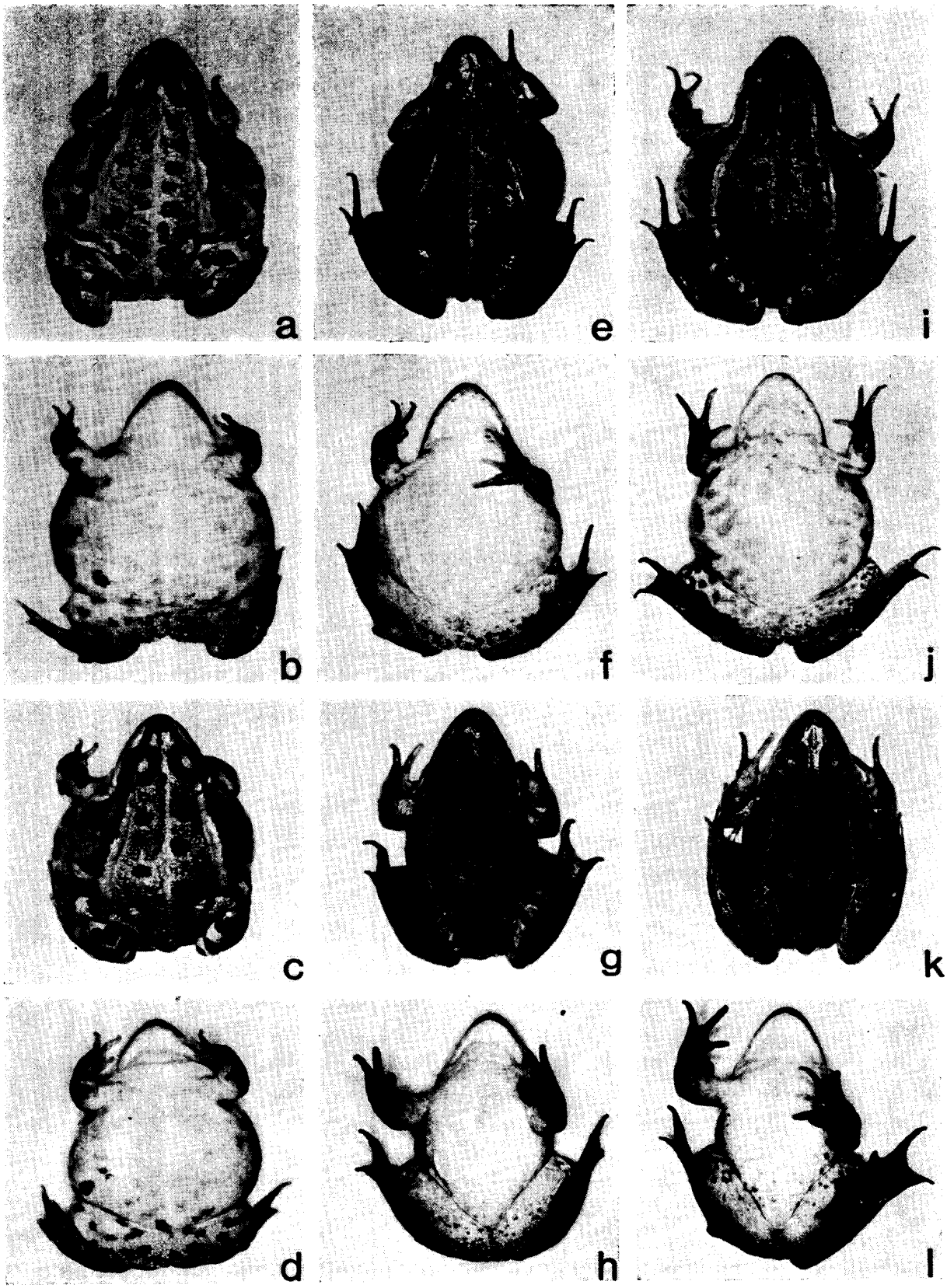
c, d. Male from Luxembourg, *les* L.W75♂, No. 2.

e, f. Female from Italy, *les* I.W77♀, No. 1 (green-type).

g, h. Male from Italy, *les* I.W77♂, No. 1 (green-type).

i, j. Female from Italy, *les* I.W77♀, No. 2 (brown-type).

k, l. Male from Italy, *les* I.W77♂, No. 2 (green-type).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stripe and several brown-black spots on the back which were roundish and somewhat larger than those of *Rana lessonae* (RR-type). Although there were two female *Rana ridibunda* from France, these frogs were not utilized in the present study, as their eggs were very low in fertility. These females had no dorso-median stripe, while they had several roundish brown-black spots on the back.

The four males were 62.0～76.5 mm, 70.3 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, their distal ends overlapped each other (RR-type) in three (Nos. 1, 2 and 4) of the four males, while they barely came into contact (RL-type) in the remaining male. The inner metatarsal tubercle of the first-toe was distinctly smaller than that of *Rana lessonae* (Figs. 1 and 2). The ratio b/c was 8.5～10.5, 9.1 on the average, and the ratio d/c was 8.0～9.8, 9.0 on the average. The ratio b/e was 25.7～31.5, 28.2 on the average (Table 9; Fig. 4a～d).

d. *Rana ridibunda* from Turkey

The external characters of *Rana ridibunda* from Turkey were observed in two females, *rid* T.W76♀, Nos. 1 and 2, and three males, *rid* T.W76♂, Nos. 1～3. All these five frogs were grayish brown in dorsal ground color and had a light green or light olive dorso-median stripe and several roundish brown-black spots on the back which were remarkably larger than those of *Rana lessonae* (RR-type).

They were 61.0～86.0 mm, 79.8 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, their distal ends overlapped each other (RR-type) in all the five frogs. The inner metatarsal tubercle was small (Figs. 1 and 2). The ratio b/c was 9.3～11.1, 10.1 on the average, and the ratio d/c was 8.2～10.8, 9.6 on the average. The ratio b/e was 20.0～27.3, 23.4 on the average (Table 9; Fig. 4e～h).

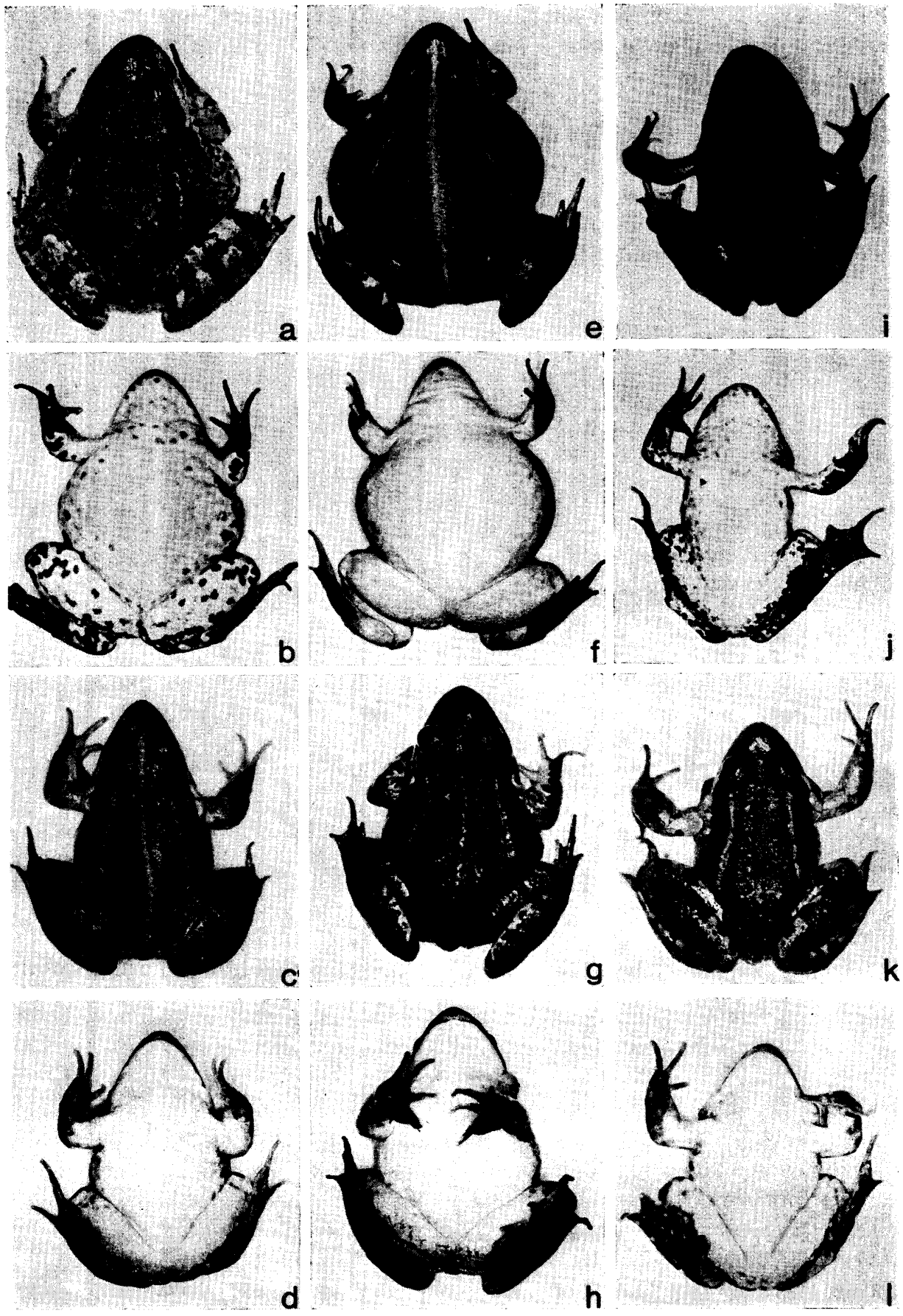
e. *Rana ridibunda* from Soviet Union

A female *Rana ridibunda* (*rid* S.W76♀, No. 1) collected in 1976 from Soviet Union was olive brown in dorsal ground color and had a light-olive dorso-median stripe and several somewhat large, roundish brown-black spots on the back (RR-type). A male *Rana ridibunda* (*rid* S.W76♂, No. 1) collected in 1976 from Soviet Union was grayish brown in dorsal ground color and had no dorso-median stripe, while there were several large, roundish brown-black spots (RR-type).

They were 85.0 mm and 75.0 mm, 80.0 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, their distal ends overlapped each other (RR-type). The inner metatarsal tubercle was small

Fig. 4. Dorsal and ventral views of *Rana ridibunda* from France, Turkey and Soviet Union.

a, b. Female from France, *rid* F.W74♀, No. 1.
c, d. Male from France, *rid* F.W74♂, No. 3.
e, f. Female from Turkey, *rid* T.W76♀, No. 1.
g, h. Male from Turkey, *rid* T.W76♂, No. 2.
i, j. Female from Soviet Union, *rid* S.W76♀, No. 1.
k, l. Male from Soviet Union, *rid* S.W76♂, No. 1.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(RR-type). The ratio b/c was 10.5 or 10.9, 10.7 on the average, the ratio d/c was 9.8 or 9.9, and the ratio b/e was 27.6 or 39.8, 33.7 on the average (Table 9; Fig. 4i~l).

f. *Rana esculenta* from West Germany

Two male *Rana esculenta* (*esc* G.W76♂, Nos. 1 and 2) collected in 1976 from West Germany were green in dorsal ground color and had a light yellowish-green dorso-median stripe and several brown-black spots on the back (RL-type). These spots were small, although somewhat larger than those of *Rana lessonae*.

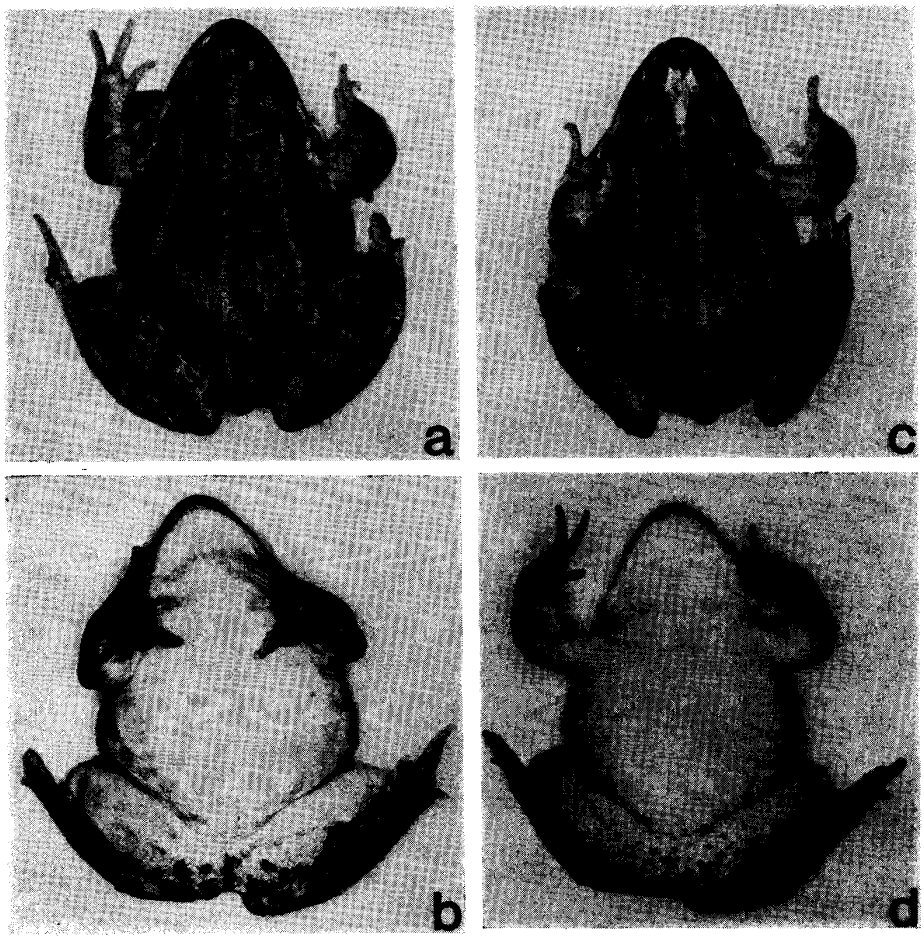

Fig. 5. Dorsal and ventral views of *Rana esculenta* from West Germany.
a, b. Male, *esc* G.W76♂, No. 1. c, d. Male, *esc* G.W76♂, No. 2.

They were 64.5 mm and 58.5 mm, 61.5 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, their distal ends overlapped each other in one (No. 1) of the two males, while they barely came into contact with each other in the other male (No. 2). The ratio b/c was 7.9 or 10.3, 9.1 on the average, the ratio d/c was 7.6 or 10.2, 8.9 on the average, and the ratio b/e was 19.8 or 17.1, 18.5 on the average (Table 9; Fig. 5).

2. Inter- and intraspecific hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

a. Controls, *les* L♀ × *les* L♂

The external characters of 32 offspring obtained from four control matings which were made in 1975, 1976 and 1977 between four females (*les* L♀, Nos. 1～4) and three males (*les* L♂, Nos. 1～3) were observed in 1978. These offspring were one, two or three years old and consisted of 15 females and 17 males.

They were all yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). Five 3-year-old offspring were 46.5～51.0 mm, 49.2 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, their distal ends did not come into contact (LL-type). The ratio b/c was 5.7～7.4, 6.5 on the average, thc ratio d/c was 5.7～8.0, 6.9 on the average, and the ratio b/e was 9.8～14.7, 11.8 on the average.

Ten 2-year-old offspring were 55.5～66.5 mm, 59.9 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, their distal ends did not come into contact with each other (LL-type). The ratios b/c and d/c were 5.3～6.2, 5.5 on the average, and 4.9～6.4, 5.4 on the average, respectively. The ratio b/e was 9.2～10.9, 10.3 on the average. Ten other 2-year-old offspring were 45.0～53.5 mm, 49.7 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in four of the 10 offspring, while they barely came into contact with each other (LR-type) in the remaining six. The ratios b/c and d/c were 5.8～7.3, 6.3 on the average, and 5.4～7.5, 6.4 on the average, respectively. The ratio b/e was 9.2～11.7, 10.4 on the average.

Seven 1-year-old offspring were 48.0～52.5 mm, 50.0 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in two of the seven offspring, while they barely came into contact with each other (LR-type) in the remaining five. The ratios b/c and d/c were 6.4～7.0, 6.6 on the average, and 6.2～7.3, 6.6 on the average, respectively. The ratio b/e was 11.4～13.3, 12.6 on the average (Table 10; Fig. 6a).

b. Interspecific hybrids, *les* L♀ × *rid* F♂

The external characters of 30 hybrids obtained in 1975 and 1976 from three matings between three female *Rana lessonae* from Luxembourg and two male *Rana ridibunda* from France were observed in 1978. They consisted of 15 females and 15 males. These hybrids were green in dorsal ground color. They had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). Ten 3-year-old hybrids produced in 1975 were remarkably larger than the control *Rana lessonae*, being 67.0～81.0 mm, 72.7 mm on the average, in body length. When their tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in

TABLE 10

External characters of the mature hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

Kinds	No. of frogs	Age (years)	External appearance (Type)	Body lengths (mm)	Femur lengths (mm)	Tibia lengths (mm)	Type of hind legs			b/c	d/c	b/e
							LL	LR	RR			
75 *les* L ♀1×*les* L ♂1	5 (♀3, ♂2)	3	LL	46.5~51.0 (49.2)	20.0~26.0 (22.6)	17.0~23.0 (19.8)	5	—	—	5.7~7.4 (6.5)	5.7~8.0 (6.9)	9.8~14.7 (11.8)
75 *les* L ♀1×*rid* F ♂1	10 (♀5, ♂5)	3	LR	67.0~81.0 (72.7)	25.5~32.5 (28.4)	24.5~32.5 (28.2)	6	4	—	5.6~6.4 (5.82±0.12)	5.1~6.1 (5.49±0.16)	11.2~14.3 (12.57±0.40)
76 *les* L ♀2×*les* L ♂2	10 (♀5, ♂5)	2	LL	55.5~66.5 (59.9)	21.5~24.0 (22.5)	20.5~22.0 (21.1)	10	—	—	5.3~6.2 (5.49±0.11)	4.9~6.4 (5.36±0.13)	9.2~10.9 (10.28±0.19)
76 *les* L ♀2×*rid* F ♂2	10 (♀5, ♂5)	2	LR	61.5~70.5 (66.8)	22.5~30.0 (26.9)	22.5~29.0 (25.7)	9	1	—	5.7~7.1 (6.61±0.16)	5.5~7.3 (6.17±0.23)	11.8~15.6 (13.44±0.39)
76 *les* L ♀2×*rid* T ♂1	10 (♀5, ♂5)	2	LR	65.0~74.5 (70.1)	30.0~35.5 (31.9)	28.0~33.0 (29.7)	9	1	—	6.0~7.4 (6.84±0.14)	5.9~7.0 (6.50±0.13)	12.7~14.8 (13.44±0.21)
76 *les* L ♀3×*les* L ♂2	10 (♀5, ♂5)	2	LL	45.0~53.5 (49.7)	17.5~20.5 (18.9)	17.5~21.0 (18.9)	4	6	—	5.8~7.3 (6.29±0.13)	5.4~7.5 (6.42±0.21)	9.2~11.7 (10.44±0.24)
76 *les* L ♀3×*rid* F ♂2	10 (♀5, ♂5)	2	LR	57.0~71.5 (64.8)	23.0~30.0 (26.1)	22.0~29.5 (24.7)	9	1	—	6.2~7.4 (6.69±0.14)	5.9~7.1 (6.62±0.10)	12.6~19.2 (15.70±0.21)
76 *les* L ♀3×*rid* T ♂1	10 (♀5, ♂5)	2	LR	60.5~69.0 (64.2)	24.0~31.5 (27.1)	23.0~30.0 (26.1)	8	2	—	6.6~7.1 (6.83±0.04)	6.6~7.6 (7.22±0.11)	17.5~20.8 (19.00±0.37)
77 *les* L ♀4×*les* L ♂3	7 (♀2, ♂5)	1	LL	48.0~52.5 (50.0)	20.0~22.0 (21.0)	20.0~22.0 (21.1)	2	5	—	6.4~7.0 (6.61±0.08)	6.2~7.3 (6.64±0.11)	11.4~13.3 (12.58±0.27)
77 *les* L ♀4×*les* I ♂1	3 (♂3)	1	LL	47.0~51.5 (49.7)	20.5~24.0 (22.2)	21.5~23.0 (22.5)	2	1	—	6.3~7.7 (7.2)	6.7~8.1 (7.4)	10.2~12.9 (11.5)
77 *les* L ♀4×*esc* G ♂1	5 (♀5)	1	LR	49.0~62.0 (55.0)	20.5~25.5 (22.7)	21.5~27.0 (24.3)	—	5	—	6.1~7.5 (7.0)	6.3~6.9 (6.6)	11.9~13.4 (12.5)
	5 (♂5)	1	LL	45.0~54.5 (49.9)	19.0~24.0 (21.5)	19.0~23.0 (20.4)	4	1	—	5.4~6.6 (6.0)	5.6~6.3 (6.1)	9.1~11.6 (10.0)

b/c, the ratio of tibia length to the length of the inner metatarsal tubercle

d/c, the ratio of first-toe length to the length of the inner metatarsal tubercle

b/e, the ratio of tibia length to the height of the inner metatarsal tubercle

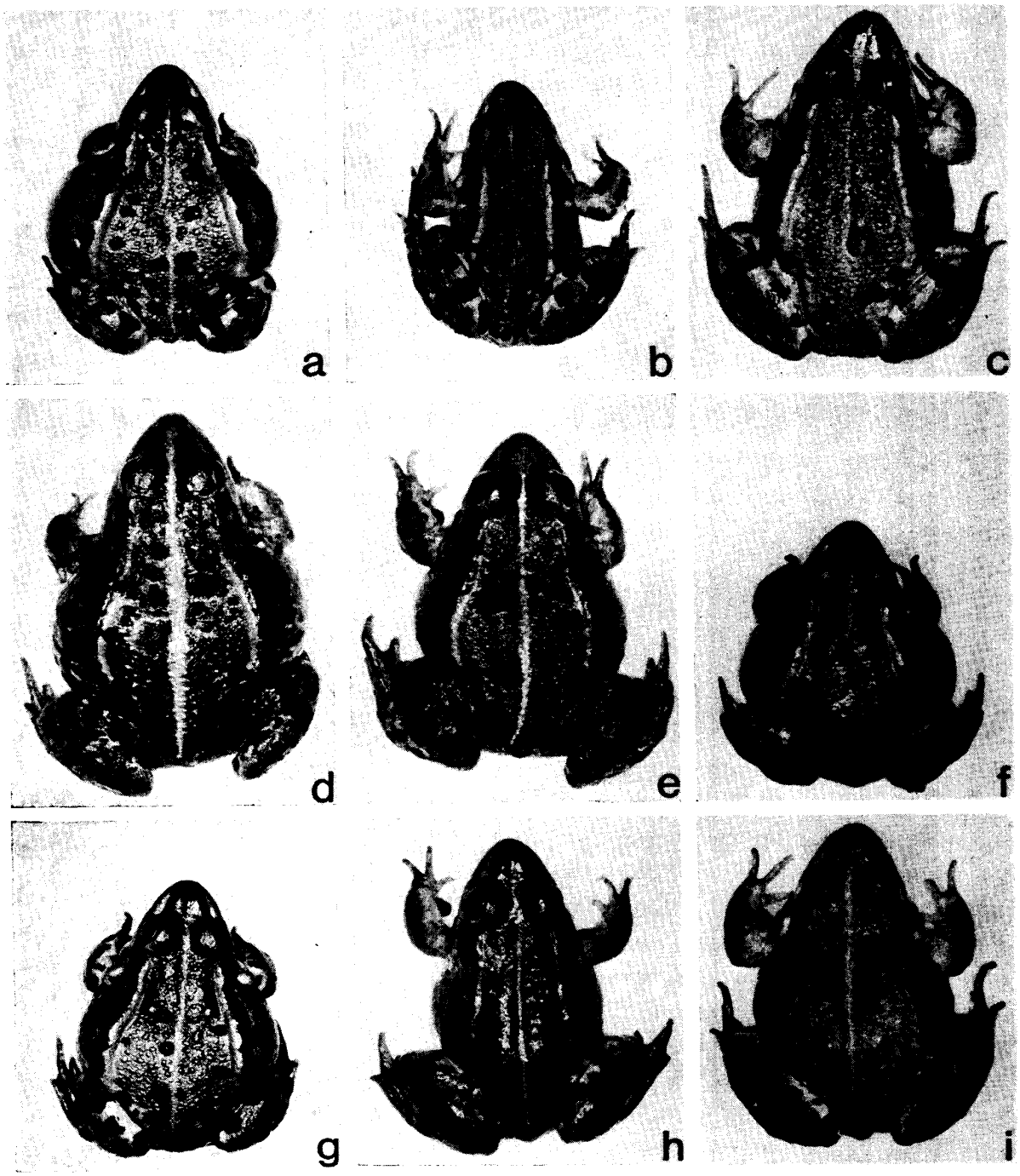

Fig. 6. Inter- and intraspecific hybrids between female *Rana lessonae* from Luxembourg and four kinds of males and the control. ×0.7

a. Control female, 1 year old, produced in 1977 from *les* L♀, No. 4×*les* L♂, No. 3.
b. Male hybrid, 1 year old, produced in 1977 from *les* L♀, No. 4×*les* I♂, No. 1.
c. Male hybrid, 2 years old, produced in 1976 from *les* L♀, No. 2×*rid* F♂, No. 2.
d. Female hybrid, 2 years old, produced in 1976 from *les* L♀, No. 2×*rid* T♂, No. 1.
e. Male hybrid, 2 years old, produced in 1976 from *les* L♀, No. 2×*rid* T♂, No. 1.
f, g. Male hybrids (LL-type), 1 year old, produced in 1977 from *les* L♀, No. 4×*esc* G♂, No. 1.
h. Male hybrid (LR-type), 1 year old, produced in 1977 from *les* L♀, No. 4×*esc* G♂, No. 1.
i. Male hybrid (LR-type), 3 years old, produced in 1977 from *les* L♀, No. 4×*esc* G♂, No. 1.

six of the 10 hybrids, while they barely came into contact with each other (LR-type) in the remaining four. The ratios b/c and d/c were 5.6～6.4, 5.8 on the average, and 5.1～6.1, 5.5 on the average, respectively. The ratio b/e was 11.2～14.3, 12.6 on the average.

Twenty 2-year-old hybrids produced in 1976 from two matings between two females, *les* L♀, Nos. 2 and 3, and a male, *rid* F♂, No. 2, were 61.5～70.5 mm, 66.8 mm on the average, and 57.0～71.5 mm, 64.8 mm on the average, in body length, respectively. When their tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in 18 of the 20 hybrids, while they barely came into contact with each other (LR-type) in the remaining two. In 10 hybrids produced from female *les* L♀, No. 2, the ratios b/c and d/c were 5.7～7.1, 6.6 on the average, and 5.5～7.3, 6.2 on the average, respectively. The ratio b/e was 11.8～15.6, 13.4 on the average. In the other 10 hybrids produced from female *les* L♀, No. 3, the ratios b/c and d/c were 6.2～7.4, 6.7 on the average, and 5.9～7.1, 6.6 on the average, respectively. The ratio b/e was 12.6～19.2, 15.7 on the average (Table 10; Fig. 6c).

c. Interspecific hybrids, *les* L♀ × *rid* T♂

Two mating experiments were made in 1976 between the two females, *les* L♀, Nos. 2 and 3, and a male, *rid* T♂, No. 1. Twenty 2-year-old hybrids obtained from these matings consisted of 10 females and 10 males. They were green in dorsal ground color and had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). Ten of these hybrids were 65.0～74.5 mm, 70.1 mm on the average, while the other ten were 60.5～69.0 mm, 64.2 mm on the average, in body length. When their tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other in 17 of the 20 hybrids (LL-type), while they barely came into contact with each other in the other three (LR-type).

In ten hybrids produced from female *les* L♀, No. 2, the ratios b/c and d/c were 6.0～7.4, 6.8 on the average, and 5.9～7.0, 6.5 on the average, respectively. The ratio b/e was 12.7～14.8, 13.4 on the average. In the other ten hybrids produced from female *les* L♀, No. 3, the ratios b/c and d/c were 6.6～7.1, 6.8 on the average, and 6.6～7.6, 7.2 on the average, respectively. The ratio b/e was 17.5～20.8, 19.0 on the average (Table 10; Fig. 6d, e).

d. Intraspecific hybrids, *les* L♀ × *les* I♂

Three 1-year-old male offspring produced in 1977 from a mating between the female, *les* L♀, No. 4, and a male, *les* I♂, No. 1, were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). They were 47.0～51.5 mm, 49.7 mm on the average, in body length. When their tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in two of the three offspring, while they barely came into contact with each other (LR-type) in the remainder. The ratios b/c and d/c were 6.3～7.7, 7.2 on

the average, and 6.7～8.1, 7.4 on the average, respectively. The ratio b/e was 10.2～12.9, 11.5 on the average (Table 10; Fig. 6b).

e. Interspecific hybrids, *les* L♀ × *esc* G♂

Of ten 1-year-old hybrids obtained from a mating made in 1977 between the female, *les* L♀, No. 4 and a male, *esc* G♂, No. 1, five were females which were green in dorsal ground color and had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). They were 49.0～62.0 mm, 55.0 mm on the average, in body length. When their tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type). The inner metatarsal tubercle was comparatively small (LR-type). The ratios b/c and d/c were 6.1～7.5, 7.0 on the average, and 6.3～6.9, 6.6 on the average, respectively. The ratio b/e was 11.9～13.4, 12.5 on the average. The other five hybrids were all males which were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). They were comparatively small, being 45.0～54.5 mm, 49.9 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in four of the five hybrids, while they barely come into contact with each other (LR-type) in the remainder. The inner metatarsal tubercles were generally larger than those of the other five hybrids. The ratios b/c and d/c were 5.4～6.6, 6.0 on the average, and 5.6～6.3, 6.1 on the average, respectively. The ratio b/e was 9.1～11.6, 10.0 on the average (Table 10; Fig. 6f～i).

3. Inter- and intraspecific hybrids between female *Rana lessonae* from Italy and five kinds of males

a. Controls, *les* I♀ × *les* I♂

Two control matings were made in 1977 between two females, *les* I♀, Nos. 1 and 2, and a male, *les* I♂, No. 1. A total of 20 one-year-old offspring were obtained from these matings. They consisted of 10 females and 10 males, all of which were yellowish green or yellowish brown in dorsal ground color. They had a light yellowish-green dorso-median stripe and some small, irregularly shaped brown-black spots on the back (LL-type). Of these offspring, 10 produced from female *les* I♀, No. 1 were 46.5～57.0 mm, 52.5 mm on the average, in body length and the other 10 obtained from female *les* I♀, No. 2 were 50.0～56.0 mm, 52.7 mm on the average, in body length. When the tibias of the former 10 offspring were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in one of the offspring, while they barely came into contact with each other (LR-type) in the other nine. The ratios b/c and d/c were 6.5～7.7, 7.0 on the average, and 6.6～7.9, 7.3 on the average, respectively. The ratio b/e was 11.8～13.7, 12.9 on the average. When the tibias of the other 10 offspring were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in one of the 10 offspring, while they

TABLE 11

External characters of the mature hybrids between female *Rana lessonae* from Italy and five kinds of males

Kinds	No. of frogs	Age (years)	External appearance (Type)	Body lengths (mm)	Femur lengths (mm)	Tibia lengths (mm)	Type of hind legs			b/c	d/c	b/e
							LL	LR	RR			
77 *les* I ♀1×*les* I ♂1	10	1	LL	46.5~57.0	19.5~26.0	20.0~27.0	1	9	—	6.5~ 7.7	6.6~ 7.9	11.8~13.7
	(♀ 5, ♂5)			(52.5)	(23.2)	(23.5)				(7.02±0.15)	(7.26±0.18)	(12.88±0.16)
77 *les* I ♀1×*les* L ♂3	9	1	LL	40.5~50.0	16.5~21.0	17.0~21.5	1	8	—	6.5~ 7.5	6.5~ 7.8	11.3~13.9
	(♀ 1, ♂8)			(46.6)	(19.9)	(20.3)				(7.01±0.11)	(7.14±0.14)	(13.04±0.26)
77 *les* I ♀1×*rid* T ♂2	8	1	LR	50.0~61.0	22.0~26.5	23.5~28.5	—	8	—	7.5~ 8.9	6.7~ 8.9	15.0~23.7
	(♀ 1, ♂7)			(53.9)	(24.2)	(25.4)				(8.39±0.17)	(7.95±0.25)	(18.39±0.94)
77 *les* I ♀1×*esc* G ♂1	10	1	LR	50.5~60.0	22.0~27.0	22.5~28.5	2	8	—	7.4~ 9.4	6.9~ 9.2	14.7~19.1
	(♀10)			(54.4)	(24.3)	(25.5)				(8.30±0.20)	(7.91±0.24)	(16.39±0.49)
	5	3	LL	58.0~74.0	27.0~33.5	25.5~32.5	4	1	—	5.3~ 7.2	3.7~ 6.5	10.3~11.0
	(♂5)			(64.0)	(29.8)	(28.6)				(6.5)	(5.6)	(10.8)
77 *les* I ♀2×*les* I ♂1	10	1	LL	50.0~56.0	21.0~26.0	21.5~26.0	1	9	—	6.1~ 7.1	6.3~ 7.0	11.3~13.0
	(♀ 5, ♂5)			(52.7)	(23.4)	(23.6)				(6.72±0.08)	(6.60±0.11)	(12.37±0.16)
77 *les* I ♀2×*les* L ♂3	10	1	LL	44.0~61.0	18.0~26.5	17.5~25.5	8	2	—	5.8~ 7.3	6.0~ 7.4	9.7~12.0
	(♀ 5, ♂5)			(52.5)	(22.2)	(21.7)				(6.68±0.16)	(6.64±0.17)	(10.57±0.21)
77 *les* I ♀2×*rid* F ♂4	10	1	LR	42.0~59.5	16.0~25.5	16.5~26.5	—	10	—	8.0~11.5	8.6~11.7	20.0~28.6
	(♀ 5, ♂5)			(48.9)	(20.2)	(20.9)				(9.99±0.39)	(9.39±0.44)	(22.95±0.72)
77 *les* I ♀2×*rid* T ♂3	10	1	LR	38.5~56.0	16.0~24.0	16.5~26.0	—	6	4	8.7~ 9.8	7.4~ 9.1	20.0~23.6
	(♀ 5, ♂5)			(47.6)	(20.0)	(21.2)				(9.21±0.11)	(8.33±0.18)	(21.66±0.39)
77 *les* I ♀2×*rid* S ♂1	6	1	LR	47.0~61.0	21.0~28.5	21.5~29.5	—	6	—	8.0~ 9.8	8.0~ 9.2	14.4~19.6
	(♂6)			(56.1)	(26.0)	(26.6)				(8.77±0.27)	(8.35±0.21)	(16.50±0.76)
77 *les* I ♀2×*esc* G ♂1	8	1	LL	50.5~54.5	21.0~23.0	20.0~22.5	8	—	—	5.6~ 6.6	5.5~ 6.0	10.5~11.8
	(♂8)			(51.4)	(22.1)	(21.1)				(6.10±0.10)	(5.76±0.12)	(11.48±0.32)
	2	1	LR	51.0, 58.5	21.0, 23.5	22.0, 24.0	—	2	—	7.4, 8.0	6.5, 8.3	17.0, 18.5
	(♂2)			(54.8)	(22.3)	(23.0)				(7.7)	(7.4)	(17.75)
	10	3	LL	53.5~57.0	24.5~27.0	19.5~24.0	10	—	—	4.3~ 5.3	4.0~ 4.9	7.2~ 9.6
	(♂10)			(55.9)	(25.2)	(21.8)				(4.86±0.12)	(4.48±0.10)	(8.44±0.37)
	5	3	LR	60.5~72.0	28.0~33.5	28.5~34.5	—	5	—	6.2~ 7.6	6.0~ 6.9	13.0~15.8
	(♂5)			(66.1)	(31.1)	(32.1)				(6.6)	(6.4)	(14.8)
	10	3	LR	72.0~80.5	32.0~36.5	33.5~38.0	—	10	—	6.3~ 7.4	5.7~ 7.1	12.8~16.3
	(♀10)			(76.4)	(34.7)	(35.3)				(6.82±0.12)	(6.39±0.16)	(14.57±0.40)
77 *les* I ♀3×*esc* G ♂1	5	3	LL	52.0~59.0	22.0~25.5	18.0~21.0	5	—	—	3.8~ 5.3	3.3~ 5.3	7.6~ 9.0
	(♂5)			(55.8)	(23.6)	(19.7)				(4.5)	(4.1)	(8.0)
	1	3	LR	66.5	28.0	28.5	—	1	—	6.3	6.0	15.8
	(♂1)											
	4	3	LR	61.0~65.0	24.0~27.5	26.5~29.5	—	4	—	6.0~ 7.9	5.8~ 7.3	11.0~13.0
	(♀ 4)			(63.6)	(26.1)	(28.0)				(6.9)	(6.5)	(11.9)

b/c, the ratio of tibia length to the length of the inner metatarsal tubercle

d/c, the ratio of first-toe length to the length of the inner metatarsal tubercle

b/e, the ratio of tibia length to the height of the inner metatarsal tubercle

barely came into contact with each other in the other nine (LR-type). The ratios b/c and d/c were 6.1～7.1, 6.7 on the average, and 6.3～7.0, 6.6 on the average, respectively. The ratio b/e was 11.3～13.0, 12.4 on the average (Table 11; Fig. 7a).

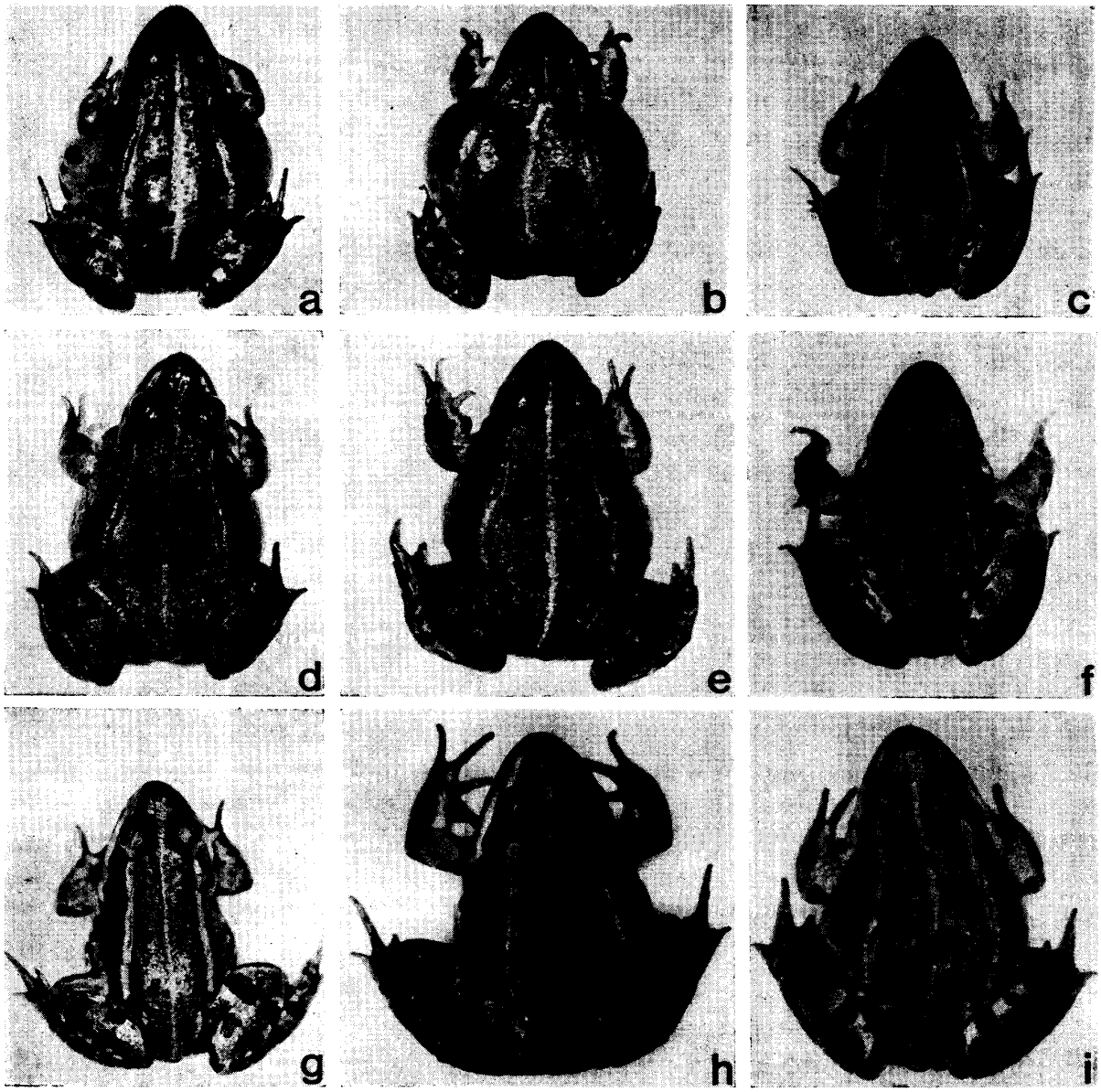

Fig. 7. Inter- and intraspecific hybrids, 1 year old, produced in 1977 between female *Rana lessonae* from Italy and five kinds of males and the control. ×0.7

a. Control female produced from *les* I ♀, No. 1 × *les* I ♂, No. 1.
b. Female hybrid produced from *les* I ♀, No. 2 × *les* L ♂, No. 3.
c. Male hybrid produced from *les* I ♀, No. 2 × *les* L ♂, No. 3.
d. Male hybrid produced from *les* I ♀, No. 2 × *rid* F ♂, No. 4.
e. Male hybrid produced from *les* I ♀, No. 2 × *rid* T ♂, No. 3.
f. Male hybrid produced from *les* I ♀, No. 2 × *rid* S ♂, No. 1.
g. Male hybrid (LL-type) produced from *les* I ♀, No. 2 × *esc* G ♂, No. 1.
h. Male hybrid (LR-type) produced from *les* I ♀, No. 1 × *esc* G ♂, No. 1.
i. Male hybrid (LR-type) produced from *les* I ♀, No. 2 × *esc* G ♂, No. 1.

b. Intraspecific hybrids, *les* I♀ × *les* L♂

A total of 19 one-year-old offspring produced from two matings between the two females, *les* I♀, Nos. 1 and 2, and a male, *les* L♂, No. 3, consisted of six females and 13 males. All of them were yellowish green in dorsal ground color. They had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). Of these offspring, nine obtained from female *les* I♀, No. 1 were 40.5～50.0 mm, 46.6 mm on the average, in body length, while the other 10 offspring obtained from female *les* I♀, No. 2 were 44.0～61.0 mm, 52.5 mm on the average, in body length. When the tibias of the former nine offspring were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in one of the nine offspring, while they barely came into contact with each other (LR-type) in the other eight. The ratios b/c and d/c were 6.5～7.5, 7.0 on the average, and 6.5～7.8, 7.1 on the average, respectively. The ratio b/e was 11.3～13.9, 13.0 on the average. When the tibias of the other 10 offspring were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in eight of the 10 offspring, while they barely came into contact with each other (LR-type) in the other two. The ratios b/c and d/c were 5.8～7.3, 6.7 on the average, and 6.0～7.4, 6.6 on the average, respectively. The ratio b/e was 9.7～12.0, 10.6 on the average (Table 11; Fig. 7b, c).

c. Interspecific hybrids, *les* I♀ × *rid* T♂

A total of 18 one-year-old hybrids produced in 1977 from two matings between the two females, *les* I♀, Nos. 1 and 2, and two males, *rid* T♂, Nos. 2 and 3, were observed. These hybrids were green or brown in dorsal ground color. They had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). Eight green hybrids were 50.0～61.0 mm, 53.9 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type) in all of the eight hybrids. The ratios b/c and d/c were 7.5～8.9, 8.4 on the average, and 6.7～8.9, 8.0 on the average, respectively. The ratio b/e was 15.0～23.7, 18.4 on the average. The other 10 brown hybrids were 38.5～56.0 mm, 47.6 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type) in six of the 10 hybrids, while they overlapped each other (RR-type) in the other four. The ratios b/c and d/c were 8.7～9.8, 9.2 on the average, and 7.4～9.1, 8.3 on the average, respectively. The ratio b/e was 20.0～23.6, 21.7 on the average (Table 11; Fig. 7e).

d. Interspecific hybrids, *les* I♀ × *rid* F♂

Ten 1-year-old hybrids produced in 1977 from a mating between the female, *les* I♀, No. 2, and a male, *rid* F♂, No. 4, consisted of five females and five males. These hybrids were green in dorsal ground color and had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type).

They were 42.0～59.5 mm, 48.9 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type) in all the 10 hybrids. The ratios b/c and d/c were 8.0～11.5, 10.0 on the average, and 8.6～11.7, 9.4 on the average, respectively. The ratio b/e was 20.0～28.6, 23.0 on the average (Table 11; Fig. 7d).

e. Interspecific hybrids, *les* I♀ × *rid* S♂

Six 1-year-old male hybrids produced in 1977 from a mating between the female, *les* I♀, No. 2, and a male, *rid* S♂, No. 1, were green in dorsal ground color and had a light green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). They were 47.0～61.0 mm, 56.1 mm on the average, in body length. When tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type) in all the six hybrids. The ratios b/c and d/c were 8.0～9.8, 8.8 on the average, and 8.0～9.2, 8.4 on the average, respectively. The ratio b/e was 14.4～19.6, 16.5 on the average (Table 11; Fig. 7f).

f. Interspecific hybrids, *les* I♀ × *esc* G♂

A total of 60 one- or 3-year-old hybrids produced in 1977 from three matings between three females, *les* I♀, Nos. 1～3, and a male, *esc* G♂, No. 1, were observed. Of 15 hybrids produced from female *les* I♀, No. 1, 10 were one year old and all females. They were green in dorsal ground color and had a light green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). They were 50.5～60.0 mm, 54.4 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in two of the 10 hybrids, while they barely came into contact with each other (LR-type) in the other eight. The ratios b/c and d/c were 7.4～9.4, 8.3 on the average, and 6.9～9.2, 7.9 on the average, respectively. The ratio b/e was 14.7～19.1, 16.4 on the average (Table 11; Fig. 7h).

The remaining five of the 15 hybrids were 3-year-old males. They were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). They were 58.0～74.0 mm, 64.0 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in four of the five hybrids, while they barely came into contact with each other (LR-type) in the remainder. The ratios b/c and d/c were 5.3～7.2, 6.5 on the average, and 3.7～6.5, 5.6 on the average, respectively. The ratio b/e was 10.3～11.0, 10.8 on the average (Table 11).

Of 35 hybrids produced from female *les* I♀, No. 2, 10 were 1-year-old males, 15 were 3-year-old males and 10 were 3-year-old females. Of the 10 one-year-old males, eight were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). They were 50.5～54.5 mm, 51.4 mm on the average, in body length. When the

tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in all the eight hybrids. The ratios b/c and d/c were 5.6～6.6, 6.1 on the average, and 5.5～6.0, 5.8 on the average, respectively. The ratio b/e was 10.5～11.8, 11.5 on the average. The remaining two 1-year-old males were green in dorsal ground color and had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). These two were 51.0 mm and 58.5 mm, 54.8 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type). The ratios b/c and d/c were 7.4 and 8.0, 7.7 on the average, and 6.5 and 8.3, 7.4 on the average, respectively. The ratio b/e was 17.0 and 18.5, 17.8 on the average (Table 11; Fig. 7g, i).

Of the 15 three-year-old males, 10 were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). They were 53.5～57.0 mm, 55.9 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in all the 10 hybrids. The ratios b/c and d/c were 4.3～5.3, 4.9 on the average, and 4.0～4.9, 4.5 on the average, respectively. The ratio b/e was 7.2～9.6, 8.4 on the average. The remaining five 3-year-old males were green or brown in dorsal ground color and had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). They were 60.5～72.0 mm, 66.1 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type) in all the five hybrids. The ratios b/c and d/c were 6.2～7.6, 6.6 on the average, and 6.0～6.9, 6.4 on the average, respectively. The ratio b/e was 13.0～15.8, 14.8 on the average (Table 11).

The 10 three-year-old females were green or brown in dorsal ground color and had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). They were 72.0～80.5 mm, 76.4 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type) in all the 10 hybrids. The ratios b/c and d/c were 6.3～7.4, 6.8 on the average, and 5.7～7.1, 6.4 on the average, respectively. The ratio b/e was 12.8～16.3, 14.6 on the average (Table 11).

Ten 3-year-old hybrids produced from female *les* I♀, No. 3 consisted of six males and four females. Five of the six males were yellowish green in dorsal ground color and had a light yellowish-green dorso-median stripe and some small brown-black spots on the back (LL-type). They were 52.0～59.0 mm, 55.8 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type). The ratios b/c and d/c were 3.8～5.3, 4.5 on the average, and 3.3～5.3, 4.1 on the average, respectively. The ratio b/e was 7.6～9.0, 8.0 on the average. The remaining one male was brown in the dorsal ground color and had a light yellowish-

green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). This male was 66.5 mm in body length. When his tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type). The ratios b/c and d/c were 6.3 and 6.0, respectively. The ratio b/e was 15.8 (Table 11).

The four females were green or brown in dorsal ground color and had a light yellowish-green dorso-median stripe and somewhat large brown-black spots on the back (LR-type). They were 61.0~65.0 mm, 63.6 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (LR-type). The ratios b/c and d/c were 6.0~7.9, 6.9 on the average, and 5.8~7.3, 6.5 on the average, respectively. The ratio b/e was 11.0~13.0, 11.9 on the average (Table 11).

4. Inter- and intraspecific hybrids between female *Rana ridibunda* from Turkey and five kinds of males

a. Controls, *rid* T♀ × *rid* T♂

Sixteen offspring obtained in 1977 and 1978 from two control matings between two females, *rid* T♀, Nos. 1 and 2, and two males, *rid* T♂, Nos. 2 and 4, consisted of 11 females and five males. Five 1-year-old offspring obtained in 1977 were all males. All these controls were grayish brown in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). They were 36.0~52.5 mm, 45.2 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in three of the five offspring, while they overlapped each other (RR-type) in the other two. The ratios b/c and d/c were 9.3~13.4, 10.3 on the average, and 9.0~13.3, 10.4 on the average, respectively. The ratio b/e was 24.9~37.8, 36.3 on the average. Eleven 7-year-old offspring obtained in 1978 were all females. They were 75.0~102.0 mm, 83.7 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in one of the offspring, barely came into contact with each other (RL-type) in six others, and overlapped each other (RR-type) in the remaining four. The ratios b/c and d/c were 6.8~10.5, 7.9 on the average, and 5.3~8.9, 6.2 on the average, respectively. The ratio b/e was 17.8~26.9, 21.9 on the average (Table 12; Fig. 8a, b).

b. Intraspecific hybrids, *rid* T♀ × *rid* F♂

Five 1-year-old males produced in 1977 from a mating between the female, *rid* T♀, No. 1, and a male, *rid* F♂, No. 3, were grayish brown in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). They were 57.0~59.0 mm, 57.8 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in all the five hybrids. The ratios b/c and d/c were 8.8~10.4, 9.6 on the average, and

TABLE 12

External characters of the mature hybrids between female *Rana ridibunda* from Turkey and five kinds of males

Kinds	No. of frogs	Age (years)	External appearance (Type)	Body lengths (mm)	Femur lengths (mm)	Tibia lengths (mm)	Type of hind legs			b/c	d/c	b/e
							LL	RL	RR			
77 *rid* T ♀1×*rid* T ♂2	5	1	RR	36.0~52.5	18.0~25.0	19.0~27.0	—	3	2	9.3~13.4	9.0~13.3	24.9~37.8
	(♂5)			(45.2)	(22.3)	(23.4)				(10.3)	(10.4)	(36.3)
77 *rid* T ♀1×*rid* F ♂3	5	1	RR	57.0~59.0	27.0~28.5	28.0~29.5	—	5	—	8.8~10.4	8.4~9.4	18.9~22.3
	(♂5)			(57.8)	(27.6)	(28.6)				(9.6)	(8.9)	(20.6)
77 *rid* T ♀1×*rid* S ♂1	6	1	RR	59.0~60.5	28.5~30.0	30.0~32.5	—	—	6	8.6~10.5	8.0~9.8	25.1~30.0
	(♀6)			(60.1)	(29.3)	(31.7)				(9.18±0.44)	(8.76±0.38)	(28.17±0.71)
77 *rid* T ♀1×*les* L ♂3	8	1	RL	40.0~55.0	15.5~26.5	16.5~27.5	—	8	—	8.1~9.8	7.9~10.2	15.0~23.6
	(♀2, ♂6)			(45.3)	(20.7)	(22.1)				(9.21±0.13)	(9.33±0.16)	(18.21±0.74)
77 *rid* T ♀1×*les* I ♂1	9	1	RL	39.0~55.5	16.5~26.0	16.5~27.0	—	9	—	8.3~10.3	8.6~12.0	15.3~21.1
	(♀2, ♂7)			(45.0)	(20.3)	(21.1)				(9.31±0.25)	(10.15±0.21)	(17.71±0.36)
77 *rid* T ♀1×*esc* G ♂1	5	1	RR	47.0~60.0	20.0~29.0	22.5~29.0	—	—	5	9.7~11.2	9.4~10.8	27.3~28.0
	(♀2, ♂3)			(53.2)	(24.4)	(25.7)				(10.5)	(10.1)	(27.7)
	2	1	RL	45.5, 53.0	21.0, 25.5	23.0, 27.5	—	5	—	6.6, 7.9	6.3, 7.7	13.7, 20.0
	(♂2)			(49.3)	(21.3)	(25.3)				(7.3)	(7.0)	(16.8)
78 *rid* T ♀2×*rid* T ♂4	11	7	RR	75.0~102.0	33.0~46.0	33.5~47.5	1	6	4	6.8~10.5	5.3~8.9	17.8~26.9
	(♀11)			(83.7±2.2)	(36.0±1.1)	(37.0±1.2)				(7.89±0.32)	(6.24±0.29)	(21.92±0.89)
78 *rid* T ♀2×*rid* S ♂2	10	7	RR	70.0~84.5	29.5~40.0	31.0~41.5	—	3	7	6.9~8.8	5.7~7.5	20.0~29.0
	(♀10)			(76.3±1.5)	(33.7±1.0)	(34.8±0.9)				(8.00±0.17)	(6.7±0.19)	(25.23±1.30)
78 *rid* T ♀2×*les* L ♂5	10	7	RL	58.5~74.0	28.0~34.0	25.5~31.5	10	—	—	6.5~8.4	5.9~7.0	12.9~15.8
	(♀5, ♂5)			(66.8±2.2)	(30.3±0.7)	(27.8±0.6)				(7.34±0.17)	(6.61±0.17)	(13.86±0.28)
78 *rid* T ♀2×*les* I ♂3	10	7	RL	62.0~76.5	29.5~33.5	28.0~34.5	5	1	4	6.8~8.6	6.1~7.6	12.7~15.0
	(♀5, ♂5)			(70.2±1.4)	(31.5±0.4)	(31.2±0.6)				(7.59±0.17)	(6.90±0.15)	(14.13±0.26)
78 *rid* T ♀2×*esc* G ♂2	10	7	RR	75.5~82.5	33.0~37.0	33.0~38.0	—	5	5	7.7~8.7	6.6~7.5	23.3~31.7
	(♀10)			(78.9±0.7)	(34.3±0.5)	(35.3±0.5)				(8.26±0.11)	(7.10±0.11)	(27.35±0.88)
	2	5	RR	71.0, 72.5	32.5, 33.0	34.5, 35.0	—	—	2	8.0, 8.2	7.9, 8.1	27.6, 31.2
	(♂2)			(71.8)	(32.8)	(34.8)				(8.1)	(8.0)	(29.4)

b/c, the ratio of tibia length to the length of the inner metatarsal tubercle

d/c, the ratio of first-toe length to the length of the inner metatarsal tubercle

b/e, the ratio of tibia length to the height of the inner metatarsal tubercle

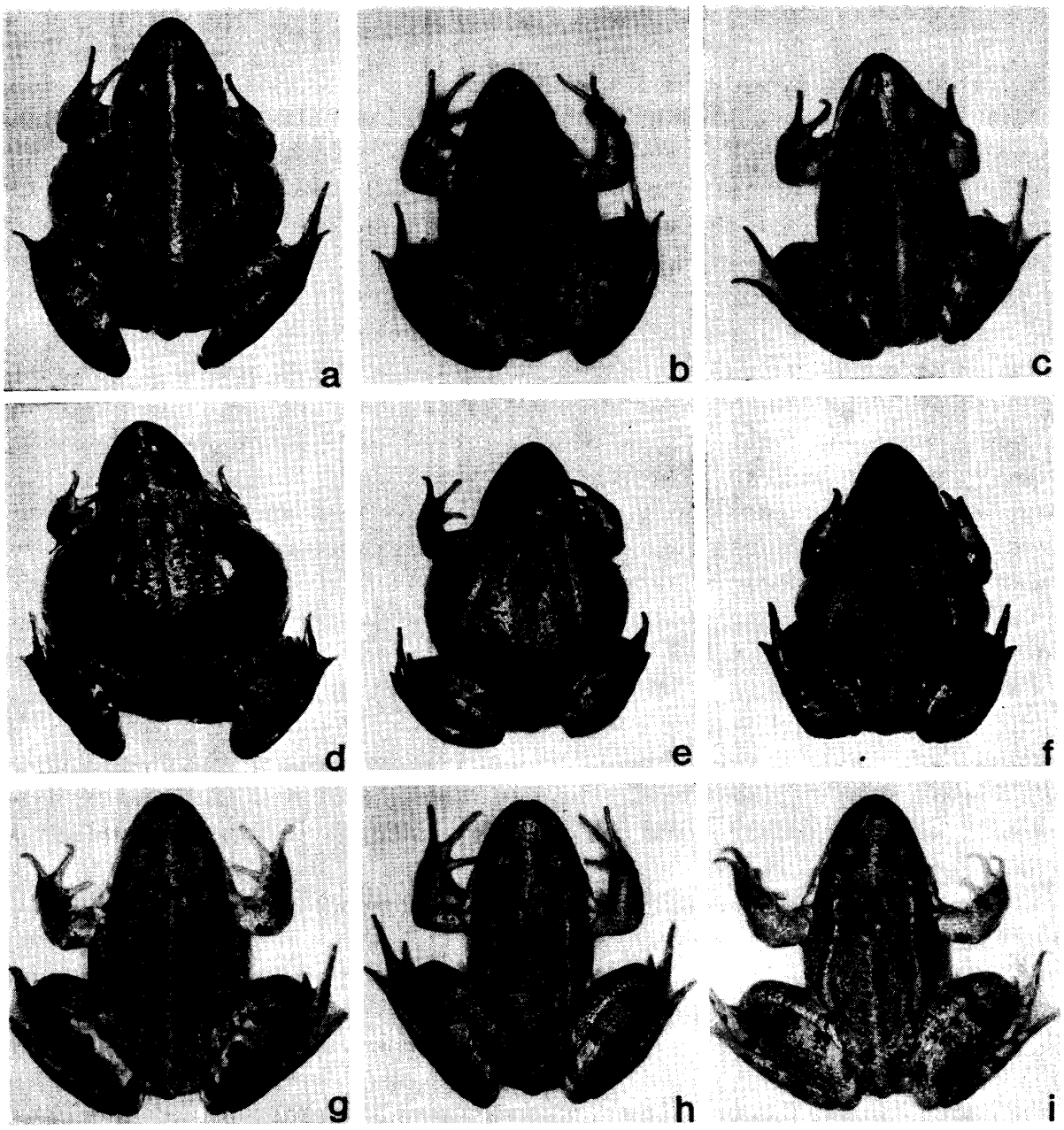

Fig. 8. Inter- and intraspecific hybrids between a female *Rana ridibunda* from Turkey and five kinds of males and the controls. ×0.7

a. Control female, 3 years old, produced in 1978 from *rid* T♀, No. 2 × *rid* T♂, No. 4.
b. Control male, 1 year old, produced in 1977 from *rid* T♀, No. 1 × *rid* T♂, No. 2.
c. Male hybrid, 2 years old, produced in 1977 from *rid* T♀, No. 1 × *rid* F♂, No. 3.
d. Female hybrid, 2 years old, produced in 1977 from *rid* T♀, No. 1 × *rid* S♂, No. 1.
e. Male hybrid, 1 year old, produced in 1977 from *rid* T♀, No. 1 × *les* L♂, No. 3.
f. Male hybrid, 1 year old, produced in 1977 from *rid* T♀, No. 1 × *les* I♂, No. 1.
g. Male hybrid (RR-type), 1 year old, produced in 1977 from *rid* T♀, No. 1 × *esc* G♂, No. 1.
h. Male hybrid (RL-type), 1 year old, produced in 1977 from *rid* T♀, No. 1 × *esc* G♂, No. 1.
i. Male hybrid (RL-type), 1 year old, produced in 1977 from *rid* T♀, No. 1 × *esc* G♂, No. 1.

8.4～9.4, 8.9 on the average, respectively. The ratio b/e was 18.9～22.3, 20.6 on the average (Table 12; Fig. 8c).

c. Intraspecific hybrids, *rid* T♀ × *rid* S♂

Sixteen offspring produced in 1977 and 1978 from two matings between the two females, *rid* T♀, Nos. 1 and 2, and two males, *rid* S♂, Nos. 1 and 2, were grayish brown in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). Six of these offspring were 1-year-old females, which were 59.0～60.5 mm, 60.1 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends overlapped each other (RR-type). The ratios b/c and d/c were 8.6～10.5, 9.2 on the average, and 8.0～9.8, 8.8 on the average, respectively. The ratio b/e was 25.1～30.0, 28.2 on the average. The other 10 offspring were 7-year-old females, which were 70.0～84.5 mm, 76.3 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in three of the 10 offspring, while they overlapped each other (RR-type) in the other seven. The ratios b/c and d/c were 6.9～8.8, 8.0 on the average, and 5.7～7.5, 6.7 on the average, respectively. The ratio b/e was 20.0～29.0, 25.2 on the average (Table 12; Fig. 8d).

d. Interspecific hybrids, *rid* T♀ × *les* L♂

A total of 18 hybrids produced in 1977 and 1978 from two matings between the two females, *rid* T♀, Nos. 1 and 2, and two males, *les* L♂, Nos. 3 and 5, were green in dorsal ground color and had a light green dorso-median stripe and somewhat large brown-black spots on the back (RL-type). Eight of the 18 hybrids were one year old and consisted of two females and six males. They were 40.0～55.0 mm, 45.3 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in all the hybrids. The ratios b/c and d/c were 8.1～9.8, 9.2 on the average, and 7.9～10.2, 9.3 on the average, respectively. The ratio b/e was 15.0～23.6, 18.2 on the averge (Table 12; Fig. 8e).

The other 10 hybrids produced in 1978 were seven years old and consisted of five females and five males. They were 58.5～74.0 mm, 66.8 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in all the 10 hybrids. The ratios b/c and d/c were 6.5～8.4, 7.3 on the average, and 5.9～7.0, 6.6 on the average, respectively. The ratio b/e was 12.9～15.8, 13.9 on the average (Table 12).

e. Interspecific hybrids, *rid* T♀ × *les* I♂

A total of 19 hybrids produced in 1977 and 1978 from two matings between the two females, *rid* T♀, Nos. 1 and 2, and two males, *les* I♂, Nos. 1 and 3, were green in dorsal ground color and had a light green dorso-median stripe and some-

what large brown-black spots on the back (RL-type). Nine of the 19 hybrids were one year old and consisted of two females and seven males. They were 39.0～55.5 mm, 45.0 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in all the hybrids. The ratios b/c and d/c were 8.3～10.3, 9.3 on the average, and 8.6～12.0, 10.2 on the average, respectively. The ratio b/e was 15.3～21.1, 17.7 on the average (Table 12; Fig. 8f).

The other ten 7-year-old hybrids produced from a mating between the female, *rid* T♀, No. 2, and a male, *les* I♂, No. 3, consisted of five females and five males. They were 62.0～76.5 mm, 70.2 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other in five hybrids (LL-type), barely came into contact (RL-type) in another hybrid and overlapped each other (RR-type) in the remaining four hybirds. The ratios b/c and d/c were 6.8～8.6, 7.6 on the average, and 6.1～7.6, 6.9 on the average, respectively. The ratio b/e was 12.7～15.0, 14.1 on the average (Table 12).

f. Interspecific hybrids, *rid* T♀ × *esc* G♂

A total of 19 hybrids produced in 1977 and 1978 from two matings between the two females, *rid* T♀, Nos. 1 and 2, and two males, *esc* G♂, Nos. 1 and 2, were observed. Five of seven 1-year-old hybrids obtained in 1977 consisted of two females and three males which were olive in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). These five hybrids were 47.0～60.0 mm, 53.2 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends overlapped each other (RR-type). The ratios b/c and d/c were 9.7～11.2, 10.5 on the average, and 9.4～10.8, 10.1 on the average, respectively. The ratio b/e was 27.3～28.0, 27.7 on the average. The other two 1-year-old hybrids were males which were green or brown in dorsal ground color and had a light green dorso-median stripe and somewhat large brown-black spots on the back (RR- or RL-type). They were 45.5 mm and 53.0 mm, 49.3 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in the two hybrids. The ratios b/c and d/c were 6.6 and 7.9, 7.3 on the average, and 6.3 and 7.7, 7.0 on the average, respectively. The ratio b/e was 13.7 and 20.0, 16.8 on the average.

Ten of the remaining 12 hybrids obtained in 1978 were 7-year-old females which were grayish brown in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). They were 75.5～82.5 mm, 78.9 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in five of the 10 hybrids, while they overlapped each other (RR-type) in the other five. The ratios b/c and d/c were 7.7～8.7, 8.3 on the average, and 6.6～7.5, 7.1 on the average, respectively. The

ratio b/e was 23.3~31.7, 27.4 on the average. The remaining two hybrids obtained in 1978 were 5-year-old males which were grayish brown in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). They were 71.0 mm and 72.5 mm, 71.8 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends overlapped each other (RR-type). The ratios b/c and d/c were 8.0 and 8.2, 8.1 on the average, and 7.9 and 8.1, 8.0 on the average, respectively. The ratio b/e was 27.6 and 31.2, 29.4 on the average (Table 12; Fig. 8g~i).

5. Inter- and intraspecific hybrids between a female *Rana ridibunda* from Soviet Union and four kinds of males

a. Controls, *rid* S♀ × *rid* S♂

Six 1-year-old offspring produced in 1977 from a mating between a female, *rid* S♀, No. 1, and a male, *rid* S♂, No. 1, were males which were grayish brown or olive in dorsal ground color and had several large roundish brown-black spots on the back (RR-type). While two of them had a light olive dorso-median stripe, the other four had no dorso-median stripe. The six offspring were 55.0~61.0 mm, 56.9 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends overlapped each other (RR-type). The ratios b/c and d/c were 8.6~8.8, 8.7 on the average, and 8.0~8.6, 8.4 on the average, respectively. The ratio b/e was 25.0~30.0, 28.4 on the average (Table 13; Fig. 9a).

b. Intraspecific hybrids, *rid* S♀ × *rid* F♂

Seven 1-year-old offspring produced in 1977 from a mating between the female, *rid* S♀, No. 1, and a male, *rid* F♂, No. 3, consisted of one female and six males. They were olive brown or grayish brown in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). They were 49.5~66.0 mm, 57.6 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends overlapped each other (RR-type). The ratios b/c and d/c were 8.6~10.0, 9.3 on the average, and 8.2~9.3, 8.6 on the average, respectively. The ratio b/e was 20.3~23.3, 22.1 on the average (Table 13; Fig. 9b, c).

c. Intraspecific hybrids, *rid* S♀ × *rid* T♂

A total of 17 offspring were obtained in 1977 from a mating between the female, *rid* S♀, No. 1, and a male, *rid* T♂, No. 2. They were grayish brown or grayish olive in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). Ten of them were one year old and consisted of four females and six males. They were 50.5~59.0 mm, 56.4 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends overlapped each other (RR-type) in all of them. The ratios b/c and d/c were 9.4~10.9, 10.2 on the average, and 8.3~9.4,

TABLE 13

External characters of the mature hybrids between a female *Rana ridibunda* from Soviet Union and four kinds of males

Kinds	No. of frogs	Age (years)	External appearance (Type)	Body lengths (mm)	Femur lengths (mm)	Tibia lengths (mm)	Type of hind legs			b/c	d/c	b/e
							LL	RL	RR			
77 *rid* S ♀1×*rid* S ♂1	6	1	RR	55.0~61.0	28.0~30.0	30.0~32.5	—	—	6	8.6~8.8	8.0~8.6	25.0~30.0
	(♂6)			(56.9)	(28.8)	(30.9)				(8.73±0.04)	(8.37±0.06)	(28.37±0.77)
77 *rid* S ♀1×*rid* F ♂3	7	1	RR	49.5~66.0	23.0~27.0	24.5~31.0	—	—	7	8.6~10.0	8.2~9.3	20.3~23.3
	(♀1, ♂6)			(57.6)	(24.7)	(27.8)				(9.28±0.21)	(8.58±0.20)	(22.13±0.27)
77 *rid* S ♀1×*rid* T ♂2	10	1	RR	50.5~59.0	22.5~27.5	24.5~30.0	—	—	10	9.4~10.9	8.3~9.4	24.5~30.5
	(♀4, ♂6)			(56.4)	(25.7)	(28.6)				(10.16±0.13)	(8.99±0.10)	(27.67±0.60)
	7	3	RR	67.5~83.0	31.0~36.5	33.5~37.0	—	7	—	6.2~8.6	5.6~8.1	21.7~27.5
	(♀4, ♂3)			(77.8)	(34.6)	(35.3)				(7.50±0.37)	(6.83±0.39)	(24.11±0.42)
77 *rid* S ♀1×*les* L ♂3	6	1	RL	65.0~70.5	30.5~34.5	32.0~36.5	1	4	1	7.2~8.3	6.9~7.8	14.9~16.4
	(♂6)			(67.5)	(32.6)	(33.8)				(7.60±0.15)	(7.33±0.13)	(15.82±0.24)
77 *rid* S ♀1×*esc* G ♂1	6	1	RR	48.0~69.5	22.0~30.0	24.5~34.5	—	—	6	8.0~11.1	7.9~10.5	24.2~28.0
	(♀4, ♂2)			(60.4)	(26.9)	(29.3)				(9.70±0.40)	(9.18±0.34)	(25.47±0.37)
	4	1	RL	57.0~61.5	26.5~27.5	27.0~28.5	—	4	—	6.6~8.0	6.3~7.5	15.1~18.3
	(♂4)			(59.4)	(26.9)	(27.8)				(7.2)	(6.5)	(17.1)

b/c, the ratio of tibia length to the length of the inner metatarsal tubercle

d/c, the ratio of first-toe length to the length of the inner metatarsal tubercle

b/e, the ratio of tibia length to the height of the inner metatarsal tubercle

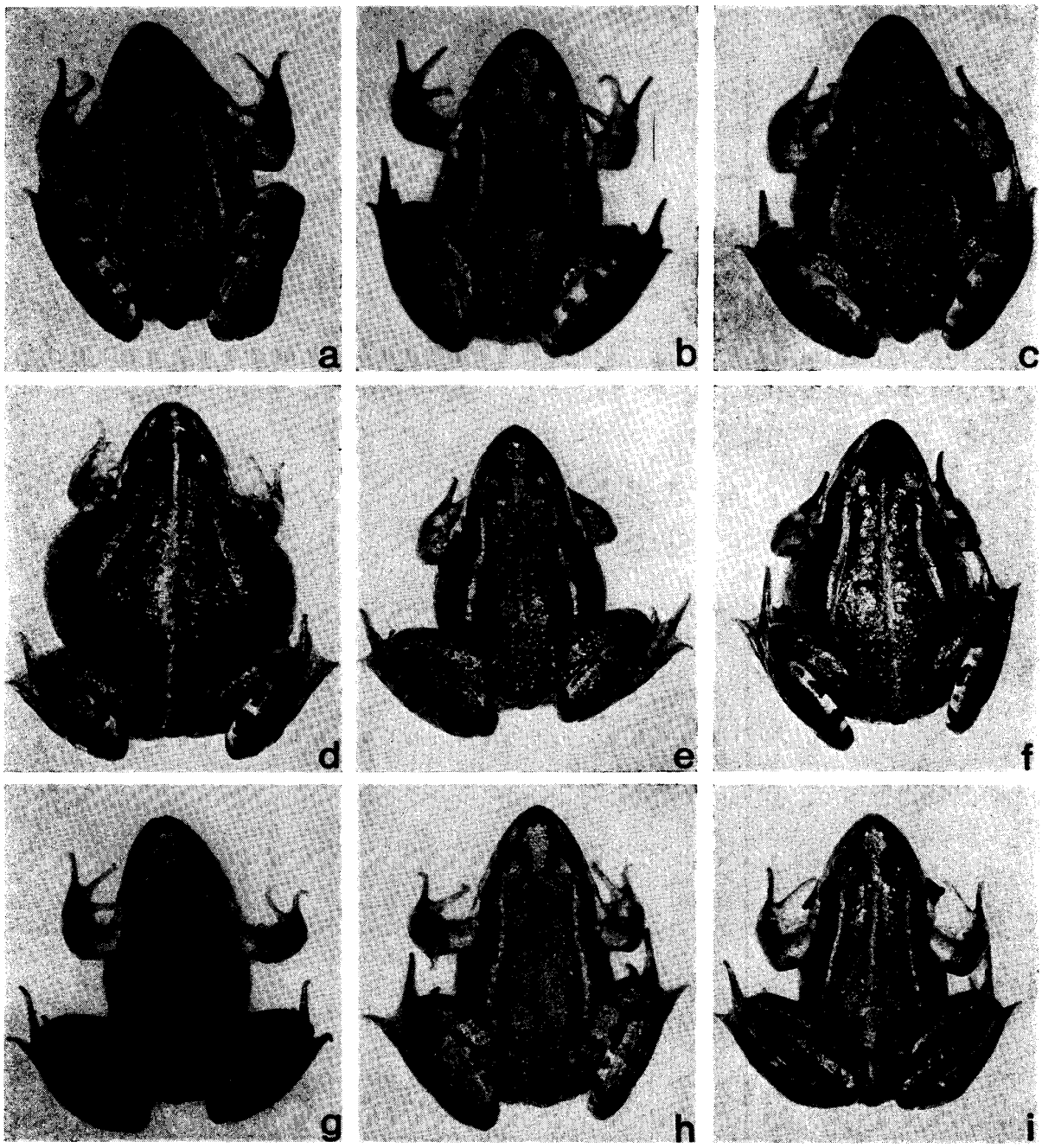

Fig. 9. Inter- and intraspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and four kinds of males and the control. ×0.7

a. Control male, 1 year old, produced from *rid* S♀, No. 1 × *rid* S♂, No. 1.
b. Male hybrid, 1 year old, produced from *rid* S♀, No. 1 × *rid* F♂, No. 3.
c. Male hybrid, 1 year old, produced from *rid* S♀, No. 1 × *rid* F♂, No. 3.
d. Female hybrid, 2 years old, produced from *rid* S♀, No. 1 × *rid* T♂, No. 2.
e. Male hybrid, 1 year old, produced from *rid* S♀, No. 1 × *rid* T♂, No. 2.
f. Male hybrid, 1 year old, produced from *rid* S♀, No. 1 × *les* L♂, No. 3.
g. Male hybrid (RR-type), 1 year old, produced from *rid* S♀, No. 1 × *esc* G♂, No. 1.
h. Male hybrid (RR-type), 1 year old, produced from *rid* S♀, No. 1 × *esc* G♂, No. 1.
i. Male hybrid (RL-type), 1 year old, produced from *rid* S♀, No. 1 × *esc* G♂, No. 1.

9.0 on the average, respectively. The ratio b/e was 24.5～30.5, 27.7 on the average. The remaining seven offspring were three years old and consisted of four females and three males. They were 67.5～83.0 mm, 77.8 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type). The ratios b/c and d/c were 6.2～8.6, 7.5 on the average, and 5.6～8.1, 6.8 on the average, respectively. The ratio b/e was 21.7～27.5, 24.1 on the average (Table 13; Fig. 9d, e).

d. Interspecific hybrids, *rid* S♀ × *les* L♂

Six 1-year-old male hybrids produced from a mating between the female, *rid* S♀, No. 1 and a male, *les* L♂, No. 3, were green in dorsal ground color and had a light green dorso-median stripe and somewhat large brown-black spots on the back (RL-type). They were 65.0～70.5 mm, 67.5 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends did not come into contact with each other (LL-type) in one of the six hybrids, barely came into contact with each other (RL-type) in four others and overlapped each other (RR-type) in the remainder. The ratios b/c and d/c were 7.2～8.3, 7.6 on the average, and 6.9～7.8, 7.3 on the average, respectively. The ratio b/e was 14.9～16.4, 15.8 on the average (Table 13; Fig. 9f).

e. Interspecific hybrids, *rid* S♀ × *esc* G♂

Of ten 1-year-old hybrids produced in 1977 from a mating between the female, *rid* S♀, No. 1, and a male, *esc* G♂, No. 1, six consisting of four females and two males were grayish brown in dorsal ground color and had a light olive dorso-median stripe and several large roundish brown-black spots on the back (RR-type). They were 48.0～69.5 mm, 60.4 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends overlapped each other (RR-type) in all the six hybrids. The ratios b/c and d/c were 8.0～11.1, 9.7 on the average, and 7.9～10.5, 9.2 on the average, respectively. The ratio b/e was 24.2～28.0, 25.5 on the average. The remaining four hybrids were all males, which were green in dorsal ground color and had a light green dorso-median stripe and somewhat large brown-black spots on the back (RL-type). They were 57.0～61.5 mm, 59.4 mm on the average, in body length. When the tibias were placed at a right angle to the body axis, the distal ends barely came into contact with each other (RL-type) in all the four hybrids. The ratios b/c and d/c were 6.6～8.0, 7.2 on the average, and 6.3～7.5, 6.5 on the average, respectively. The ratio b/e was 15.1～18.3, 17.1 on the average (Table 13; Fig. 9g～i).

IV. Electrophoretic patterns of hybrids

1. Mature frogs used in crossing experiments

a. *Rana lessonae* from Luxembourg

Electrophoretic patterns of 10 mature *Rana lessonae* from Luxembourg were

observed. Of these frogs, three females, *les* L.W72♀, No. 1 and *les* L.W75♀, Nos. 2 and 3, and two males, *les* L.W72♂, No. 1 and *les* L.W75♂, No. 2, were collected from the field. The other five frogs included two females, *les* L. 75♀, Nos. 4 and 5, two males, *les* L.75♂, Nos. 3 and 4, produced in 1975 from a mating between a female, *les* L.W72♀, No. 1, and a male, *les* L.W72♂, No. 1, and one male, *les* L. 76♂, No. 5, produced in 1976 from a mating between a female, *les* L. W75♀, No. 2, and a male, *les* L. W75♂, No. 2.

Hemoglobin (Hb), serum albumin (Ab) and 18 kinds of enzymes extracted from the skeletal muscles and livers of these ten frogs were analyzed by the method of starch-gel electrophoresis. A total of 26 loci of these blood proteins and enzymes were examined. These loci were Hb, Ab, LDH–A, LDH–B, PGM, 6–PGD, MPI, ME–A, ME–B, ALD, Pep–A, ADH–B, SOD–A, SOD–B, α–GDH, GPI, AAT–A, AAT–B, ADA, AK, Fum, MDH–A, MDH–B, CK, IDH–A and IDH–B. It was found that all these loci consisted of homozygous alleles except ME–B which showed three phenotypes due to two alleles, *c* and *d*. These electrophoretic patterns of *Rana lessonae* from Luxembourg are called the $L^L \cdot L^L$-type (Table 14; Figs. 10 and 11).

b. *Rana lessonae* from Italy

The electrophoretic patterns of the above 26 loci were examined in six *Rana lessonae* from Italy including three females, *les* I.W77♀, Nos. 1～3 and three males, *les* I.W77♂, Nos. 1～3. All these frogs were collected from the field. The results showed that 24 of the 26 loci analyzed consisted of homozygous alleles, while the alleles of the other two loci, MPI and α-GDH, were heterozygous in a single female, *les* I.W77♀, No. 2. These two loci were *hi* and *ce* in phenotype, respectively.

When the electrophoretic patterns of *Rana lessonae* from Italy are called the $L^I \cdot L^I$-type, and compared with those of the $L^L \cdot L^L$-type found in *Rana lessonae* from Luxembourg, there are distinct differences between them in two loci. While loci ADH–B and AAT–B in the $L^I \cdot L^I$-type electrophoretic patterns are occupied by homozygous alleles *cc* and *bb*, respectively, those in the $L^L \cdot L^L$-type ones are occupied by homozygous alleles *bb* and *cc*, respectively. There is also a remarkable difference between the electrophoretic patterns of the two populations. In the Italy population, locus ME–B is occupied by homozygous alleles *cc*, in contrast to two alleles, *c* and *d*, in the Luxembourg population. The two populations are nearly the same as each other in the electrophoretic patterns of the other 23 loci (Table 14; Figs. 10 and 11).

c. *Rana ridibunda* from France

In four male *Rana ridibunda* from France, *rid* F.W74♂, Nos. 1～4, the electrophoretic patterns of the above 26 loci were examined. These four males were all collected from the field. The electrophoretic patterns of *Rana ridibunda* did not differ from those of *Rana lessonae* in 12 of the 26 loci, while they completely differed from the latter in 11 loci, Hb, Ab, LDH–B, PGM, 6–PGD, MPI, ME–B,

ALD, Pep–A, ADH–B and SOD–A. They slightly differed from those of *Rana lessonae* from Italy in loci GPI and AAT–B. In a male, *rid* F.W74♂, No. 2, these two loci consisted of heterozygous alleles *bd* and *bc*, respectively, in contrast to homozygous alleles *dd* and *bb* in the other three males. The electrophoretic patterns of *Rana ridibunda* from France also slightly differed from those of *Rana lessonae* from Italy in locus α–GDH. While locus α–GDH of *Rana ridibunda* consisted of homozygous alleles *ee* in phenotype, that of a female, *les* I.W77♀, No. 2, of *Rana lessonae* from Italy consisted of *ce*.

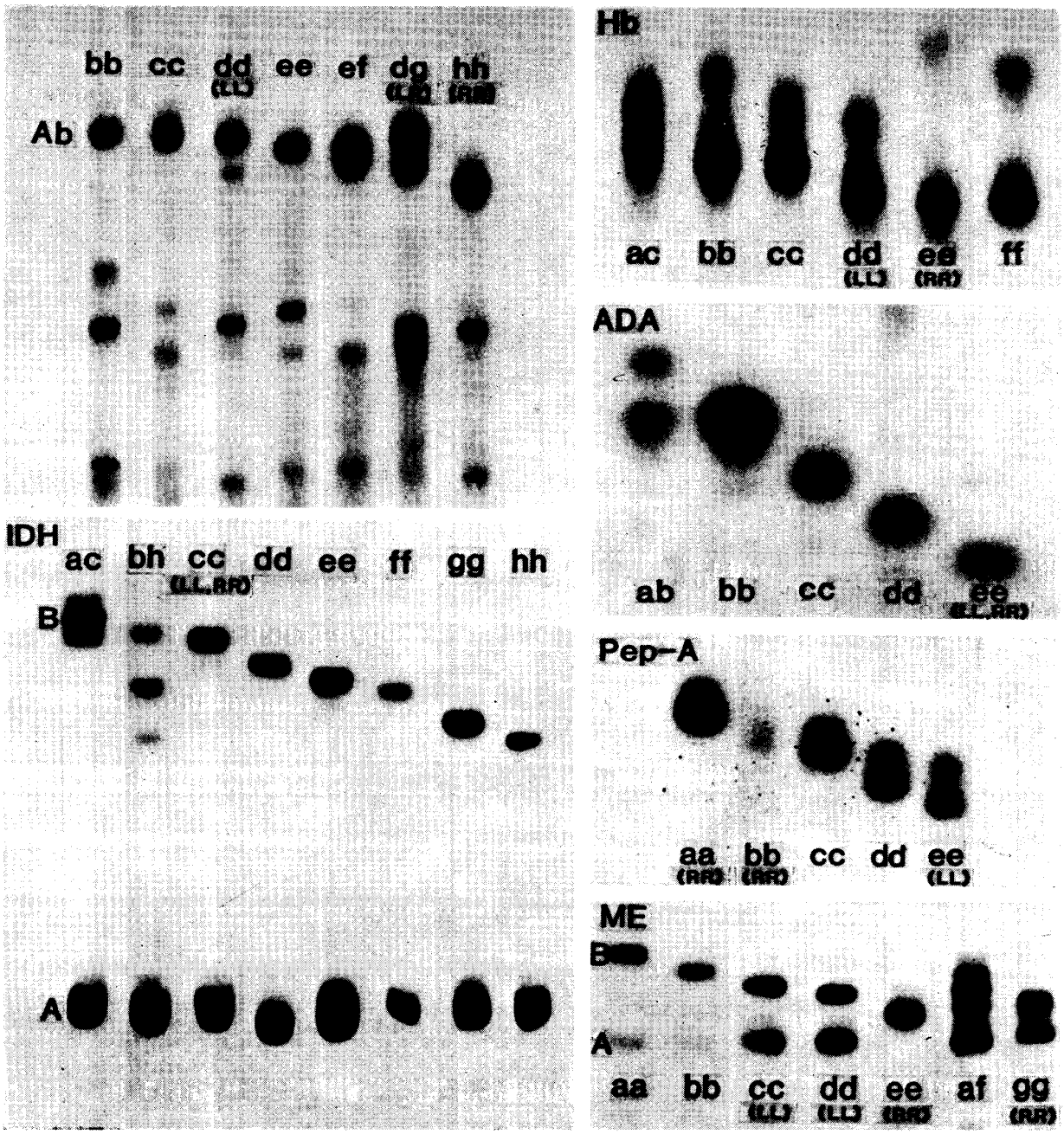

Fig. 10. Electrophoretic patterns of two blood proteins and four enzymes from green frogs in the Palearctic region.

TABLE 14

Electrophoretic patterns of the mature frogs used in crossing experiments

	Hb	Ab	LDH-B	PGM	6-PGD	MPI	ME-B	ALD	Pep-A	ADH-B	SOD-A	α-GDH	GPI	AAT-B	Type
les L.W72♀, No. 1	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L.W75♀, No. 2	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L.W75♀, No. 3	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L. 75♀, No. 4	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L. 75♀, No. 5	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	$L^L \cdot L^L$
les L.W72♂, No. 1	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L.W75♂, No. 2	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L. 75♂, No. 3	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L. 75♂, No. 4	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les L. 76♂, No. 5	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*	
les I.W77♀, No. 1	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*cc*	*cc*	*ee*	*dd*	*bb*	
les I.W77♀, No. 2	*dd*	*dd*	*ee*	*bb*	*bb*	*hi*	*cc*	*dd*	*ee*	*cc*	*cc*	*ce*	*dd*	*bb*	
les I.W77♀, No. 3	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*cc*	*cc*	*ee*	*dd*	*bb*	$L^I \cdot L^I$
les I.W77♂, No. 1	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*cc*	*cc*	*ee*	*dd*	*bb*	
les I.W77♂, No. 2	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*cc*	*cc*	*ee*	*dd*	*bb*	
les I.W77♂, No. 3	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*cc*	*cc*	*ee*	*dd*	*bb*	
rid F.W74♂, No. 1	*ee*	*gg*	*bd*	*cc*	*ee*	*ac*	*ee*	*aa*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid F.W74♂, No. 2	*ee*	*fh*	*dd*	*cc*	*ee*	*bc*	*ee*	*gg*	*ab*	*gg*	*aa*	*ee*	*bd*	*bc*	$R^F \cdot R^F$
rid F.W74♂, No. 3	*ee*	*gf*	*bd*	*cc*	*ee*	*ac*	*ee*	*aa*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid F.W74♂, No. 4	*ee*	*ff*	*bb*	*cc*	*ee*	*aa*	*ee*	*aa*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid T.W76♀, No. 1	*ee*	*hh*	*dd*	*cc*	*ee*	*ff*	*gg*	*cg*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid T.W76♀, No. 2	*ee*	*hh*	*dd*	*cc*	*ee*	*cf*	*eg*	*cc*	*ab*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid T.W76♂, No. 1	*ee*	*hh*	*dd*	*cc*	*ee*	*bf*	*ee*	*cg*	*aa*	*gg*	*aa*	*ee*	*bd*	*bb*	$R^T \cdot R^T$
rid T.W76♂, No. 2	*ee*	*hh*	*dd*	*cc*	*ee*	*bf*	*eg*	*cg*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid T.W76♂, No. 3	*ee*	*hh*	*dd*	*cc*	*ee*	*bf*	*ee*	*cc*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid T. 77♂, No. 4	*ee*	*hh*	*dd*	*cc*	*ee*	*bf*	*eg*	*cc*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	
rid S.W76♀, No. 1	*ee*	*gh*	*bd*	*cc*	*ee*	*cc*	*ee*	*cg*	*bb*	*gg*	*aa*	*ee*	*bd*	*bb*	
rid S.W76♂, No. 1	*ee*	*hh*	*bb*	*bb*	*ee*	*ff*	*ee*	*gg*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*	$R^S \cdot R^S$
rid S. 77♂, No. 2	*ee*	*gh*	*bd*	*bc*	*ee*	*cf*	*ee*	*gg*	*bb*	*gg*	*aa*	*ee*	*bd*	*bb*	
esc G.W76♂, No. 1	*ed*	*gd*	*be*	*cb*	*eb*	*fh*	*ec*	*gd*	*be*	*gb*	*ac*	*ce*	*bd*	*bc*	$R^G \cdot L^G$
esc G.W76♂, No. 2	*ed*	*gd*	*be*	*cb*	*eb*	*fh*	*ec*	*gd*	*be*	*gb*	*ac*	*ce*	*bd*	*bc*	

Of the 14 loci which completely or slightly differed from those of *Rana lessonae*, Ab and MPI were occupied by three alleles, *f*, *g* and *h*, and *a*, *b* and *c*, respectively. Five loci, LDH–B, ALD, Pep–A, GPI and AAT–B, were occupied by two alleles, *b* and *d*, *a* and *g*, *a* and *b*, *b* and *d*, and *b* and *c*, respectively. The remaining 19 loci always consisted of homozygous alleles. These electrophoretic patterns of *Rana ridibunda* from France are called the $R^F \cdot R^F$-type (Table 14; Figs. 10 and 11).

d. *Rana ridibunda* from Turkey

The electrophoretic patterns of the foregoing 26 loci were examined in a total of six *Rana ridibunda* from Turkey, including two females, *rid* T.W76♀, Nos. 1 and 2, and three males, *rid* T.W76♂, Nos. 1～3, collected from the field, and a male, *rid* T.77♂, No. 4, produced from a mating between a female, *rid* T.W76♀, No. 1, and a male, *rid* T.W76♂, No. 2. It was found that 21 of the 26 loci examined consisted of homozygous alleles, while locus MPI was occupied by three alleles, *b*, *c* and *f*, and the remaining four loci, ME–B, ALD, Pep–A and GPI, were occupied by two alleles, *e* and *g*, *c* and *g*, *a* and *b*, and *b* and *d*, respectively.

The electrophoretic patterns of six loci, Pep–A, Hb, PGM, 6–PGD, ADH–B and SOD–A, were identical with those of *Rana ridibunda* from France and completely differed from those of *Rana lessonae*. On the other hand, the electrophoretic patterns of five loci, Ab, LDH–B, MPI, ME–B and ALD, also completely differed from those of *Rana lessonae*. However, they were not identical with those of *Rana ridibunda* from France, although one or two common alleles were found in each kind of these loci of the two populations of *Rana ridibunda*. The electrophoretic patterns of locus AAT–B were the same as those of *Rana lessonae* from Italy, but completely differed from those of *Rana lessonae* from Luxembourg. No differences could be found between *Rana lessonae* and *Rana ridibunda* in the electrophoretic patterns of the remaining 14 loci. The electrophoretic patterns of *Rana ridibunda* from Turkey are called the $R^T \cdot R^T$-type (Table 14; Figs. 10 and 11).

e. *Rana ridibunda* from Soviet Union

The electrophoretic patterns of the foregoing 26 loci were examined in three *Rana ridibunda* from Soviet Union, including a female, *rid* S.W76♀, No. 1 and a male, *rid* S.W76♂, No. 1, collected from the field, and a male, *rid* S.77♂, No. 2, produced from a mating between these female and male frogs. The results of analyses showed that 20 loci consisted of homozygous alleles and the other six loci, Ab, LDH–B, PGM, MPI, ALD and GPI, were occupied by two alleles, *g* and *h*, *b* and *d*, *c* and *b*, *c* and *f*, *c* and *g*, and *b* and *d*, respectively. The electrophoretic patterns of 10 loci, Hb, Ab, LDH–B, 6–PGD, MPI, ME–B, ALD, Pep–A, ADH–B and SOD–A, completely differed from those of *Rana lessonae*, but they were identical with those of *Rana ridibunda* from France and Turkey or had an allele or alleles common to the three populations of *Rana ridibunda* in each kind of these loci. The electrophoretic patterns of the other 16 loci were the same as those of *Rana lessonae* and *Rana ridibunda* from the other localities. Such electrophoretic patterns of *Rana ridibunda* from Soviet Union are called the

$R^S \cdot R^S$-type (Table 14).

f. *Rana esculenta* from West Germany

The electrophoretic patterns of the foregoing 26 loci were examined in two field-caught *Rana esculenta* from West Germany, *esc* G.W76♂, Nos. 1 and 2. It was found that 14 loci, Hb, Ab, LDH–B, PGM, 6–PGD, MPI, ME–B, ALD, Pep–A, ADH–B, SOD–A, α–GDH, GPI and AAT–B, showed hybrid patterns consisting of two alleles derived from *Rana ridibunda* and *Rana lessonae*. The other 12 loci consisted of homozygous alleles, as the electrophoretic patterns of these loci in *Rana ridibunda* were the same as those in *Rana lessonae*. Such electrophoretic patterns are called the $R^G \cdot L^G$-type (Table 14).

2. Inter- and intraspecific hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

a. Controls, *les* L♀ × *les* L♂

Five matings were made between five females, *les* L♀, Nos. 1～5, and four males, *les* L♂, Nos. 1～4, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type). A total of 27 one- or 3-year-old mature female and male offspring obtained from these matings were used in examining electrophoretic patterns of 26 loci controlling two kinds of blood proteins, Hb and Ab, and 18 kinds of enzymes extracted from the skeletal muscles and livers. It was found that 25 of the 26 loci were occupied by homozygous alleles, and the remaining locus ME–B showed three kinds of phenotypes, *cc*, *dd* and *cd* (Table 15).

b. Intraspecific hybrids, *les* L♀ × *les* I♂

The electrophoretic patterns of nine mature offspring produced from two matings between two females, *les* L♀, Nos. 4 and 5, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type) and two males, *les* I♂, Nos. 1 and 2, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type) were examined. There were no differences in electrophoretic patterns of 23 of the 26 loci examined between *Rana lessonae* from Luxembourg and the same species from Italy, while these two populations differed from each other in three loci, ME–B, ADH–B and AAT–B. The electrophoretic pattern of locus ME–B revealed three kinds of phenotypes, *cc*, *dd* and *cd*, in the Luxembourg population, while it revealed *cc* in the Italy population. The electrophoretic patterns of loci ADH–B and AAT–B of the Luxembourg population showed *bb* and *cc* in phenotype, respectively, while those of the Italy population showed *cc* and *bb* in phenotype, respectively.

Of the 26 loci of the offspring between the two populations, locus ME–B showed *cc* and *dc*, ADH–B showed *bc*, and AAT–B showed *cb* in phenotype, as expected. The other 23 loci were all occupied by homozygous alleles. Thus, the electrophoretic patterns of the offspring were of the $L^L \cdot L^I$-type (Table 15).

c. Interspecific hybrids, *les* L♀ × *rid* F♂

The electrophoretic patterns of 30 mature female and male offspring produced

TABLE 15

Electrophoretic patterns of the mature hybrids between female *Rana lessonae* from Luxembourg or Italy and four or five kinds of males and between female *Rana ridibunda* from Turkey or Soviet Union and five kinds of males

	Type	Hb	Ab	LDH-B	PGM	6-PGD	MPI	ME-B	ALD	Pep-A	ADH-B	SOD-A	α-GDH	GPI	AAT-B
les L ♀1~5×*les* L ♂1~4	$L^L \cdot L^L$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc dd cd*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*
les L ♀4, 5×*les* I ♂1, 2	$L^L \cdot L^I$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc dc*	*dd*	*ee*	*bc*	*cc*	*ee*	*dd*	*cb*
les L ♀1~3×*rid* F ♂1, 2	$L^L \cdot R^F$	*de*	*df dg dh*	*eb ed*	*bc*	*be*	*ha hb hc*	*ce de*	*da dg*	*ea eb*	*bg*	*ca*	*ee*	*dd db*	*cc cb*
les L ♀2, 3×*rid* T ♂1	$L^L \cdot R^T$	*de*	*dh*	*ed*	*bc*	*be*	*hf hb*	*ce de*	*dc dg*	*ea*	*bg*	*ca*	*ee*	*dd*	*cb*
les L ♀4 ×*esc* G ♂1	$L^L \cdot R^G$	*de*	*dg*	*eb*	*bc*	*be*	*hf*	*ce de*	*dg*	*eb*	*bg*	*ca*	*ec*	*db*	*cb*
〃	$L^L \cdot L^G$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc dc*	*dd*	*ee*	*bb*	*cc*	*ee*	*dd*	*cc*
les I ♀1~3×*les* I ♂1, 2	$L^I \cdot L^I$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh ih*	*cc*	*dd*	*ee*	*cc*	*cc*	*ee ce*	*dd*	*bb*
les I ♀1, 2×*les* L ♂3	$L^I \cdot L^L$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh ih*	*cd*	*dd*	*ee*	*cb*	*cc*	*ee ce*	*dd*	*bc*
les I ♀1, 2×*rid* F ♂3, 4	$L^I \cdot R^F$	*de*	*dg df*	*eb ed*	*bc*	*be*	*ha hc ia*	*ce*	*da*	*eb*	*cg*	*ca*	*ee ce*	*dd*	*bb*
les I ♀1, 2×*rid* T ♂2, 3	$L^I \cdot R^T$	*de*	*dh*	*ed*	*bc*	*be*	*hb hf*	*ce cg*	*dc dg*	*eb*	*cg*	*ca*	*ee*	*dd*	*bb*
les I ♀2 ×*rid* S ♂1	$L^I \cdot R^S$	*de*	*dh*	*eb*	*bb*	*be*	*hf if*	*ce*	*dg*	*eb*	*cg*	*ca*	*ee ce*	*dd*	*bb*
les I ♀1 ×*esc* G ♂1	$L^I \cdot R^G$	*de*	*dg*	*eb*	*bc*	*be*	*hf*	*ce*	*dg*	*eb*	*cg*	*ca*	*ec*	*db*	*bb*
〃	$L^I \cdot L^G$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*cb*	*cc*	*ee*	*dd*	*bc*
les I ♀2 ×*esc* G ♂1	$L^I \cdot R^G$	*de*	*dg*	*eb*	*bc*	*be*	*hf if*	*ce*	*dg*	*eb*	*cg*	*ca*	*cc ec*	*db*	*bb*
〃	$L^I \cdot L^G$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh ih*	*cc*	*dd*	*ee*	*cb*	*cc*	*ee ce*	*dd*	*bc*
les I ♀3 ×*esc* G ♂1	$L^I \cdot R^G$	*de*	*dg*	*eb*	*bc*	*be*	*hf*	*ce*	*dg*	*eb*	*cg*	*ca*	*ec*	*db*	*bb*
〃	$L^I \cdot L^G$	*dd*	*dd*	*ee*	*bb*	*bb*	*hh*	*cc*	*dd*	*ee*	*cb*	*cc*	*ee*	*dd*	*bc*
rid T ♀1 ×*rid* T ♂2	$R^T \cdot R^T$	*ee*	*hh*	*dd*	*cc*	*ee*	*ff fb*	*gg ge*	*cc gg cg*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*
rid T ♀1 ×*rid* F ♂3	$R^T \cdot R^F$	*ee*	*hg hf*	*dd db*	*cc*	*ee*	*fa fc*	*ge*	*ca ga*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*
rid T ♀1 ×*rid* S ♂1	$R^T \cdot R^S$	*ee*	*hh*	*db*	*cb*	*ee*	*ff*	*ge*	*cg gg*	*bb*	*gg*	*aa*	*ee*	*dd*	*bb*
rid T ♀1 ×*les* L ♂3	$R^T \cdot L^L$	*ed*	*hd*	*de*	*cb*	*eb*	*fh*	*gd*	*cd gd*	*be*	*gb*	*ac*	*ee*	*dd*	*bc*
rid T ♀1 ×*les* I ♂1	$R^T \cdot L^I$	*ed*	*hd*	*de*	*cb*	*eb*	*fh*	*gc*	*cd gd*	*be*	*gc*	*ac*	*ee*	*dd*	*bb*
rid T ♀1 ×*esc* G ♂1	$R^T \cdot L^G$	*ed*	*hd*	*de*	*cb*	*eb*	*fh*	*gc*	*cd gd*	*be*	*gb*	*ac*	*ee*	*dd*	*bc*
〃	$R^T \cdot R^G$	*ee*	*hg*	*db*	*cc*	*ee*	*ff*	*ge*	*cg gg*	*bb*	*gg*	*aa*	*ec*	*db*	*bb*
rid T ♀2 ×*rid* T ♂4	$R^T \cdot R^T$	*ee*	*hh*	*dd*	*cc*	*ee*	*cb cf fb ff*	*ee eg gg*	*cc*	*ab bb*	*gg*	*aa*	*ee*	*dd*	*bb*
rid T ♀2 ×*rid* S ♂2	$R^T \cdot R^S$	*ee*	*hg*	*db*	*cc cb*	*ee*	*cc cf ff*	*ee ge*	*cg*	*ab bb*	*gg*	*aa*	*ee*	*bd dd*	*bb*
rid T ♀2 ×*les* L ♂5	$R^T \cdot L^L$	*ed*	*hd*	*de*	*cb*	*eb*	*ch fh*	*ec ed gc gd*	*cd*	*ae be*	*gb*	*ac*	*ee*	*dd*	*bc*
rid T ♀2 ×*les* I ♂3	$R^T \cdot L^I$	*ed*	*hd*	*de*	*cb*	*eb*	*ch fh*	*ec gc*	*cd*	*ae be*	*gc*	*ac*	*ee*	*dd*	*bb*
rid T ♀2 ×*esc* G ♂2	$R^T \cdot R^G$	*ee*	*hg*	*db*	*cc*	*ee*	*cf ff*	*ee ge*	*cg*	*ab bb*	*gg*	*aa*	*ac*	*bd*	*bb*
rid S ♀1 ×*rid* S ♂1	$R^S \cdot R^S$	*ee*	*gh hh*	*bb db*	*cb*	*ee*	*cf*	*ee*	*cg gg*	*bb*	*gg*	*aa*	*ee*	*bd*	*bb*
rid S ♀1 ×*rid* F ♂3	$R^S \cdot R^F$	*ee*	*gg gf hg hf*	*bb bd dd*	*cc*	*ee*	*ca cc*	*ee*	*ca ga*	*bb*	*gg*	*aa*	*ee*	*bd dd*	*bb*
rid S ♀1 ×*rid* T ♂2	$R^S \cdot R^T$	*ee*	*gh hh*	*bd dd*	*cc*	*ee*	*cb cf*	*ee eg*	*gg cg*	*bb*	*gg*	*aa*	*ee*	*bd dd*	*bb*
rid S ♀1 ×*les* L ♂3	$R^S \cdot L^L$	*ed*	*gd hd*	*be de*	*cb*	*eb*	*ch*	*ed*	*cd gd*	*be*	*gb*	*ac*	*ee*	*bd dd*	*bc*
rid S ♀1 ×*les* I ♂1	$R^S \cdot L^I$	*ed*	*gd hd*	*be de*	*cb*	*eb*	*ch*	*ec*	*cd gd*	*be*	*gc*	*ac*	*ee*	*bd dd*	*bb*
rid S ♀1 ×*esc* G ♂1	$R^S \cdot L^G$	*ed*	*gd hd*	*be*	*cb*	*eb*	*ch*	*ec*	*cd gd*	*be*	*gb*	*ac*	*ee*	*bd dd*	*bc*
〃	$R^S \cdot R^G$	*ee*	*gg gh*	*bb db*	*cc*	*ee*	*cf*	*ee*	*cg gg*	*bb*	*gg*	*aa*	*ec*	*bb db*	*bb*

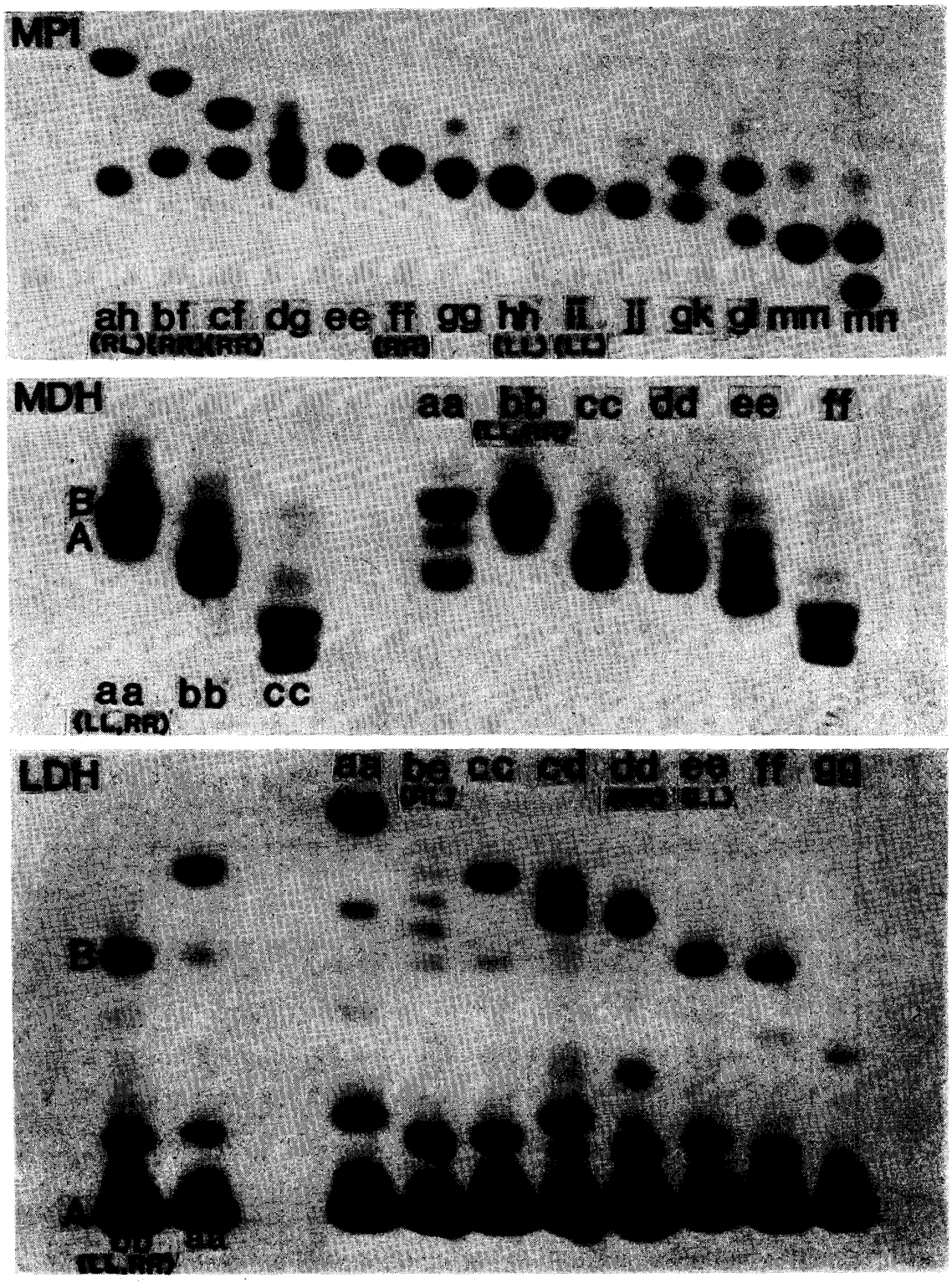

Fig. 11. Electrophoretic patterns of three enzymes from green frogs in the Palearctic region.

from three matings between three females, *les* L♀, Nos. 1~3, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type) and two males, *rid* F♂, Nos. 1 and 2, of *Rana ridibunda* from France ($R^F \cdot R^F$-type) were examined. It was found that 13 of the 26 loci analyzed had homozygous alleles, as there were no differences in electro-

phoretic patterns between *Rana lessonae* from Luxembourg and *Rana ridibunda* from France. Of the remaining 13 loci, five loci, Hb, PGM, 6–PGD, ADH–B and SOD–A, showed hybrid bands, *de*, *bc*, *be*, *bg* and *ca*, respectively, in phenotype, as these loci consisted of homozygous alleles in each of the two species. The hybrids were polymorphic in the following eight loci; Ab was *df*, *dg* and *dh*, LDH–B was *eb* and *ed*, MPI was *ha*, *hb* and *hc*, ME–B was *ce* and *de*, ALD was *da* and *dg*, Pep–A was *ea* and *eb*, GPI was *dd* and *db*, and AAT–B was *cc* and *cb* in phenotype.

In the offspring produced in 1975 from mating with a male, *rid* F♂, No. 1, loci LDH–B and MPI of six males showed *eb* and *ha*, respectively, while those of six females showed *ed* and *hc*, respectively. On the other hand, in the offspring produced from mating with the other male, *rid* F♂, No. 2, locus MPI revealed *hc* in phenotype in eight of 10 males and *hb* in the other two, while *hb* in all eight females. No sexual differences were found in the other loci. All the offspring produced from the matings between female *Rana lessonae* from Luxembourg and male *Rana ridibunda* from France were of the $L^L \cdot R^F$-type in electrophoretic patterns (Table 15).

d. Interspecific hybrids, *les* L♀ × *rid* T♂

The electrophoretic patterns of 20 mature female and male hybrids produced from two matings between two females, *les* L♀, Nos. 2 and 3, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type) and a male, *rid* T♂, No. 1, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) were examined. It was found that 14 of the 26 loci analyzed had homozygous alleles, as there were no differences in electrophoretic patterns between the two parental species. Nine of the other 12 loci, Hb, Ab, LDH–B, PGM, 6–PGD, Pep–A, ADH–B, SOD–A and AAT–B, showed hybrid bands, *de*, *dh*, *ed*, *bc*, *be*, *ea*, *bg*, *ca* and *cb* in phenotype, respectively. The remaining three loci, MPI, ME–B and ALD, showed two kinds of phenotypes, *hf* and *hb*, *ce* and *de*, and *dc* and *dg*, respectively. Thus, the electrophoretic patterns of these hybrids were all of the $L^L \cdot R^T$-type (Table 15).

e. Interspecific hybrids, *les* L♀ × *esc* G♂

Of 32 mature hybrids produced from a mating between a female, *les* L♀, No. 4, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type), and a male, *esc* G♂, No. 1, of *Rana esculenta* from West Germany ($R^G \cdot L^G$-type), 12 females and five males were of the LR-type in external characters, while the other 15 males were of the LL-type. The electrophoretic patterns of five of the 12 LR-type females and three of the five LR-type males, and five of the 15 LL-type males were examined.

The results showed that the five LL-type males were all of the $L^L \cdot L^L$-type in phenotype. Of the foregoing 26 loci, 25 consisted of homozygous alleles, while the remaining locus ME–B showed *cc* and *dc* in phenotype, as the locus of the female parent, *les* L♀, No. 4, had heterozygous alleles *c* and *d*. In the five LR-type females and three LR-type males, 12 of the 26 loci analyzed had homozygous alleles, as there were no differences in the phenotypes of these loci between

the two parental species. Of the other 14 loci, 13 loci, Hb, Ab, LDH–B, PGM, 6–PGD, MPI, ALD, Pep–A, ADH–B, SOD–A, α–GDH, GPI and AAT–B, revealed hybrid bands, *de*, *dg*, *eb*, *bc*, *be*, *hf*, *dg*, *eb*, *bg*, *ca*, *ec*, *db* and *cb* in phenotype, respectively. The remaining locus ME–B showed two kinds of phenotypes, *ce* and *de*. These electrophoretic patterns showing hybrid bands were due to the alleles derived from both *Rana lessonae* from Luxembourg and *Rana esculenta* from West Germany. Thus, the electrophoretic patterns of these LR-type hybrids were of the $L^L \cdot R^G$-type (Table 15).

3. Inter- and intraspecific hybrids between female *Rana lessonae* from Italy and five kinds of males

a. Controls, *les* I♀ × *les* I♂

Three matings were made between three females, *les* I♀, Nos. 1~3, and two males, *les* I♂, Nos. 1 and 2, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type). A total of 26 loci of blood proteins, Hb and Ab, and 18 kinds of enzymes extracted from the skeletal muscles and livers were analyzed in 12 mature offspring obtained from the above control matings. The results indicated that 24 of the 26 loci consisted of homozygous alleles. Of the remaining two loci, MPI showed *hh* and *ih* in phenotype and α–GDH showed *ee* and *ce* (Table 15).

b. Intraspecific hybrids, *les* I♀ × *les* L♂

The electrophoretic patterns of 10 mature offspring produced from two matings between two females, *les* I♀, Nos. 1 and 2, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type) and a male, *les* L♂, No. 3, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type) were examined. It was found that 21 of the 26 loci analyzed consisted of homozygous alleles. Of the remaining five loci, ME–B, ADH–B and AAT–B showed hybrid bands, *cd*, *cb* and *bc* in phenotype, respectively. Loci MPI and α-GDH showed two kinds of phenotypes, *hh* and *ih*, and *ee* and *ce*, respectively. Thus, these offspring between the two populations of *Rana lessonae* were of the $L^I \cdot L^L$-type in electrophoretic patterns (Table 15).

c. Interspecific hybrids, *les* I♀ × *rid* F♂

The electrophoretic patterns of 10 mature hybrids produced from two matings between two females, *les* I♀, Nos. 1 and 2, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type) and two males, *rid* F♂, Nos. 3 and 4, of *Rana ridibunda* from France ($R^F \cdot R^F$-type) were examined. Most of these hybrids were males. It was found that 14 of the 26 loci analyzed consisted of homozygous alleles. Eight of the other 12 loci, Hb, PGM, 6–PGD, ME–B, ALD, Pep–A, ADH–B and SOD–A, showed hybrid bands, *de*, *bc*, *be*, *ce*, *da*, *eb*, *cg* and *ca* in phenotype, respectively. Of the remaining four loci, Ab, LDH–B and α–GDH showed two kinds of phenotypes, *dg* and *df*, *eb* and *ed*, and *ee* and *ce*, respectively. Locus MPI showed three kinds of phenotypes, *ha*, *hc* and *ia*. Thus, these hybrids were of the $L^I \cdot R^F$-type in electrophoretic patterns (Table 15).

d. Interspecific hybrids, *les* I♀ × *rid* T♂

The electrophoretic patterns of 12 mature hybrids produced from two matings between two females, *les* I♀, Nos. 1 and 2, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type) and two males, *rid* T♂, Nos. 2 and 3, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) were examined. Ten of these mature hybrids were males. The results showed that 15 of the 26 loci analyzed consisted of homozygous alleles. Of the other 11 loci, eight including Hb, Ab, LDH–B, PGM, 6–PGD, Pep–A, ADH–B and SOD–A showed hybrid bands, *de*, *dh*, *ed*, *bc*, *be*, *eb*, *cg* and *ca* in phenotype, respectively. The remaining three loci, MPI, ME–B and ALD, revealed two kinds of phenotypes, *hb* and *hf*, *ce* and *cg*, and *dc* and *dg*, respectively. Thus, the electrophoretic patterns of these hybrids were of the $L^I \cdot R^T$-type (Table 15).

e. Interspecific hybrids, *les* I♀ × *rid* S♂

Twelve mature male hybrids were obtained from a mating between a female, *les* I♀, No. 2, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type) and a male, *rid* S♂, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type). The electrophoretic patterns of five of these hybrids were examined. The results indicated that 15 of the 26 loci analyzed consisted of homozygous alleles. Nine other loci, Hb, Ab, LDH–B, 6–PGD, ME–B, ALD, Pep–A, ADH–B and SOD–A, showed hybrid bands, *de*, *dh*, *eb*, *be*, *ce*, *dg*, *eb*, *cg* and *ca* in phenotype, respectively. The remaining two loci, MPI and α–GDH, revealed two kinds of phenotypes, *hf* and *if*, and *ee* and *ce*, respectively. Thus, the electrophoretic patterns of these hybrids were of the $L^I \cdot R^S$-type (Table 15).

f. Interspecific hybrids, *les* I♀ × *esc* G♂

Of mature hybrids produced from three matings between three females, *les* I♀, Nos. 1～3, of *Rana lessonae* from Italy and a male, *esc* G♂, No. 1, of *Rana esculenta* from West Germany, females were all of the LR-type in external characters, while males were mostly of the LL-type and only 19.5% of the males were of the LR-type. The electrophoretic patterns of 15 LR-type females, 13 LR-type males and 30 LL-type males were examined.

It was found that 12 of the 26 loci analyzed consisted of homozygous alleles in all the 58 female and male hybrids. In the 15 LR-type females and 13 LR-type males, 11 of the other 14 loci, Hb, Ab, LDH–B, PGM, 6–PGD, ME–B, ALD, Pep–A, ADH–B, SOD–A and GPI, showed hybrid bands, *de*, *dg*, *eb*, *bc*, *be*, *ce*, *dg*, *eb*, *cg*, *ca* and *db* in phenotype, respectively. Loci MPI and α-GDH, two of the other three loci, revealed *hf* and *ec* in phenotype, respectively, in the hybrids produced from females Nos. 1 and 3, while these loci revealed two kinds of phenotypes, *hf* and *if*, and *cc* and *ec*, respectively, in the hybrids produced from female No. 2. The remaining locus AAT–B consisted of homozygous alleles and showed *bb* in phenotype (Table 15).

In the LL-type male, ten of the 14 loci, Hb, Ab, LDH–B, PGM, 6–PGD, ME–B, ALD, Pep–A, SOD–A and GPI, all consisted of homozygous alleles and revealed *dd*, *dd*, *ee*, *bb*, *bb*, *cc*, *dd*, *ee*, *cc* and *dd* in phenotype, respectively. Loci

MPI and α-GDH showed *hh* and *ee* in phenotype, respectively, in the hybrids produced from females Nos. 1 and 3, while these loci revealed two kinds of phenotypes, *hh* and *ih*, and *ee* and *ce*, respectively, in the hybrids produced from female No. 2. The remaining two loci, ADH–B and AAT–B, revealed *cb* and *bc* in phenotype, respectively. Thus, it became evident that the offspring of the LR-type in external characters were of the $L^I \cdot R^G$-type in electrophoretic patterns, while the LL-type offspring were of the $L^I \cdot L^G$-type (Table 15).

4. Inter- and intraspecific hybrids between female *Rana ridibunda* from Turkey and five kinds of males

a. Controls, *rid* T♀ × *rid* T♂

A control mating was made in 1977 between a female, *rid* T♀, No. 1 and a male, *rid* T♂, No. 2, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type). As the eggs were in an inferior condition, only five mature males were produced from this mating. Electrophoretic analyses were made in these five males. It was found that 23 of the 26 loci analyzed consisted all of homozygous alleles, while the alleles of the other three loci, MPI, ME–B and ALD, were heterozygous. Loci MPI and ME–B revealed two kinds of phenotypes, *ff* and *fb*, and *gg* and *ge*, respectively, while locus ALD showed three kinds of phenotypes, *cc*, *gg* and *cg* (Table 15).

In 1978, a female, *rid* T.W76♀, No. 2, of *Rana ridibunda* collected from the field in Turkey was mated with a male, *rid* T.77♂, No. 4, of *Rana ridibunda* produced in 1977. It was found that only two of 314 sexually mature offspring were males and all the others were females. The electrophoretic patterns of 10 female and one male offspring were examined. It was found that 23 of the 26 loci analyzed consisted of homozygous alleles, while the other three consisted of heterozygous alleles. Of these loci, MPI was the most polymorphic, being *cb*, *cf*, *fb* and *ff* in phenotype. Another locus ME–B showed three kinds of phenotypes, *ee*, *eg* and *gg*, and the remaining locus Pep–A showed two kinds of phenotypes, *ab* and *bb* (Table 15).

b. Intraspecific hybrids, *rid* T♀ × *rid* F♂

The above female, *rid* T♀, No. 1, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) was mated in 1977 with a male, *rid* F♂, No. 3, of *Rana ridibunda* from France ($R^F \cdot R^F$-type). From this mating, five mature males were obtained. Electrophoretic patterns were examined in five males of these offspring. The results showed that 21 of the 26 loci analyzed had homozygous alleles. Of the other five loci, Ab, LDH–B, MPI and ALD revealed two kinds of phenotypes, *hg* and *hf*, *dd* and *db*, *fa* and *fc*, and *ca* and *ga*, respectively. The remaining locus ME–B showed *ge* in phenotype. These phenotypes were all of the $R^T \cdot R^F$-type (Table 15).

c. Intraspecific hybrids, *rid* T♀ × *rid* S♂

Six mature females were produced in 1977 from a mating between the female, *rid* T♀, No. 1, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) and a male, *rid* S♂, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type). The electro-

phoretic patterns of three of these six offspring were examined. It was found that 22 of the 26 loci analyzed consisted of homozygous alleles. Three other loci, LDH-B, PGM and ME-B, revealed hybrid bands, *db*, *cb* and *ge* in phenotype, respectively, and the remaining locus ALD showed two kinds of phenotypes, *cg* and *gg* (Table 15).

In 1978, a mating was made between the above female, *rid* T♀, No. 2, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) and a male, *rid* S♂, No. 2, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type). From this mating, 122 mature offspring including 84.4% females were produced. The electrophoretic patterns of five female offspring were examined. It was found that 18 of the 26 loci examined consisted of homozygous alleles. Three of the other eight loci, Ab, LDH-B and ALD showed hybrid bands, *hg*, *db* and *cg* in phenotype, respectively, while four other loci, PGM, ME-B, Pep-A and GPI, revealed two kinds of phenotypes, *cc* and *cb*, *ee* and *ge*, *ab* and *bb*, and *bd* and *dd*, respectively. The remaining locus MPI revealed three kinds of phenotypes, *cc*, *cf* and *ff*. These phenotypes were all of the $R^T \cdot R^S$-type (Table 15).

d. Interspecific hybrids, *rid* T♀ × *les* L♂

In 1977, two mature female and six mature male hybrids were produced from a mating between the female, *rid* T♀, No. 1, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) and a male, *les* L♂, No. 3, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type). The electrophoretic patterns of these six male hybrids were examined. It was found that 14 of the 26 loci examined were occupied by homozygous alleles, while 11 of the remaining 12 loci, Hb, Ab, LDH-B, PGM, 6-PGD, MPI, ME-B, Pep-A, ADH-B, SOD-A and AAT-B, showed hybrid bands, *ed*, *hd*, *de*, *cb*, *eb*, *fh*, *gd*, *be*, *gb*, *ac* and *bc* in phenotype, respectively. The remaining locus ALD revealed two phenotypes, *cd* and *gd*. Thus, the electrophoretic patterns of these hybrids were of the $R^T \cdot L^L$-type (Table 15).

The electrophoretic patterns of five female and five male hybrids obtained in 1978 from a mating between the female, *rid* T♀, No. 2, of *Rana ridibunda* from Turkey and a male, *les* L♂, No. 5, of *Rana lessonae* from Luxembourg were examined. The results showed that 14 of the 26 loci examined were occupied by homozygous alleles, while nine of the other 12 loci, Hb, Ab, LDH-B, PGM, 6-PGD, ALD, ADH-B, SOD-A and AAT-B, revealed hybrid bands, *ed*, *hd*, *de*, *cb*, *eb*, *cd*, *gb*, *ac* and *bc* in phenotype, respectively. The remaining three loci were polymorphic in phenotype. Loci MPI and Pep-A showed two kinds of phenotypes, *ch* and *fh*, and *ae* and *be*, respectively, and locus ME-B revealed four kinds of phenotypes, *ec*, *ed*, *gc* and *gd*. Thus, the electrophoretic patterns of these hybrids were of the $R^T \cdot L^L$-type (Table 15).

e. Interspecific hybrids, *rid* T♀ × *les* I♂

The electrophoretic patterns of five mature male hybrids obtained in 1977 from a mating between the female, *rid* T♀, No. 1, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) and a male, *les* I♂, No. 1, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type)

were examined. It was found that 15 of the 26 loci analyzed were occupied by homozygous alleles. Ten of the other 11 loci, Hb, Ab, LDH–B, PGM, 6–PGD, MPI, ME–B, Pep–A, ADH–B and SOD–A, revealed hybrid bands, *ed*, *hd*, *de*, *cb*, *eb*, *fh*, *gc*, *be*, *gc* and *ac* in phenotype, respectively. The remaining locus ALD showed two kinds of phenotypes, *cd* and *gd*. Thus, the electrophoretic patterns of these hybrids were of the $R^T \cdot L^I$-type (Table 15).

The electrophoretic patterns of five mature female and five mature male hybrids obtained in 1978 from a mating between the female, *rid* T♀, No. 2, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) and a male, *les* I♂, No. 3, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type) were examined. The results indicated that 15 of the 26 loci analyzed consisted of homozygous alleles, while eight of the other 11 loci, Hb, Ab, LDH–B, PGM, 6–PGD, ALD, ADH–B and SOD–A, revealed hybrid bands, *ed*, *hd*, *de*, *cb*, *eb*, *cd*, *gc* and *ac* in phenotype, respectively. The remaining three loci were polymorphic in phenotype. Loci MPI, ME–B and Pep–A showed two kinds of phenotypes, *ch* and *fh*, *ec* and *gc*, and *ae* and *be*, respectively. Thus, the electrophoretic patterns of these hybrids were of the $R^T \cdot L^I$-type (Table 15).

f. Interspecific hybrids, *rid* T♀ × *esc* G♂

In 1977, seven mature hybrids were obtained from a mating between the female, *rid* T♀, No. 1, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) and a male, *esc* G♂, No. 1, of *Rana esculenta* from West Germany ($R^G \cdot L^G$-type). Of these seven hybrids, two were females and five were males. The two females and three of the five males were of the RR-type in external characters, while the remaining two males were of the RL-type. Electrophoretic patterns were examined in the three RR-type males and the two RL-type males. In the three RR-type hybrids, 20 of the 26 loci analyzed consisted of homozygous alleles, while five of the other six, Ab, LDH–B, ME–B, α–GDH and GPI, revealed hybrid bands of the $R^T \cdot R^G$-type, *hg*, *db*, *ge*, *ec* and *db* in phenotype, respectively. The remaining locus ALD showed two phenotypes, *cg* and *gg*. In the two RL-type hybrids, 14 of the 26 loci analyzed consisted of homozygous alleles. Eleven of the other 12 loci, Hb, Ab, LDH–B, PGM, 6–PGD, MPI, ME–B, Pep–A, ADH–B, SOD–A and AAT–B, revealed hybrid bands, *ed*, *hd*, *de*, *cb*, *eb*, *fh*, *gc*, *be*, *gb*, *ac* and *bc* in phenotype, respectively. The remaining locus ALD showed two phenotypes, *cd* and *gd*. Thus, the phenotypes of these 12 loci were of the $R^T \cdot L^G$-type (Table 15).

In 1978, 154 mature hybrids were obtained from a mating between the female, *rid* T♀, No. 2, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type) and a male, *esc* G♂, No. 2, of *Rana esculenta* from West Germany ($R^G \cdot L^G$-type). All these hybrids were of the RR-type in external characters and only 1.3% of them were males. The electrophoretic patterns of 10 female hybrids were examined.

It was found that 18 of the 26 loci examined consisted of homozygous alleles, while five of the other eight loci, Ab, LDH–B, ALD, α–GDH and GPI, revealed hybrid bands, *hg*, *db*, *cg*, *ac* and *bd* in phenotype, respectively. The remaining three loci were polymorphic in phenotype. Loci MPI, ME–B and Pep–A showed two kinds of phenotypes, *cf* and *ff*, *ee* and *ge*, and *ab* and *bb*, respectively.

All these electrophoretic patterns were of the $R^T \cdot R^G$-type (Table 15).

It became evident that the hybrids of the RR-type and RL-type in external characters were of the $R^T \cdot R^G$- and $R^T \cdot L^G$-type in electrophoretic patterns, respectively.

5. Inter- and intraspecific hybrids between a female *Rana ridibunda* from Soviet Union and five kinds of males

a. Controls, *rid* S♀ × *rid* S♂

Six mature offspring obtained from a mating between a female, *rid* S♀, No. 1, and a male, *rid* S♂, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type) were all males. The electrophoretic patterns of three of these six offspring were examined. The results showed that 20 of the 26 loci analyzed consisted of homozygous alleles, while three of the other six loci, PGM, MPI and GPI, showed hybrid bands, *cb*, *cf* and *bd* in phenotype, respectively, and the remaining three loci, Ab, LDH–B and ALD, revealed two kinds of phenotypes, *gh* and *hh*, *bb* and *db*, and *cg* and *gg*, respectively (Table 15).

b. Intraspecific hybrids, *rid* S♀ × *rid* F♂

Only seven mature offspring were obtained from a mating between the female, *rid* S♀, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type) and a male, *rid* F♂, No. 3, of *Rana ridibunda* from France ($R^F \cdot R^F$-type). Of these offspring, one was a female and six were males. The electrophoretic patterns of five of the males were examined. It was found that 21 of the 26 loci analyzed were occupied by homozygous alleles. Of the other five loci, Ab showed four kinds of phenotypes, *gg*, *gf*, *hg* and *hf*, locus LDH–B showed three kinds of phenotypes, *bb*, *bd* and *dd*, and the remaining three loci, MPI, ALD and GPI, showed *ca* and *cc*, *ca* and *ga*, and *bd* and *dd* in phenotype, respectively. Thus, these phenotypes were of the $R^S \cdot R^F$-type (Table 15).

c. Intraspecific hybrids, *rid* S♀ × *rid* T♂

Of 29 mature offspring produced from a mating between the female, *rid* S♀, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type) and a male, *rid* T♂, No. 2, of *Rana ridibunda* from Turkey ($R^T \cdot R^T$-type), eight were females and 21 were males. Electrophoretic patterns were examined in 16 males of these offspring. The results showed that 20 of the 26 loci analyzed consisted of homozygous alleles. Each of the other six loci, Ab, LDH–B, MPI, ME–B, ALD and GPI, revealed two kinds of phenotypes, *gh* and *hh*, *bd* and *dd*, *cb* and *cf*, *ee* and *eg*, *gg* and *cg*, and *bd* and *dd*, respectively. Thus, the electrophoretic patterns of these hybrids were of the $R^S \cdot R^T$-type (Table 15).

d. Interspecific hybrids, *rid* S♀ × *les* L♂

Seven mature hybrids were obtained from a mating between the female, *rid* S♀, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type) and a male, *les* L♂, No. 3, of *Rana lessonae* from Luxembourg ($L^L \cdot L^L$-type). One of them was a female

and six were males. The electrophoretic patterns of three of these male hybrids were examined. It was found that 13 of the 26 loci analyzed were occupied by homozygous alleles. Nine of the other 13 loci, Hb, PGM, 6–PGD, MPI, ME–B, Pep–A, ADH–B, SOD–A and AAT–B, revealed hybrid bands, *ed*, *cb*, *eb*, *ch*, *ed*, *be*, *gb*, *ac* and *bc* in phenotype, respectively. The other four loci, Ab, LDH–B, ALD and GPI, showed two kinds of phenotypes, *gd* and *hd*, *be* and *de*, *cd* and *gd*, and *bd* and *dd*, respectively. It was evident that these hybrids were of the $R^S \cdot L^L$-type in electrophoretic patterns (Table 15).

e. Interspecific hybrids, *rid* S♀ × *les* I♂

Twelve mature hybrids were obtained from a mating between a female, *rid* S♀, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type) and a male, *les* I♂, No. 1, of *Rana lessonae* from Italy ($L^I \cdot L^I$-type). Two of them were females and the other 10 were males. The electrophoretic patterns of five males of these hybrids were examined. They were identical to those of the foregoing hybrids between *Rana ridibunda* from Soviet Union and *Rana lessonae* from Luxembourg in 23 of the 26 loci analyzed. The other three loci, ME–B, ADH–B and AAT–B, revealed *ec*, *gc* and *bb* in phenotype, respectively, in contrast to the latter hybrids in which the three loci showed *ed*, *gb* and *bc*, respectively. Thus, the electrophoretic patterns of these hybrids were of the $R^S \cdot L^I$-type (Table 15).

f. Interspecific hybrids, *rid* S♀ × *esc* G♂

Ten mature hybrids were obtained from a mating between a female, *rid* S♀, No. 1, of *Rana ridibunda* from Soviet Union ($R^S \cdot R^S$-type) and a male, *esc* G♂, No. 1, of *Rana esculenta* from West Germany ($R^G \cdot L^G$-type). Of these 10 hybrids, four were females and six were males. The four females and two of the six males were of the RR-type in external characters, while the remaining four males were of the RL-type. Electrophoretic patterns were examined in two of the four RR-type females and the two RR-type males as well as three of the four RL-type males.

It was found that 12 of the 26 loci analyzed consisted of homozygous alleles whose phenotypes were the same in both the RR- and RL-type frogs. In the RR-type frogs, eight of the other 14 loci were occupied by homozygous alleles, and four other loci, Ab, LDH–B, ALD and GPI, revealed two kinds of phenotypes, *gg* and *gh*, *bb* and *db*, *cg* and *gg*, and *bb* and *db*, respectively. As found in these electrophoretic patterns, one of the two kinds of phenotypes was due to homozygous alleles, while the other was due to heterozygous alleles. The remaining two loci, MPI and α–GDH, showed *cf* and *ec* in phenotype, respectively, which were of the $R^S \cdot R^G$-type.

In contrast, the RL-type males remarkably differed from the RR-type females and males in electrophoretic patterns. Ten of the above 14 loci, Hb, LDH–B, PGM, 6–PGD, MPI, ME–B, Pep–A, ADH–B, SOD–A and AAT–B, showed hybrid bands, *ed*, *be*, *cb*, *eb*, *ch*, *ec*, *be*, *gb*, *ac* and *bc* in phenotype, respectively. Another locus α–GDH consisted of homozygous alleles and the remaining three

loci, Ab, ALD and GPI, revealed two kinds of phenotypes, *gd* and *hd*, *cd* and *gd*, and *bd* and *dd*, respectively. When these $R^S \cdot L^G$-type electrophoretic patterns of the RL-type males are compared with the above $R^S \cdot L^L$-type ones, they are identical with the latter in 25 of the 26 loci examined. The only exceptional locus is ME–B, which shows *ec* in the $R^S \cdot L^G$-type phenotype, in contrast to *ed* in the $R^S \cdot L^L$-type phenotype. When they are compared with the $R^S \cdot L^I$-type electrophoretic patterns, they are identical with the latter in 24 of the 26 loci examined. The exceptional loci are ADH–B and AAT–B, which show *gb* and *bc* in the $R^S \cdot L^G$-type phenotype, respectively, in contrast to *gc* and *bb* in the $R^S \cdot L^I$-type phenotype (Table 15).

Thus, it is evident that the male, *esc* G♂, No. 1, of *Rana esculenta* from West Germany produced two kinds of spermatozoa, one of which contained *Rana ridibunda* genome and the other contained *Rana lessonae* genome, as the offspring obtained from this male by mating with female *Rana lessonae* from Luxembourg or Italy or with female *Rana ridibunda* from Turkey or Soviet Union contained two kinds of frogs, *Rana esculenta* and *Rana lessonae*, or *Rana esculenta* and *Rana ridibunda* in the external characters as well as in the electrophoretic patterns. It is also evident that the male, *esc* G♂, No. 2, of *Rana esculenta* from West Germany produced one kind of spermatozoa which contained the *Rana ridibunda* genome, as the offspring obtained from this male by mating with a female *Rana ridibunda* from Turkey were all *Rana ridibunda* in external characters as well as in electrophoretic patterns. At the same time, it seems probable that the *Rana ridibunda* genome of this male, *esc* G♂, No. 2, included no Y-chromosome, as all the offspring of this male were females, although 1.3% of them were exceptionally males.

V. Testes of mature male hybrids

1. Hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

a. Controls, *les* L♀ × *les* L♂

The testes of 11 mature males in total, including four 2-year-old males (Nos. 1～4) obtained in 1975 from a mating, *les* L♀, No. 1 × *les* L♂, No. 1, four 2-year-old males (Nos. 5～8) obtained in 1976 from a mating, *les* L♀, No. 2 × *les* L♂, No. 2 and three 2-year-old males (Nos. 9～11) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, were observed. These male frogs were 47.0～50.5 mm, 49.5 mm on the average, in body length. Their left testes were 3.0～5.5 mm, 4.6 mm on the average, in length and 2.5～3.5 mm, 3.3 mm on the average, in width, while the right testes 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. The testes of seven 1-year-old males in total, including five (Nos. 12～16) and two (Nos. 17 and 18) obtained in 1977 from matings, *les* L♀, No. 4 × *les* L♂, No. 3 and *les* L♀, No. 5 × *les* L♂, No. 4, respectively, were also observed. These males were 48.0～52.5 mm, 50.0 mm on the average, in body length. Their left testes were 4.0～4.5 mm, 4.2 mm on the average, in length and 2.5～3.5 mm, 3.2 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 2.0～3.5 mm, 2.6 mm on the average, in width.

While one testis of each male frog was used in mating experiments, the other was cut into cross-sections. The latter showed that the testes were normal in inner structure. The central lumens of the seminiferous tubules were filled with many compact bundles of normal spermatozoa and contained only a few pycnotic nuclei. There were numerous spermatocytes and secondary spermatogonia in the areas surrounding each central lumen and a few primary spermatogonia along the wall of each seminiferous tubule (Fig. 12).

b. Intraspecific hybrids, *les* L♀ × *les* I♂

The testes of 10 mature males in total, including five 1-year-old males (Nos. 1～5) obtained in 1977 from a mating, *les* L♀, No. 4 × *les* I♂, No. 1, and five 1-year-old males (Nos. 6～10) obtained in the same year from a mating, *les* L♀, No. 5 × *les* I♂, No. 2, were observed. These intraspecific hybrids were 47.0～51.5 mm, 50.2 mm on the average, in body length. Their left testes were 4.0～4.5 mm, 4.2 mm on the average, in length and 3.0～3.5 mm, 3.1 mm on the average, in width. The right testes were 3.5～4.5 mm, 3.9 mm on the average, in length and 2.5～3.0 mm, 2.8 mm on the average, in width.

While one testis of each of six males, Nos. 1～3 and 6～8, was used in mating experiments, the other testis of each male and the two testes of each of the remain-

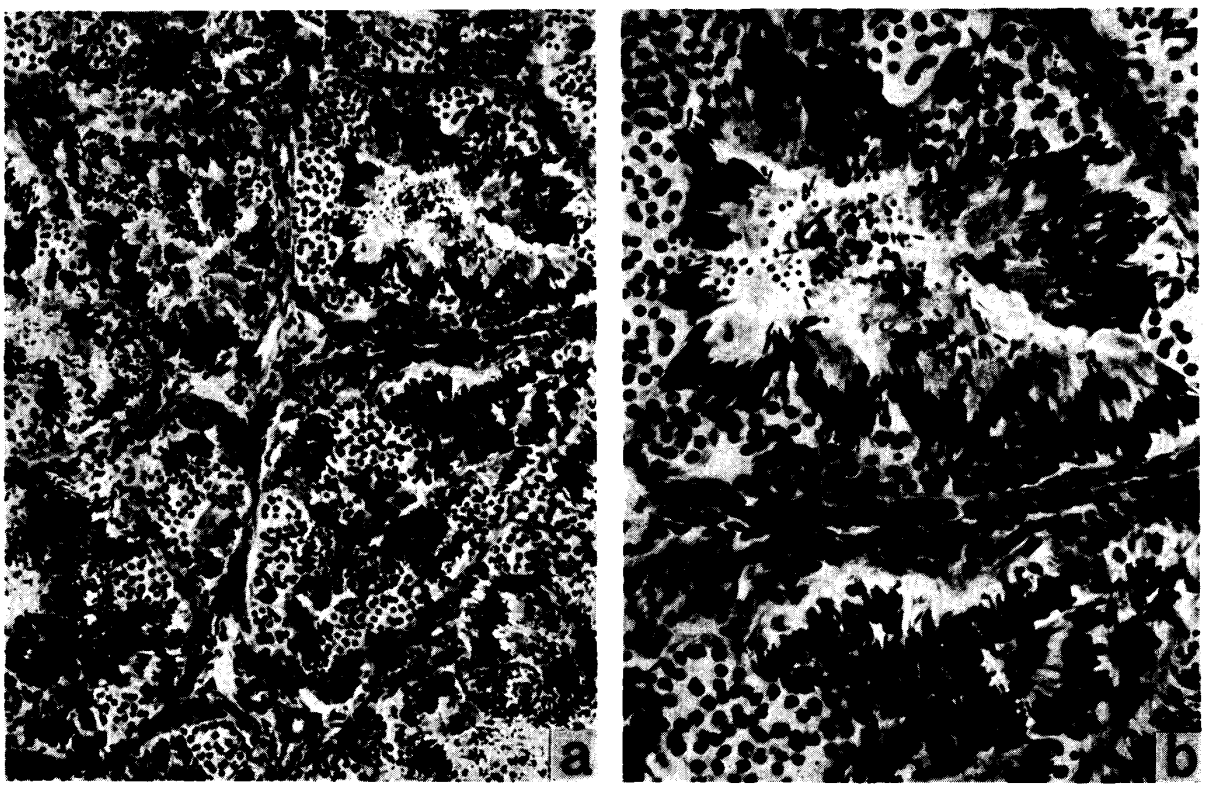

Fig. 12. Cross-sections of the testis of a male *Rana lessonae* from Luxembourg.

a. Control ♂, No. 9, 2 years old, produced in 1976 from *les* L♀, No. 3 × *les* L♂, No. 2. × 150

b. The same as (a). × 300

ing four males were cut into cross-sections. In seven (Nos. 2, 3 and 5~9) of the ten males, all the testes examined were completely normal and similar in inner structure to those of the control males. The central lumens of the seminiferous tubules were filled with many compact bundles of normal spermatozoa. In the areas surrounding each central lumen, there were numerous spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule (Fig. 13a, b). In the remaining three males (Nos. 1, 4 and 10), the testes differed from those of the foregoing males in that the spermatozoa were remarkably fewer (Fig. 13c, d).

c. Interspecific hybrids, *les* L♀ × *rid* F♂

The testes of 15 two-year-old mature male hybrids in total, including five (Nos. 1~5) obtained in 1975 from a mating, *les* L♀, No. 1 × *rid* F♂, No. 1, five (Nos. 6~10) obtained in 1976 from a mating, *les* L♀, No. 2 × *rid* F♂, No. 2 and five (Nos. 11~15) obtained in 1976 from a mating, *les* L♀, No. 3 × *rid* F♂, No. 2, were observed. These male hybrids were 57.0~68.0 mm, 64.2 mm on the average, in body length. Their left testes were 4.5~5.5 mm, 5.0 mm on the average, in length and 2.5~3.5 mm, 3.1 mm on the average, in width. The right testes were 4.0~5.5 mm, 5.2 mm on the average, in length and 2.5~3.0 mm, 2.7 mm on the average, in width.

While one testis of each male was used in mating experiments, the other was cut into cross-sections. The results of histological observations showed that the testes of all the male hybrids were abnormal. The central lumens of the seminiferous tubules contained abnormally shaped spermatozoa alone which were various in size and number. The male hybrids differed from one another in amount of abnormal spermatozoa. In the seminiferous tubules of some male hybrids, such spermatozoa were extremely few and there were many pycnotic nuclei, while in those of the other hybrids, abnormal spermatozoa were considerably numerous. In the areas surrounding each central lumen, there were abundant spermatocytes and secondary spermatogonia. A small number of primary spermatogonia were found along the wall of each seminiferous tubule (Fig. 14).

d. Interspecific hybrids, *les* L♀ × *rid* T♂

The testes of ten 2-year-old mature males in total, including five (Nos. 1~5) obtained in 1976 from a mating, *les* L♀, No. 2 × *rid* T♂, No. 1 and five (Nos. 6~10) obtained in the same year, from a mating, *les* L♀, No. 3 × *rid* T♂, No. 1, were observed. These male hybrids were 60.5~74.5 mm, 65.2 mm on the average, in body length. Their left testes were 3.0~6.5 mm, 4.3 mm on the average, in length and 2.5~4.5 mm, 3.4 mm on the average, in width. The right testes were 2.5~5.0 mm, 4.1 mm on the average, in length and 1.5~4.0 mm, 2.8 mm on the average, in width.

While one testis of each male hybrid was used in mating experiments, the other was cut into cross-sections. It was found that the testes of all the male

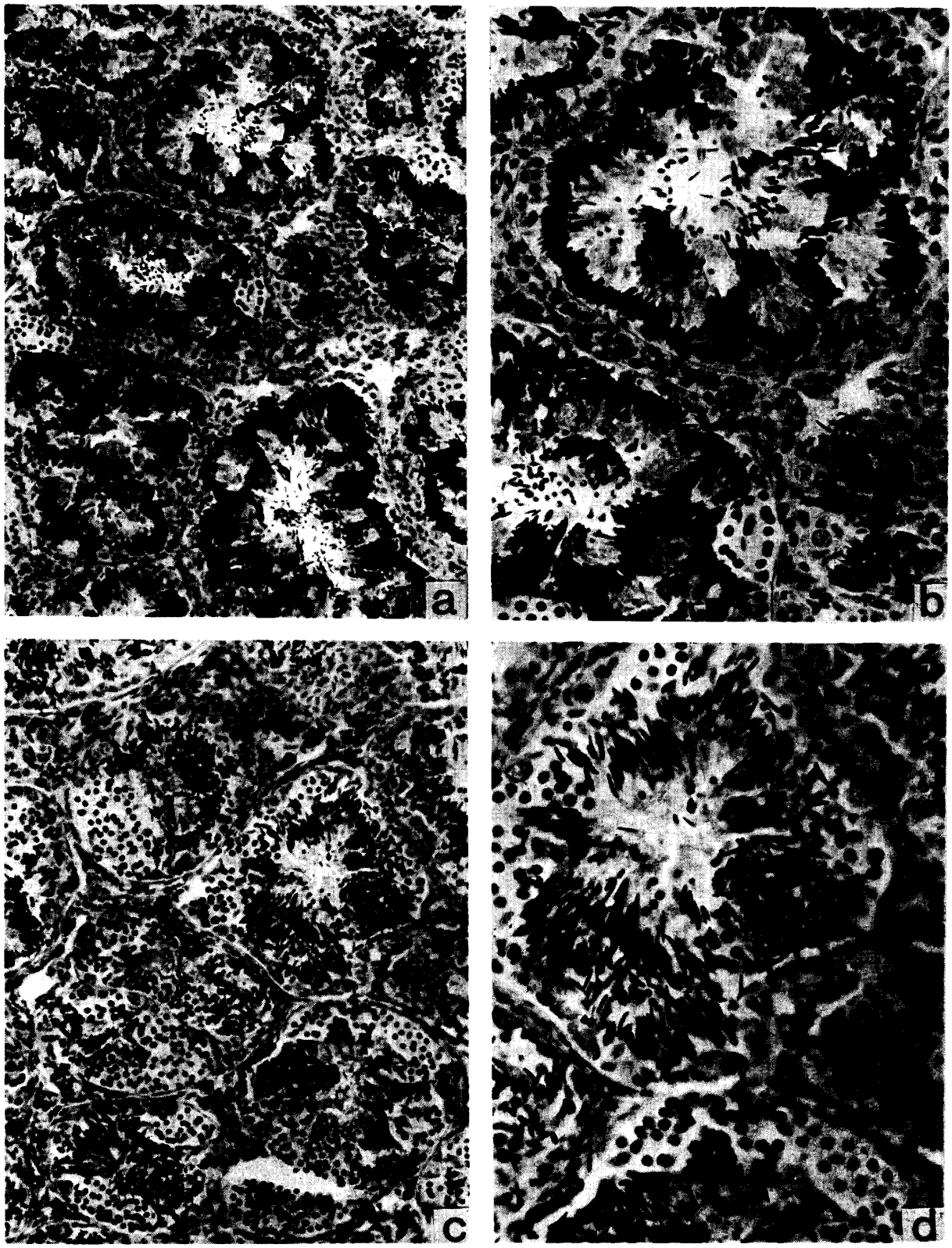

Fig. 13. Cross-sections of the testes of male intraspecific hybrids between a female *Rana lessonae* from Luxembourg and a male *Rana lessonae* from Italy.

a. Hybrid ♂, No. 2, 1 year old, produced in 1977 from *les* L♀, No. 4×*les* I♂, No. 1. ×150
b. The same as (a). ×300
c. Hybrid ♂, No. 4, 1 year old, produced in 1977 from *les* L♀, No. 4×*les* I♂, No. 1. ×150
d. The same as (c). ×300

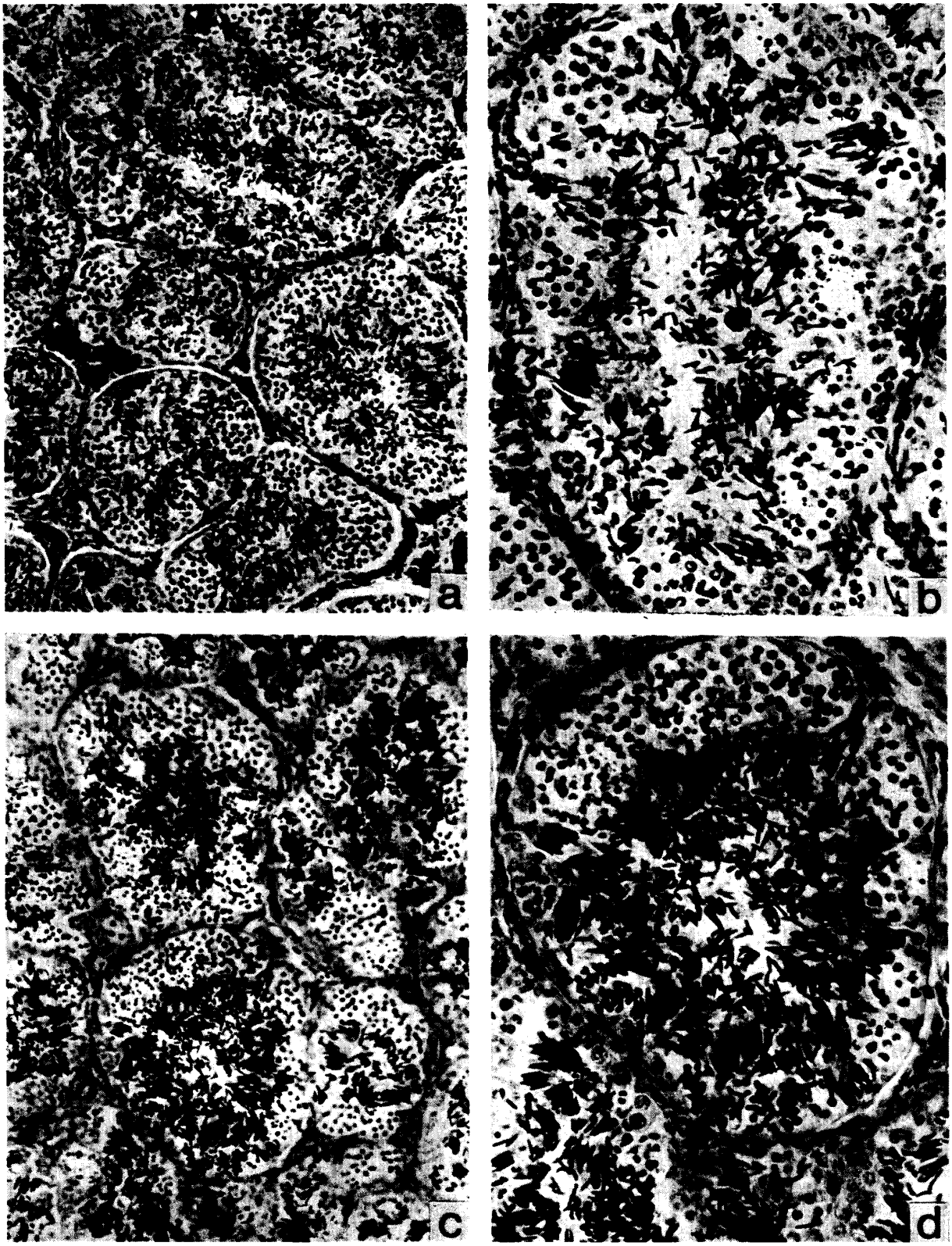

Fig. 14. Cross-sections of the testes of 2-year-old male interspecific hybrids between female *Rana lessonae* from Luxembourg and male *Rana ridibunda* from France.

a. Hybrid ♂, No. 1 produced in 1975 from *les* L♀, No. 1 × *rid* F♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 6 produced in 1976 from *les* L♀, No. 2 × *rid* F♂, No. 2. × 150
d. The same as (c). × 300

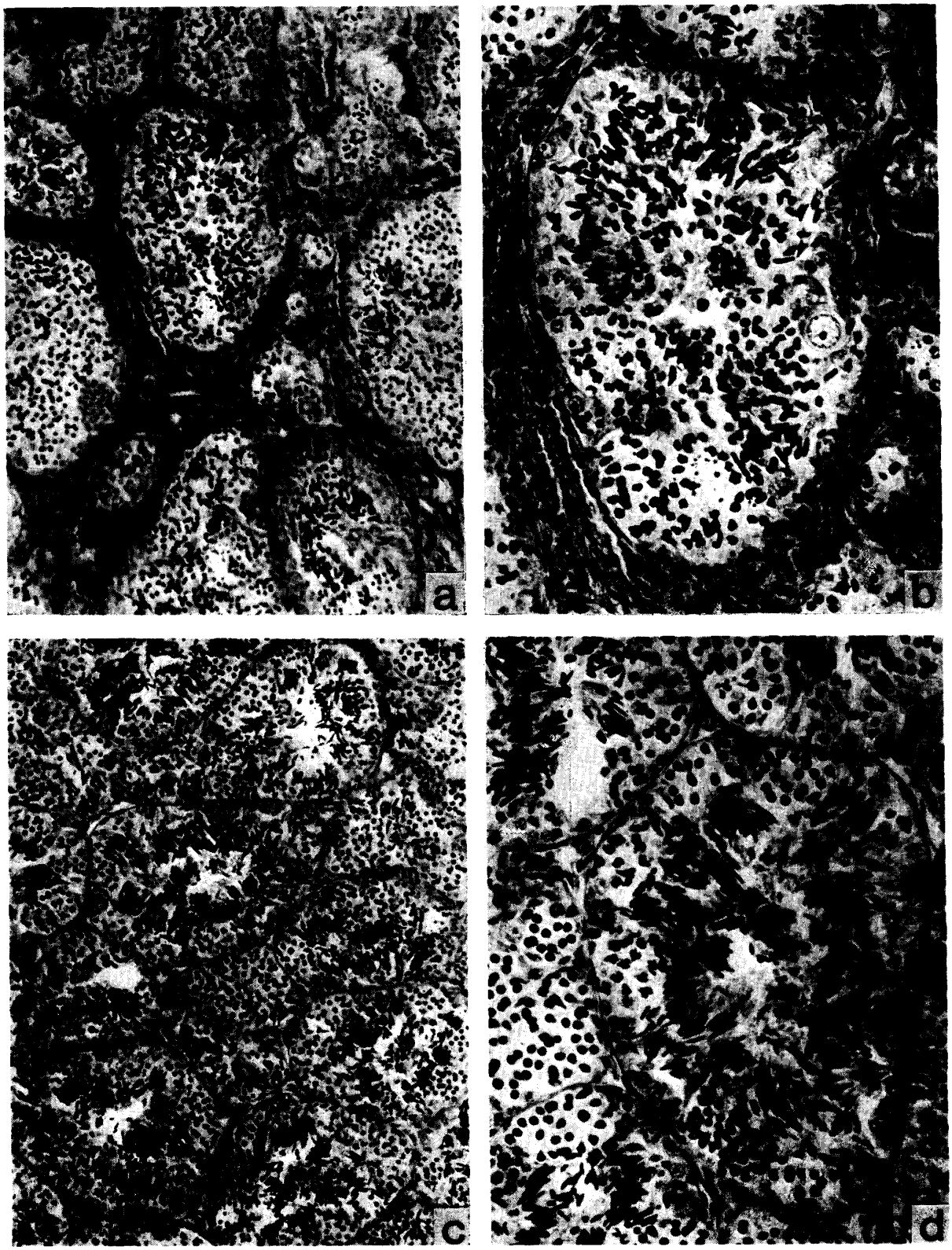

Fig. 15. Cross-sections of the testes of 2-year-old male interspecific hybrids produced in 1976 between female *Rana lessonae* from Luxembourg and a male *Rana ridibunda* from Turkey.

a. Hybrid ♂, No. 2 produced from *les* L♀, No. 2 × *rid* T♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 9 produced from *les* L♀, No. 3 × *rid* T♂, No. 1. × 150
d. The same as (c). × 300

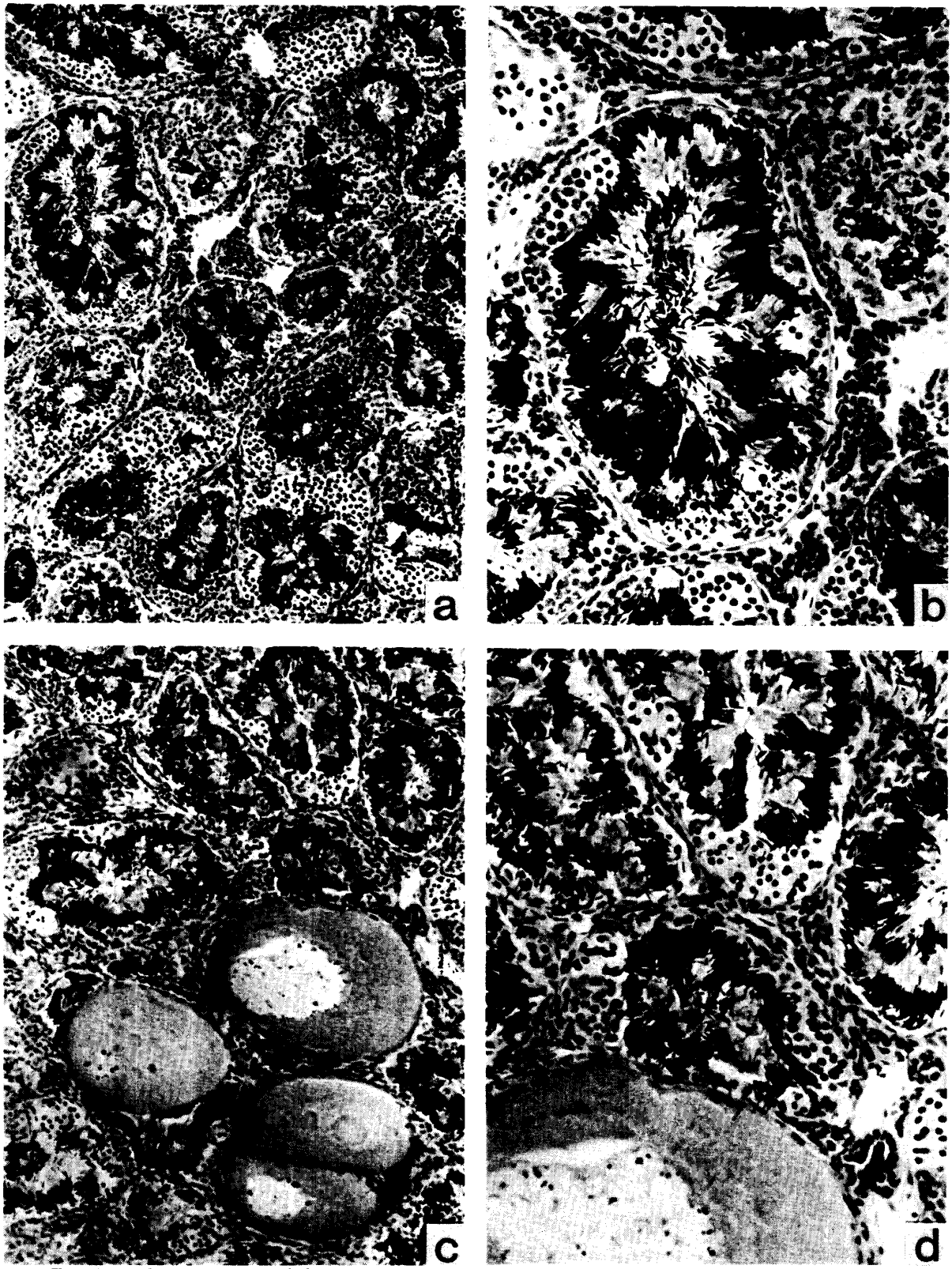

Fig. 16. Cross-sections of the testes of male interspecific hybrids between a female *Rana lessonae* from Luxembourg and a male *Rana esculenta* from West Germany.

a. Hybrid ♂, No. 1 (LL-type), 1 year old, produced in 1977 from *les* L♀, No. 4×*esc* G♂, No. 1. ×150
b. The same as (a). ×300
c. Hybrid ♂, No. 7 (LR-type), 3 years old, produced in 1977 from *les* L♀, No. 4×*esc* G♂, No. 1. ×150
d. The same as (c). ×300

hybrids were abnormal in inner structure and contained no normal spermatozoa. In the central lumens of the seminiferous tubules, there were a few abnormal spermatozoa together with abundant pycnotic nuclei or considerably numerous abnormal spermatozoa. The male hybrids differed from each other in amount of abnormal spermatozoa as found in those produced from matings, *les* L♀ × *rid* F♂. In the areas surrounding each central lumen, there were numerous spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule (Fig. 15).

e. Interspecific hybrids, *les* L♀ × *esc* G♂

The testes of five 1-year-old mature male hybrids (Nos. 1～5) produced in 1977 from a mating, *les* L♀, No. 4 × *esc* G♂, No. 1, were observed. These male hybrids were 45.0～54.5 mm, 49.9 mm on the average, in body length. Their left testes were 3.0～5.0 mm, 3.9 mm on the average, in length and 3.0～3.5 mm, 3.2 mm on the average, in width. The right testes were 3.5～5.0 mm, 4.1 mm on the average, in length and 2.5～4.0 mm, 3.0 mm on the average, in width. These five frogs were of the LL-type in external appearance and of the $L^L \cdot L^G$-type in electrophoretic patterns.

While one testis of each male hybrid was used in mating experiments, the other was cut into cross-sections. It was found that the testes of all the five male hybrids (Nos. 1～5) were completely normal in inner structure. The central lumens of the seminiferous tubules were filled with bundles of normal spermatozoa. The testes of these male hybrids did not differ from those of the control male *Rana lessonae* from Luxembourg in inner structure (Fig. 16a, b). In the areas surrounding each central lumen, there were numerous spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule.

The testes of three other 3-year-old male hybrids (Nos. 6～8) obtained from the same mating as stated above were cut into cross-sections in 1980 to examine the inner structure. Of the three hybrids, two (Nos. 6 and 7) were of the LR-type in external appearance and of the $L^L \cdot R^G$-type in electrophoretic patterns, and the other (No. 8) was of the LL-type in external appearance and of the $L^L \cdot L^G$-type in electrophoretic patterns.

The testes of two LR-type male hybrids (Nos. 6 and 7) were principally normal, although they included auxocytes everywhere in the testes. The central lumens of the seminiferous tubules were filled with bundles of normal spermatozoa as those of the above five male hybrids (Fig. 16c, d). The other male hybrid (No. 8) of the LL-type had completely normal testes. The central lumens of the seminiferous tubules were filled with bundles of normal spermatozoa.

2. Hybrids between female *Rana lessonae* from Italy and five kinds of males

a. Controls, *les* I♀ × *les* I♂

The testes of eight 1-year-old mature males in total, including four (Nos. 1～4),

two (Nos. 5 and 6) and two (Nos. 7 and 8) obtained in 1977 from three matings, *les* I♀, No. 1 × *les* I♂, No. 1, *les* I♀, No. 2 × *les* I♂, No. 1 and *les* I♀, No. 3 × *les* I♂, No. 2, respectively, were observed. These eight male frogs were 44.5～53.5 mm, 49.3 mm on the average, in body length. Their left testes were 3.5～5.0 mm, 4.4 mm on the average, in length and 2.5～3.5 mm, 3.2 mm on the average, in width. The right testes were 3.0～4.5 mm, 4.1 mm on the average, in length and 2.5～3.0 mm, 2.8 mm on the average, in width.

While one testis of each male frog was used in mating experiments, the other was cut into cross-sections. It was found that the testes of all the male frogs were normal in inner structure. The central lumens of the seminiferous tubules were filled with many bundles of normal spermatozoa. In the areas surrounding each central lumen, there were numerous spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule (Fig. 17a, b).

b. Intraspecific hybrids, *les* I♀ × *les* L♂

The testes of ten 1-year-old mature males in total, including five (Nos. 1～5) and five (Nos. 6～10) obtained in 1977 from matings, *les* I♀, No. 1 × *les* L♂, No. 3 and *les* I♀, No. 2 × *les* L♂, No. 3, respectively, were observed. These males were 43.0～53.5 mm, 49.2 mm on the average, in body length. Their left testes were 3.5～5.5 mm, 4.5 mm on the average, in length and 2.5～4.0 mm, 3.4 mm on the average, in width. The right testes were 1.5～4.5 mm, 3.8 mm on the average, in length and 1.5～4.0 mm, 2.8 mm on the average, in width.

One testis of each male was cut into cross-sections, while the other was used in mating experiments. It was found that the testes of six (Nos. 1, 2, 7～9 and 10) of the ten males were completely normal in inner structure and did not differ from those of the control males in this respect. The central lumens of the seminiferous tubules were filled with many bundles of normal spermatozoa (Fig. 17c, d). In two other males (Nos. 4 and 6), the bundles of spermatozoa in the seminiferous tubules were not so compact as those of the foregoing males (Fig. 18a, b), and in the remaining two males (Nos. 3 and 5), they were rather loosely arranged (Fig. 18c, d).

c. Interspecific hybrids, *les* I♀ × *rid* F♂

The testes of ten 1-year-old mature male hybrids in total, including five (Nos. 1～5) and five (Nos. 6～10) obtained in 1977 from matings, *les* I♀, No. 1 × *rid* F♂, No. 3 and *les* I♀, No. 2 × *rid* F♂, No. 4, respectively, were observed. These male hybrids were 44.0～59.0 mm, 50.1 mm on the average, in body length. Their left testes were 3.0～5.0 mm, 3.9 mm on the average, in length and 2.0～3.0 mm, 2.6 mm on the average, in width. The right testes were 2.5～4.0 mm, 2.9 mm on the average, in length and 1.5～3.0 mm, 2.5 mm on the average, in width.

One testis of each male hybrid was cut into cross-sections, while the other was used in mating experiments. The testes of all the males were abnormal in inner structure. In seven male hybrids (Nos. 1, 2 and 6～10), the seminiferous tubules

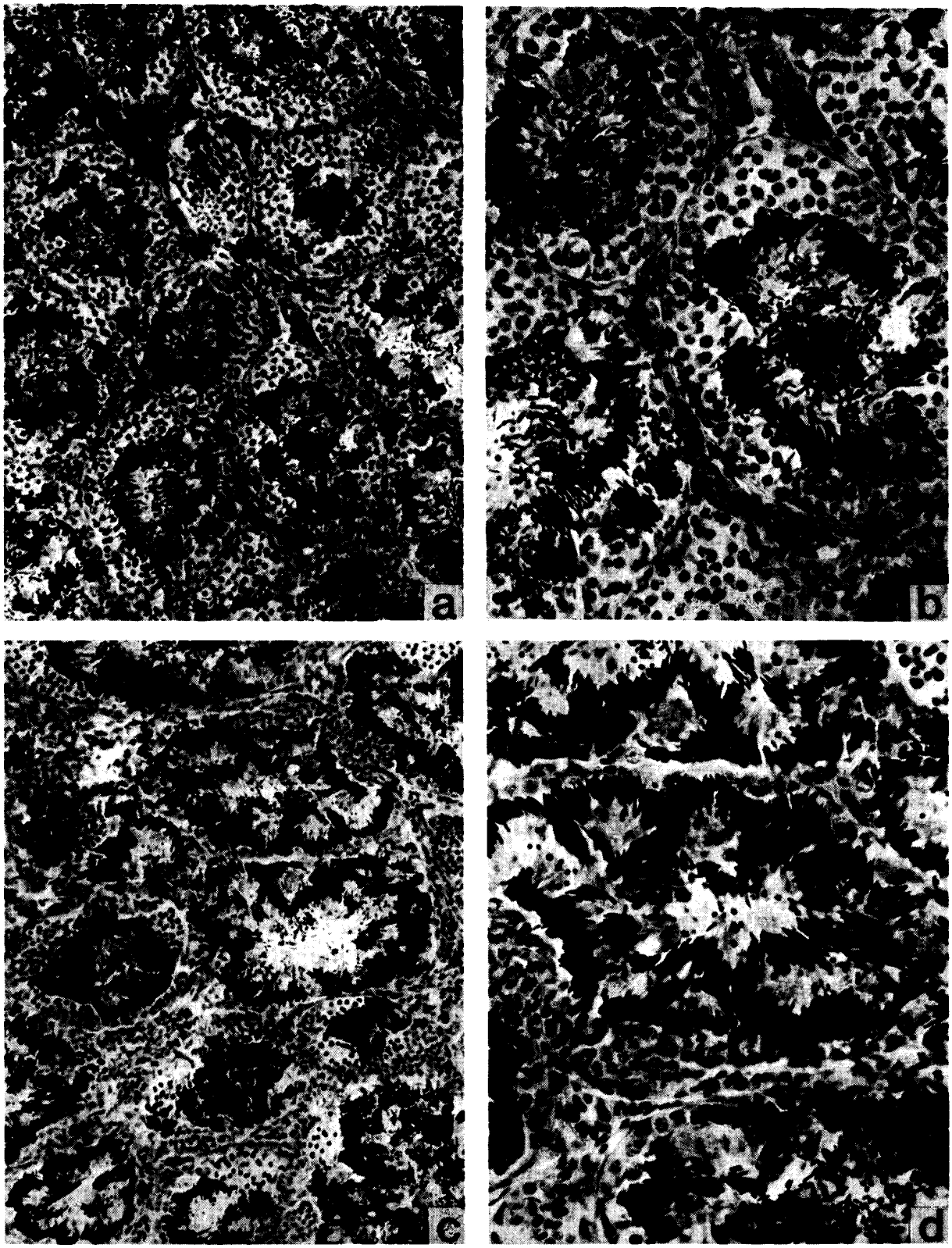

Fig. 17. Cross-sections of the testes of a male intraspecific hybrid between a female *Rana lessonae* from Italy and a male *Rana lessonae* from Luxembourg and the control male.

a. Control ♂, No. 1, 1 year old, produced in 1977 from *les* I ♀, No. 1 × *les* I ♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 1, 1 year old, produced in 1977 from *les* I ♀, No. 1 × *les* L ♂, No. 3. × 150
d. The same as (c). × 300

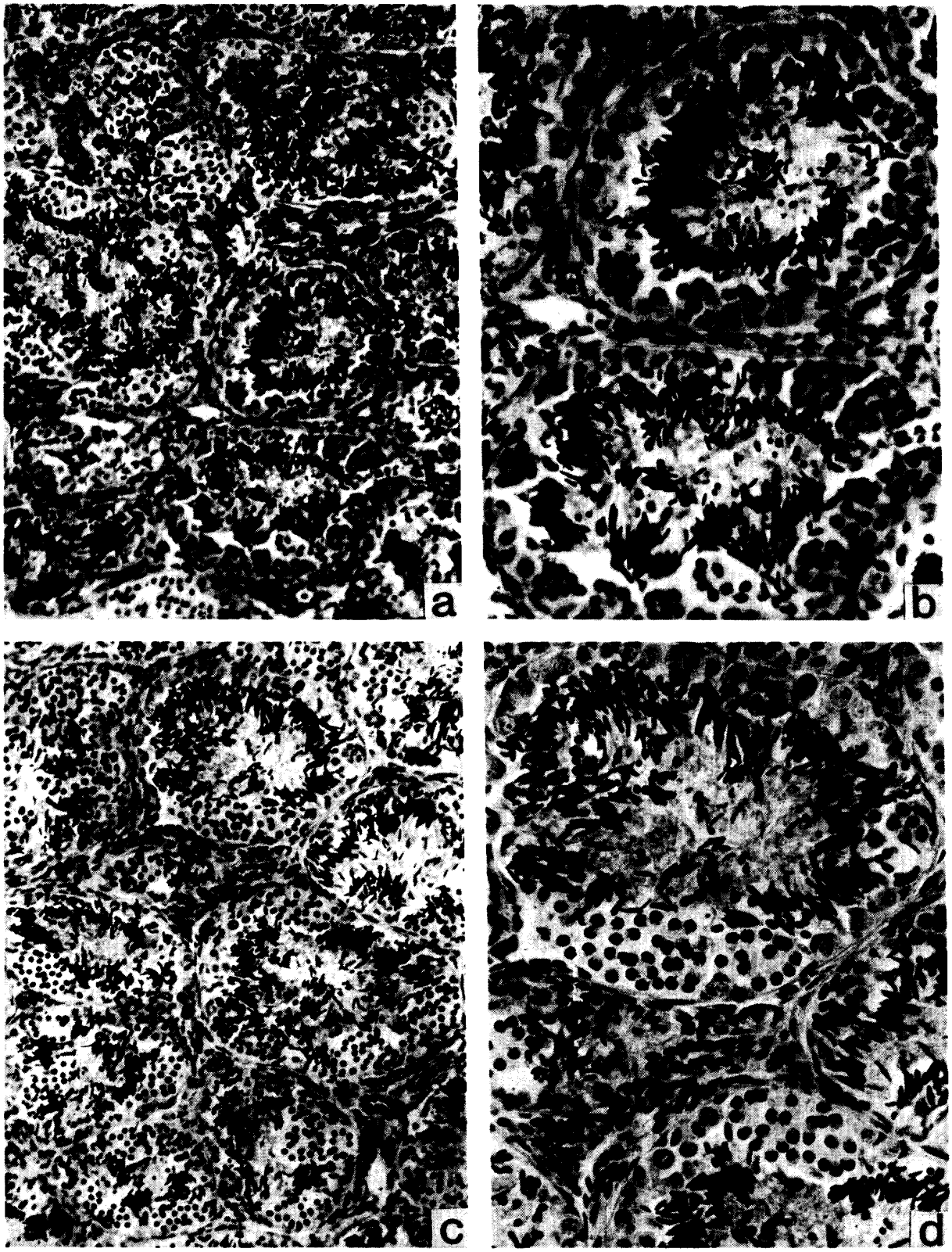

Fig. 18. Cross-sections of the testes of 1-year-old male intraspecific hybrids produced in 1977 between a female *Rana lessonae* from Italy and a male *Rana lessonae* from Luxembourg.

a. Hybrid ♂, No. 4 produced from *les* I ♀, No. 1 × *les* L ♂, No. 3. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 5 produced from *les* I ♀, No. 1 × *les* L ♂, No. 3. × 150
d. The same as (c). × 300

contained fairly numerous abnormal spermatozoa which were somewhat large and uneven in size. There were always pycnotic nuclei of various amounts together with abnormal spermatozoa. No normal spermatozoa were found. In the areas surrounding the central lumen of each seminiferous tubule, there were numerous first spermatocytes and secondary spermatogonia. Several primary spermatogonia were found along the wall of the seminiferous tubule (Fig. 19b). On the other hand, the testes of the other three male hybrids (Nos. 3, 4 and 5) were extremely abnormal in inner structure. There were only a few abnormal spermatozoa in addition to numerous pycnotic nuclei in the central lumens of seminiferous tubules. However, primary and secondary spermatogonia were abundantly found in the areas surrounding each central lumen (Fig. 19a).

d. Interspecific hybrids, *les* I♀ × *rid* T♂

The testes of ten 1-year-old mature male hybrids in total, including five (Nos. 1 ~ 5) and five (Nos. 6 ~ 10) obtained in 1977 from matings, *les* I♀, No. 1 × *rid* T♂, No. 2 and *les* I♀, No. 2 × *rid* T♂, No. 3, respectively, were observed. These male hybrids were 51.5 ~ 58.0 mm, 53.8 mm on the average, in body length. Their left testes were 2.0 ~ 5.0 mm, 3.7 mm on the average, in length and 2.0 ~ 4.0 mm, 2.7 mm on the average, in width. The right testes were 1.5 ~ 4.0 mm, 2.9 mm on the average, in length and 1.5 ~ 4.0 mm, 2.6 mm on the average, in width.

While one testis of each male hybrid was used in mating experiments, the other was cut into cross-sections. It was found that the testes of all the male hybrids were very abnormal in inner structure and contained no normal spermatozoa. Some male hybrids had fairly numerous abnormal spermatozoa and a few pycnotic nuclei, while some others had a few abnormal spermatozoa and a large amount of pycnotic nuclei. In the former case, there were numerous first spermatocytes and secondary spermatogonia in the areas surrounding the central lumen of each seminiferous tubule. In the latter case, there were abundant primary and secondary spermatogonia (Fig. 19c, d).

e. Interspecific hybrids, *les* I♀ × *rid* S♂

The testes of ten 1-year-old mature male hybrids (Nos. 1 ~ 10) obtained in 1977 from a mating, *les* I♀, No. 2 × *rid* S♂, No. 1, were observed. These male hybrids were 47.0 ~ 61.0 mm, 55.3 mm on the average, in body length. Their testes remarkably differed from each other in size. The left testes were 1.5 ~ 5.5 mm, 3.2 mm on the average, in length and 1.0 ~ 3.5 mm, 2.2 mm on the average, in width. The right testes were 1.5 ~ 3.0 mm, 2.4 mm on the average, in length and 1.0 ~ 2.5 mm, 1.6 mm on the average, in width.

While a part of each of these testes was used in mating experiments, the other part was cut into cross-sections. It was found that the testes of all the male hybrids were very abnormal. However, one (No. 1) of these hybrids had small bundles of normal spermatozoa in a small part of a seminiferous tubule, while almost all the seminiferous tubules of the testis contained many pycnotic nuclei together with a few abnormal spermatozoa in the central lumens. There were

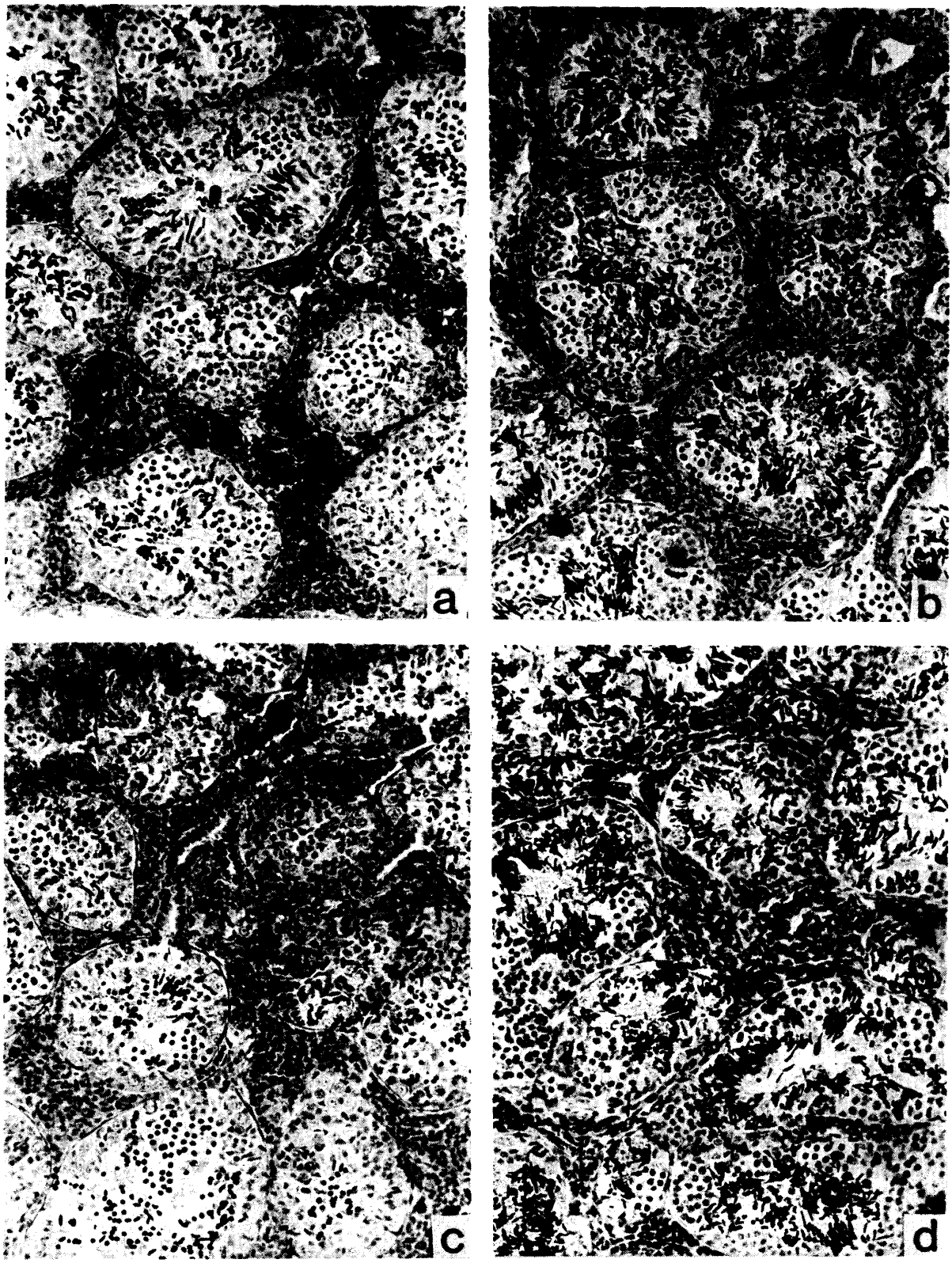

Fig. 19. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana lessonae* from Italy and a male *Rana ridibunda* from France or Turkey. ×150

a. Hybrid ♂, No. 3 produced from *les* I ♀, No. 1 × *rid* F ♂, No. 3.
b. Hybrid ♂, No. 1 produced from *les* I ♀, No. 1 × *rid* F ♂, No. 3.
c. Hybrid ♂, No. 3 produced from *les* I ♀, No. 1 × *rid* T ♂, No. 2.
d. Hybrid ♂, No. 5 produced from *les* I ♀, No. 1 × *rid* T ♂, No. 2.

numerous second spermatocytes, primary and secondary spermatogonia in the areas surrounding each central lumen (Fig. 20a, b). No normal spermatozoa were found in the testes of the other nine male hybrids. The testes of two (Nos. 4 and 9) of the latter were very small and had no germ cells in most parts of them (Fig. 20d). In the testes of male hybrids Nos. 5, 7 and 10, there were numerous pycnotic nuclei, while abnormal spermatozoa were very scarce. In the testes of the remaining four male hybrids (Nos. 2, 3, 6 and 8), there were fairly many large abnormal spermatozoa and pycnotic nuclei (Fig. 20c). The testes of all the 10 male hybrids had comparatively many primary spermatogonia along the walls of the seminiferous tubules.

f. Interspecific hybrids, *les* I♀ × *esc* G♂

The testes of 20 one-year-old mature male hybrids in total obtained in 1977, including five (Nos. 1～5), 10 (Nos. 6～15) and five (Nos. 16～20) produced from matings, *les* I♀, No. 1 × *esc* G♂, No. 1, *les* I♀, No. 2 × *esc* G♂, No. 1 and *les* I♀, No. 3 × *esc* G♂, No. 1, respectively, were observed. These male hybrids were 48.5～60.0 mm, 53.1 mm on the average, in body length. Their left testes were 2.5～5.5 mm, 3.8 mm on the average, in length and 1.5～3.5 mm, 2.6 mm on the average, in width. The right testes were 2.0～5.5 mm, 3.4 mm on the average, in length and 1.5～3.5 mm, 2.4 mm on the average, in width.

While one testis of each of 14 male hybrids (Nos. 1～4, 6～10, 16～20) was used in mating experiments, the other was cut into cross-sections together with the testes of the remaining six male hybrids. It was found that 14 male hybrids of the LL-type in external appearance and of the $L^I \cdot L^G$-type in electrophoretic patterns (Nos. 1～3, 6～9, 12, 13, 16～20) had testes which were completely normal in inner structure. The central lumens of their seminiferous tubules were filled with many compact bundles of normal spermatozoa. The areas surrounding the central lumens were occupied by first spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule. These testes scarcely differed in inner structure from those of the control male *Rana lessonae* from Luxembourg and Italy (Fig. 21a). In two other male hybrids which were of the LR-type in external appearance and of the $L^I \cdot R^G$-type in electrophoretic patterns (Nos. 4 and 11), the testes were almost similar to those of the above male hybrids in inner structure except for fewer bundles of normal spermatozoa and more abundant masses of first spermatocytes and secondary spermatogonia (Fig. 21b).

The testes of the other four male hybrids which were of the LR-type in external appearance and of the $L^I \cdot R^G$-type in electrophoretic patterns (Nos. 5, 10, 14 and 15) were very abnormal in inner structure. The cross-sections of seminiferous tubules were remarkably small and contained no normal spermatozoa. There were a few abnormal spermatozoa and pycnotic nuclei, while primary spermatogonia were comparatively numerous (Fig. 21c, d).

The testes of six 3-year-old male hybrids of the LR-type in external appearance and of the $L^I \cdot R^G$-type in electrophoretic patterns, including three (Nos. 21～23)

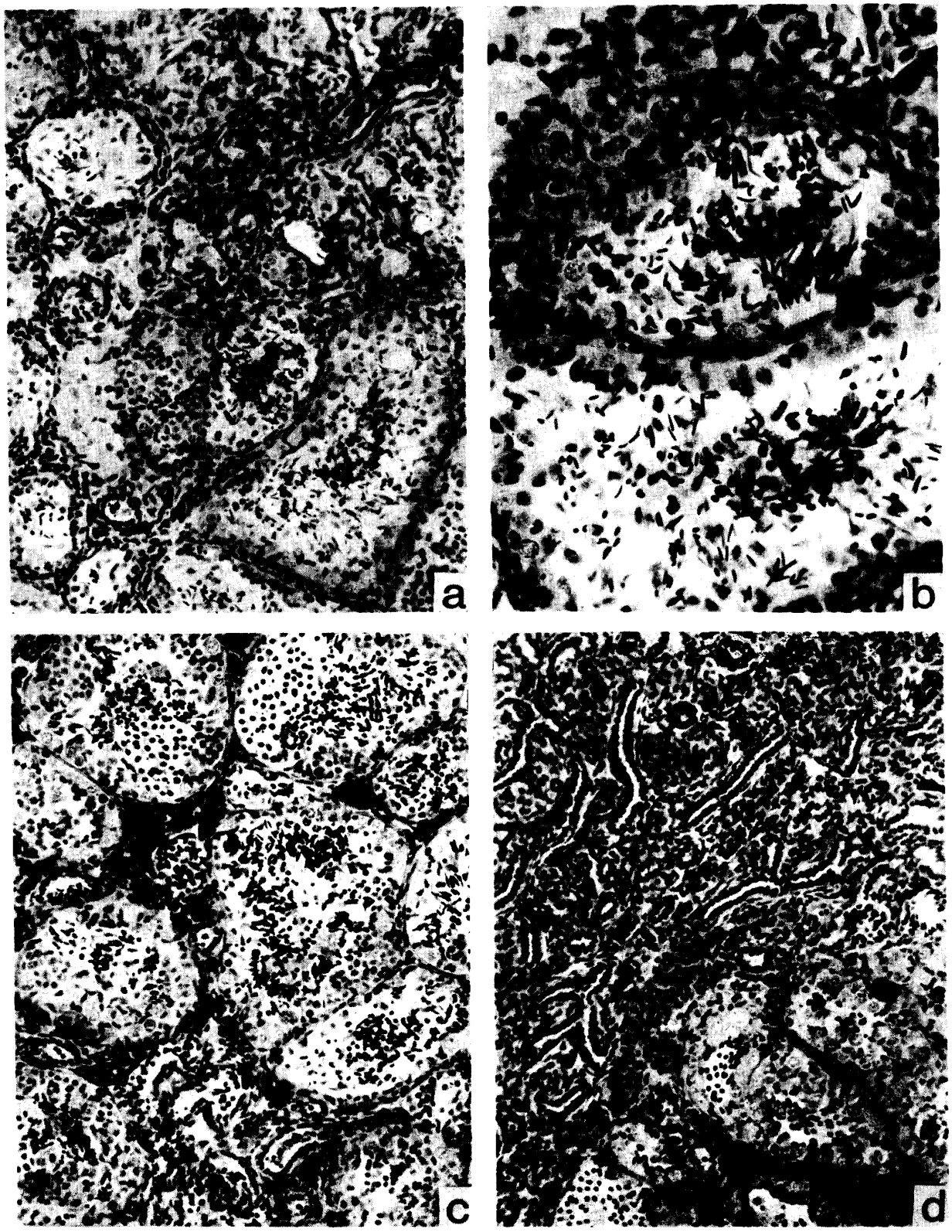

Fig. 20. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana lessonae* from Italy and a male *Rana ridibunda* from Soviet Union.

a. Hybrid ♂, No. 1 produced from *les* I ♀, No. 2 × *rid* S ♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 2 produced from *les* I ♀, No. 2 × *rid* S ♂, No. 1. × 150
d. Hybrid ♂, No. 4 produced from *les* I ♀, No. 2 × *rid* S ♂, No. 1. × 150

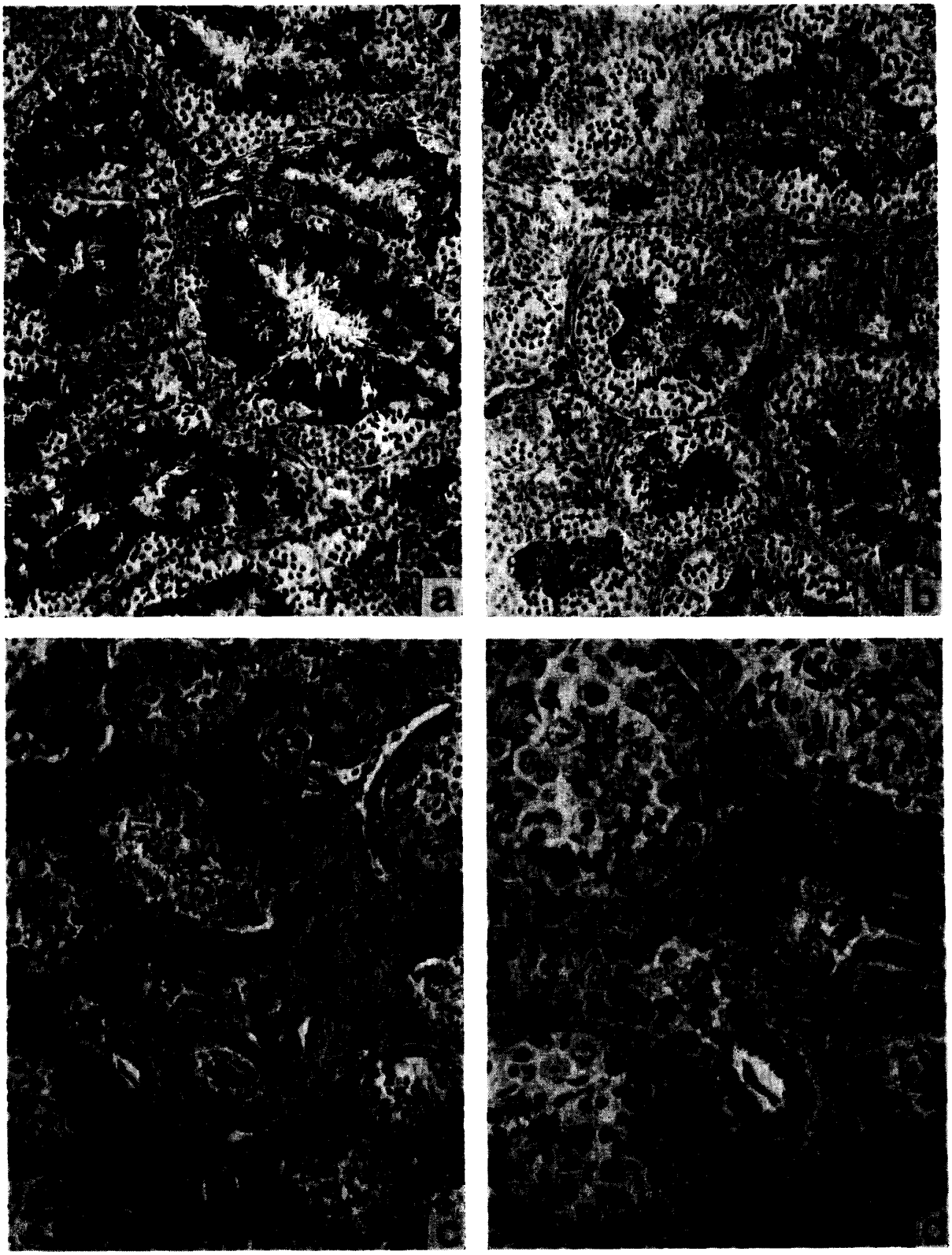

Fig. 21. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between female *Rana lessonae* from Italy and a male *Rana esculenta* from West Germany.

a. Hybrid ♂, No. 1 (LL-type) produced from *les* I♀, No. 1×*esc* G♂, No. 1. ×150
b. Hybrid ♂, No. 4 (LR-type) produced from *les* I♀, No. 1×*esc* G♂, No. 1. ×150
c. Hybrid ♂, No. 10 (LR-type) produced from *les* I♀, No. 2×*esc* G♂, No. 1. ×150
d. The same as (c). ×300

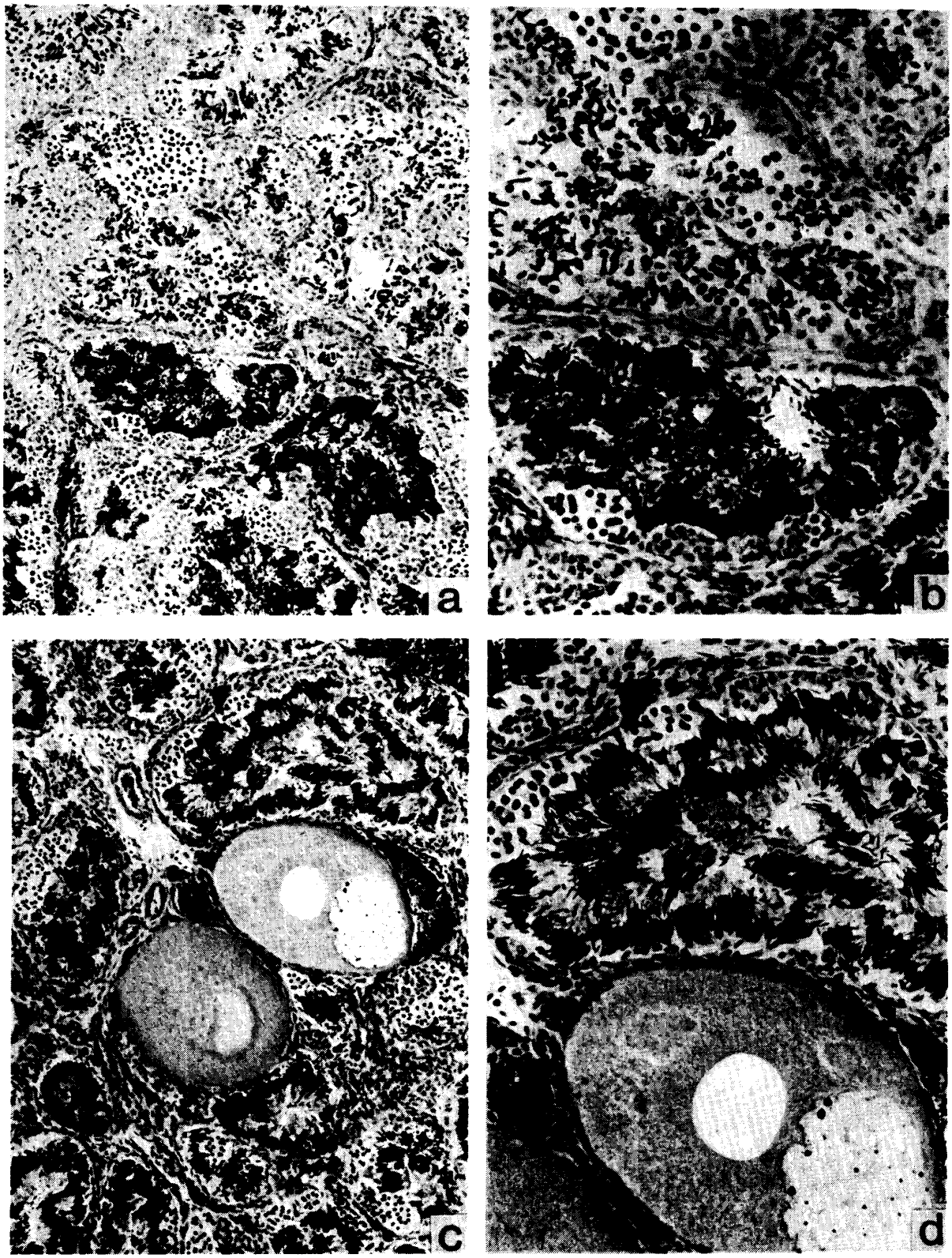

Fig. 22. Cross-sections of the testes of 3-year-old male interspecific hybrids produced in 1977 between female *Rana lessonae* from Italy and a male *Rana esculenta* from West Germany.

a. Hybrid ♂, No. 21 (LR-type) produced from *les* I ♀, No. 2 × *esc* G ♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 24 (LR-type) produced from *les* I ♀, No. 3 × *esc* G ♂, No. 1. × 150
d. The same as (c). × 300

and three (Nos. 24~26) obtained in 1977 from matings, *les* I.W77♀, No. 2×*esc* G.W76♂, No. 1 and *les* I.W77♀, No. 3×*esc* G.W76♂, No. 1, respectively, were observed. While one testis of each male hybrid was used in mating experiments, the other was cut into cross-sections. It was found that the testes of four male hybrids (Nos. 21, 22, 25 and 26) consisted of two parts, one of which consisted of normal seminiferous tubules filled with many compact bundles of normal spermatozoa, while the seminiferous tubules of the other part were abnormal and contained no normal spermatozoa, although there were many abnormal spermatozoa and pycnotic nuclei together with first spermatocytes and primary and secondary spermatogonia. This abnormal part was very similar in inner structure to the testes of male hybrids between *Rana lessonae* and *Rana ridibunda* (Fig. 22a, b).

The other two male hybrids (Nos. 23 and 24) had testes whose seminiferous tubules were filled with many compact bundles of normal spermatozoa. These testes were completely normal in inner structure except that there were many testis-ova throughout the testes (Fig. 22c, d).

3. Hybrids between female *Rana ridibunda* from Turkey and four kinds of males

a. Controls, *rid* T♀×*rid* T♂

The testes of three 1-year-old mature males obtained in 1977 from a mating, *rid* T.W76♀, No. 1×*rid* T.W76♂, No. 2, were observed. These males were 47.5~52.5 mm, 50.0 mm on the average, in body length. Their left testes were 4.0~5.5 mm, 4.7 mm on the average, in length and 2.5~3.5 mm, 3.0 mm on the average, in width. The right testes were 4.0~5.0 mm, 4.6 mm on the average, in length and 2.5~4.0 mm, 3.3 mm on the average, in width.

While one testis of each of two males was used in mating experiments, the other as well as the testes of the remaining male were cut into cross-sections. It was found that the testes of all the males were completely normal. The central lumens of the seminiferous tubules were filled with many compact bundles of normal spermatozoa. The areas surrounding the central lumens were occupied by first spermatocytes and secondary spermatogonia. There were a few primary spermatogonia along the wall of each seminiferous tubule (Fig. 23a, b).

b. Intraspecific hybrids, *rid* T♀×*rid* F♂

The testes of five 1-year-old mature males (Nos. 1~5) obtained in 1977 from a mating, *rid* T.W76♀, No. 1×*rid* F.W74♂, No. 3, were observed. These male hybrids were 57.0~59.0 mm, 57.8 mm on the average, in body length. Their left testes were 4.0~5.5 mm, 4.6 mm on the average, in length and 3.5~4.5 mm, 3.7 mm on the average, in width. The right testes were 3.0~5.0 mm, 4.2 mm on the average, in length and 2.0~4.0 mm, 3.5 mm on the average, in width.

While one testis of each of four male hybrids (Nos. 1~4) was used in mating experiments, the other was cut into cross-sections together with the testes of the remaining male hybrid (No. 5). It was found that the testes of three male

hybrids (Nos. 1～3) were normal in inner structure. The central lumens of the seminiferous tubules were filled with many compact bundles of normal spermatozoa (Fig. 23c, d). The testes of the other two male hybrids (Nos. 4 and 5) were abnormal in inner structure. A few normal spermatozoa were sparsely distributed in the central lumen of each seminiferous tubule, while abnormal spermatozoa of various sizes were comparatively abundant (Fig. 24).

c. Interspecific hybrids, *rid* T♀ × *les* L♂

The testes of five 1-year-old mature male hybrids (Nos. 1～5) obtained in 1977 from a mating, *rid* T.W76♀, No. 1 × *les* L.75♂, No. 3, were observed. The five male hybrids were 42.5～55.5 mm, 46.5 mm on the average, in body length. Their left testes were 3.5～5.0 mm, 4.2 mm on the average, in length and 2.5～4.0 mm, 3.4 mm on the average, in width. The right testes were 3.0～5.0 mm, 4.0 mm on the average, in length and 2.0～4.0 mm, 3.2 mm on the average, in width.

The testes of three 7-year-old mature male hybrids (Nos. 6～8) obtained in 1978 from a mating, *rid* T.W76♀, No. 2 × *les* L.76♂, No. 5, were also examined. These male hybrids were 59.0 mm, 60.5 mm and 63.0 mm, 60.8 mm on the average, in body length. The left testes were 5.0～6.5 mm, 5.8 mm on the average, in length and 3.5～5.0 mm, 4.2 mm on the average, in width. The right testes were 4.5～6.0 mm, 5.2 mm on the average, in length and 3.5～4.5 mm, 4.0 mm on the average, in width.

While one testis of each of the five 1-year-old mature male hybrids (Nos. 1～5) was used in mating experiments, the other was cut into cross-sections together with the testes of the remaining three 7-year-old male hybrids (Nos. 6～8). The results showed that the testes of all these male hybrids were abnormal in inner structure. In four (Nos. 1～4) of the five 1-year-old male hybrids, no normal spermatozoa were found in the seminiferous tubules, while there were numerous pycnotic nuclei and a few abnormal spermatozoa. The areas surrounding the central lumen of each seminiferous tubule were occupied by first spermatocytes and secondary spermatogonia. Some primary spermatogonia were found along the wall of each seminiferous tubule (Fig. 25a). However, in the testis of one (No. 5) of the five 1-year-old males, germ cells were scarcely found everywhere (Fig. 25b). In contrast, the testes of the three 7-year-old male hybrids (Nos. 6～8) contained somewhat numerous abnormal spermatozoa of various sizes in the seminiferous tubules (Fig. 25c, d).

d. Interspecific hybrids, *rid* T♀ × *les* I♂

The testes of three 1-year-old mature male hybrids (Nos. 1～3) obtained in 1977 from a mating, *rid* T.W76♀, No. 1 × *les* I.W77♂, No. 1, were examined. These male hybrids were 45.5 mm, 46.0 mm and 50.5 mm, 47.3 mm on the average, in body length. Their left testes were 4.5～5.5 mm, 5.0 mm on the average, in length and 3.0～3.5 mm, 3.2 mm on the average, in width. The right testes were 4.0～5.5 mm, 4.7 mm on the average, in length and 2.5～3.5 mm, 3.2 mm on the average, in width.

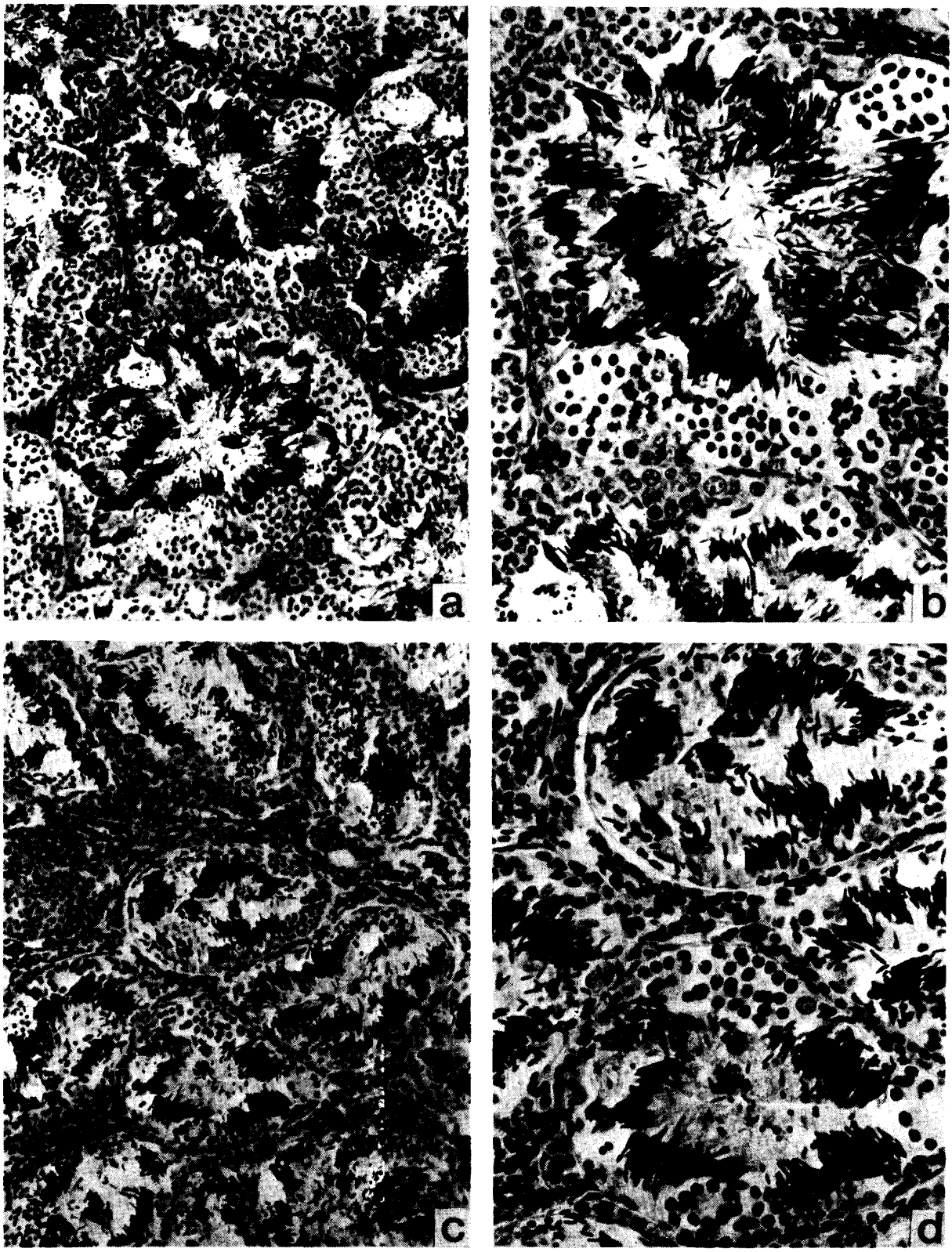

Fig. 23. Cross-sections of the testis of a 1-year-old male intraspecific hybrid produced in 1977 between a female *Rana ridibunda* from Turkey and a male *Rana ridibunda* from France and the control male.

a. Control ♂, No. 2 produced from *rid* T♀, No. 1 × *rid* T♂, No. 2. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 1 produced from *rid* T♀, No. 1 × *rid* F♂, No. 3. × 150
d. The same as (c). × 300

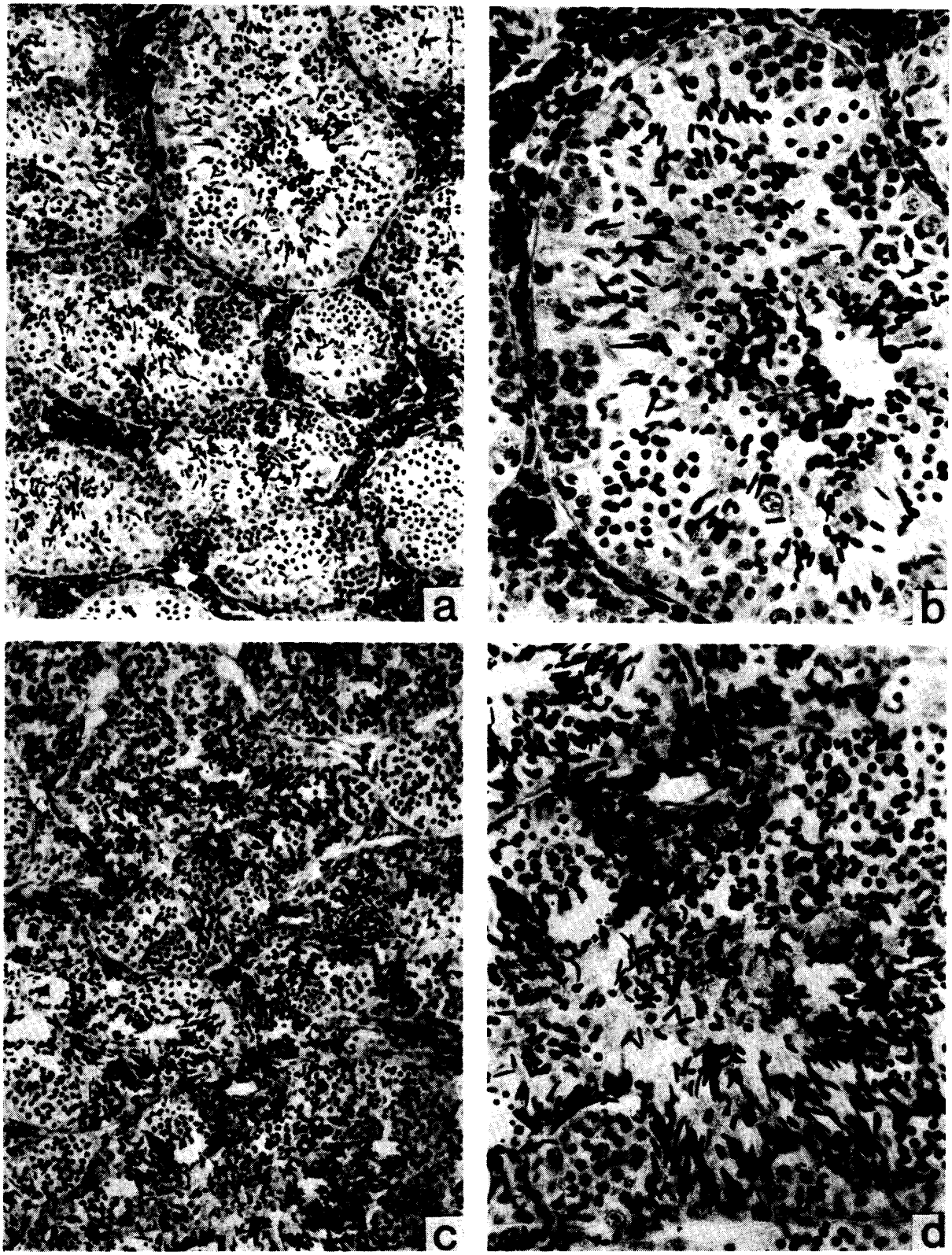

Fig. 24. Cross-sections of the testes of 1-year-old male intraspecific hybrids produced in 1977 between a female *Rana ridibunda* from Turkey and a male *Rana ridibunda* from France.

a. Hybrid ♂, No. 4 produced from *rid* T♀, No. 1 × *rid* F♂, No. 3. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 5 produced from *rid* T♀, No. 1 × *rid* F♂, No. 3. × 150
d. The same as (c). × 300

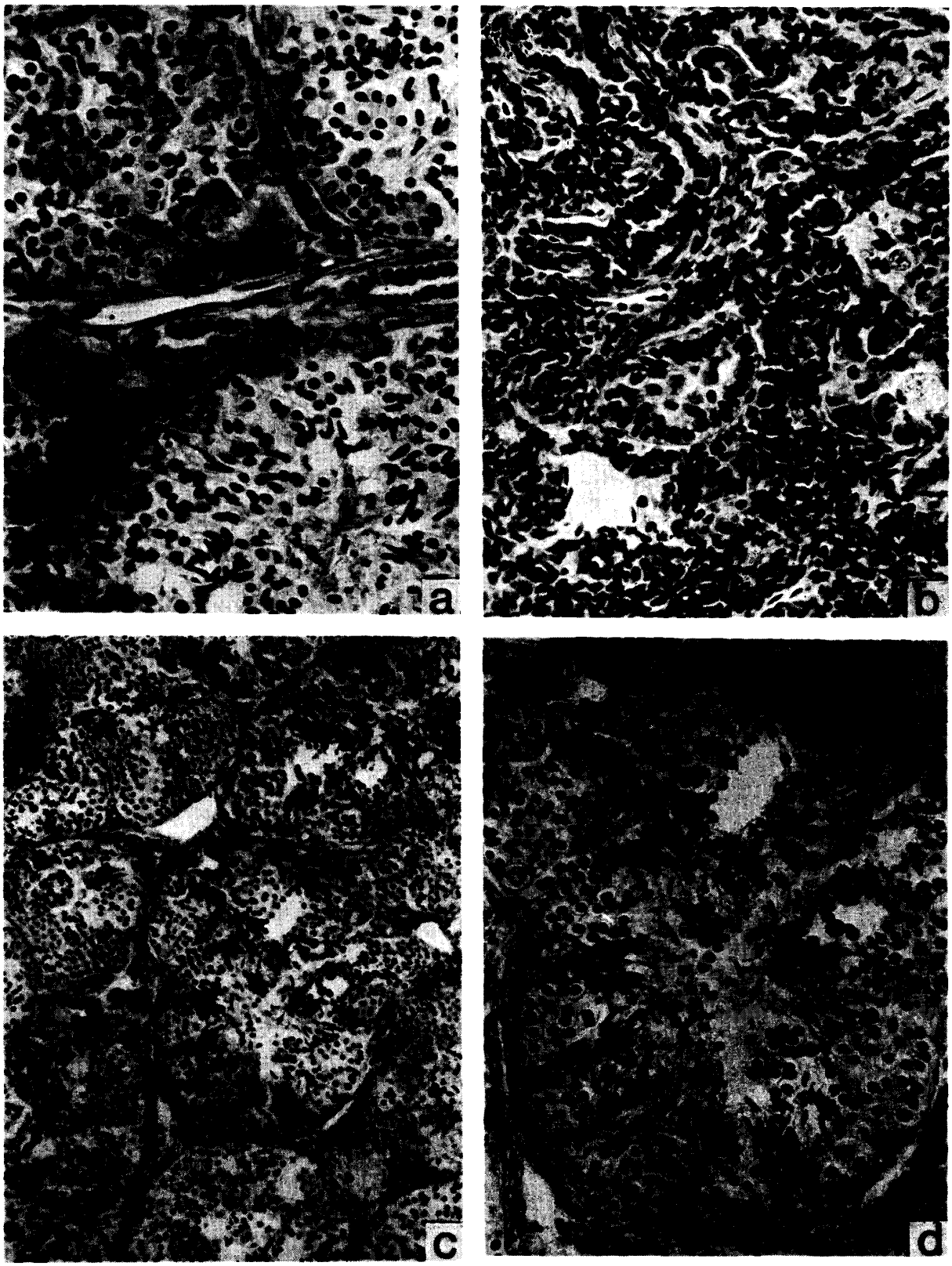

Fig. 25. Cross-sections of the testes of male interspecific hybrids between female *Rana ridibunda* from Turkey and male *Rana lessonae* from Luxembourg.

a. Hybrid ♂, No. 3, 1 year old, produced in 1977 from *rid* T ♀, No. 1 × *les* L ♂, No. 3. × 300
b. Hybrid ♂, No. 5, 1 year old, produced in 1977 from *rid* T ♀, No. 1 × *les* L ♂, No. 3. × 300
c. Hybrid ♂, No. 8, 7 years old, produced in 1978 from *rid* T ♀, No. 2 × *les* L ♂, No. 5. × 150
d. The same as (c). × 300

The testes of five 7-year-old mature male hybrids (Nos. 4～8) obtained in 1978 from a mating, *rid* T.W76♀, No. 2×*les* I.W77♂, No. 3, were examined. These male hybrids were 62.0～74.0 mm, 67.2 mm on the average, in body length. Their left testes were 4.5～6.0 mm, 5.4 mm on the average, in length and 3.5～4.0 mm, 3.7 mm on the average, in width. The right testes were 5.0～6.0 mm, 5.5 mm on the average, in length and 3.0～4.0 mm, 3.6 mm on the average, in width.

While one testis of each of the three 1-year-old male hybrids was used in mating experiments, the other was cut into cross-sections together with the testes of the other five 7-year-old male hybrids. It was found that the testes of all the male hybrids were abnormal in inner structure. In six (Nos. 1～5 and 8) of the eight male hybrids, no normal spermatozoa were found in the seminiferous tubules. The findings that the central lumens of the latter contained only pycnotic nuclei and abnormal spermatozoa were the same as those in the male hybrids between female *Rana ridibunda* from Turkey and male *Rana lessonae* from Luxembourg (Fig. 26a, b). In the remaining two 7-year-old male hybrids (Nos. 6 and 7), abnormally large spermatozoa were abundantly observed in the seminiferous tubules (Fig. 26c, d).

e. Interspecific hybrids, *rid* T♀×*esc* G♂

The testes of five 1-year-old mature male hybrids (Nos. 1～5) obtained in 1977 from a mating, *rid* T.W76♀, No. 1×*esc* G.W76♂, No. 1, were observed. These male hybrids were 45.5～60.0 mm, 53.2 mm on the average, in body length. Their left testes were 3.0～5.5 mm, 4.5 mm on the average, in length and 2.0～4.0 mm, 3.3 mm on the average, in width. The right testes of four of the five male hybrids were 3.0～4.5 mm, 3.4 mm on the average, in length and 2.0～3.5 mm, 2.9 mm on the average, in width. The remaining male hybrid (No. 5) had no right testis.

While one testis of each of four male hybrids (Nos. 1～4) and a part of the left testis of the remaining male hybrid (No. 5) were used in mating experiments, the other testis and the remaining testicular part were cut into cross-sections. It was found that the testes of three male hybrids of the RR-type in external appearance and of the $R^T \cdot R^G$-type in electrophoretic patterns (Nos. 1～3) were completely normal as those of the control males. The central lumens of the seminiferous tubules were filled with many compact bundles of normal spermatozoa (Fig. 27). The areas surrounding the central lumens were occupied by first spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule. The testis of another male hybrid (No. 4) which was of the RL-type in external appearance and of the $R^T \cdot L^G$-type in electrophoretic patterns was almost normal in inner structure, although the bundles of spermatozoa found in the central lumen of each seminiferous tubule were not so compact as those of the foregoing three male hybrids (Nos. 1～3). Abnormal spermatozoa and pycnotic nuclei were more abundantly found in some seminiferous tubules (Fig. 28a, b). In the

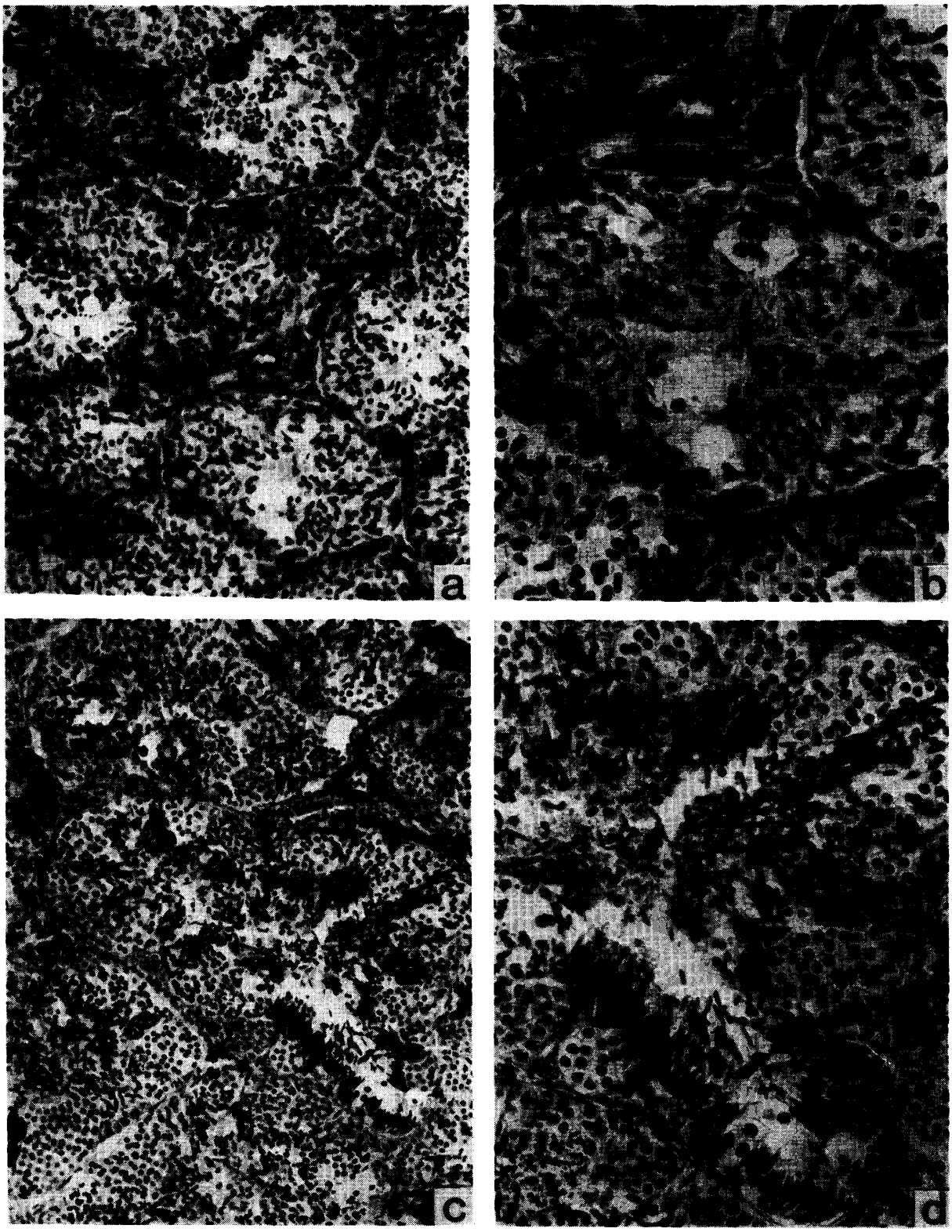

Fig. 26. Cross-sections of the testes of male interspecific hybrids between female *Rana ridibunda* from Turkey and male *Rana lessonae* from Italy.

a. Hybrid ♂, No. 1, 1 year old, produced in 1977 from *rid* T ♀, No. 1 × *les* I ♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 6, 7 years old, produced in 1978 from *rid* T ♀, No. 2 × *les* I ♂, No. 3. × 150
d. The same as (c). × 300

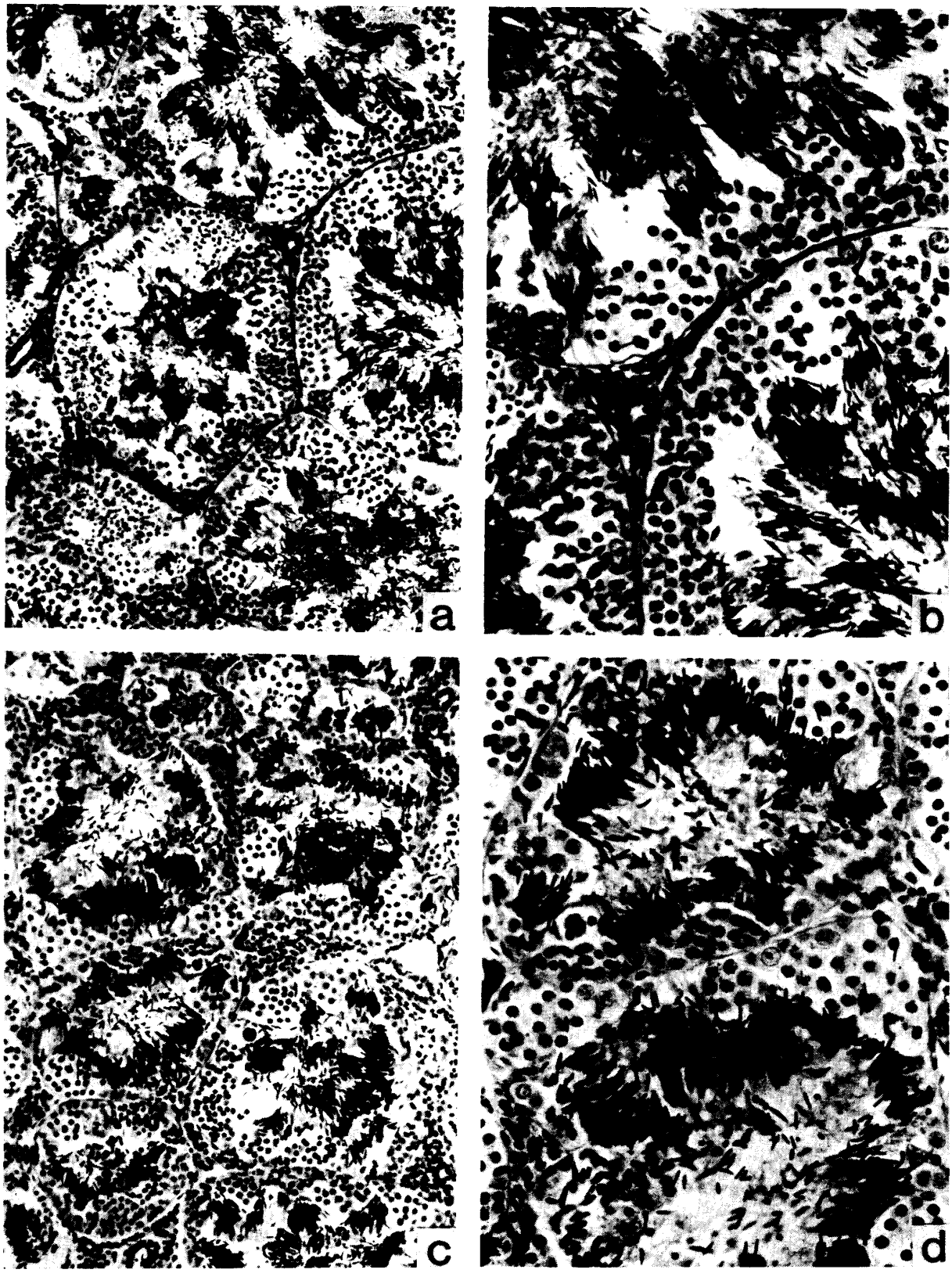

Fig. 27. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana ridibunda* from Turkey and a male *Rana esculenta* from West Germany.

a. Hybrid ♂, No. 1 (RR-type) produced from *rid* T♀, No. 1 × *esc* G♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 3 (RR-type) produced from *rid* T♀, No. 1 × *esc* G♂, No. 1. × 150
d. The same as (c). × 300

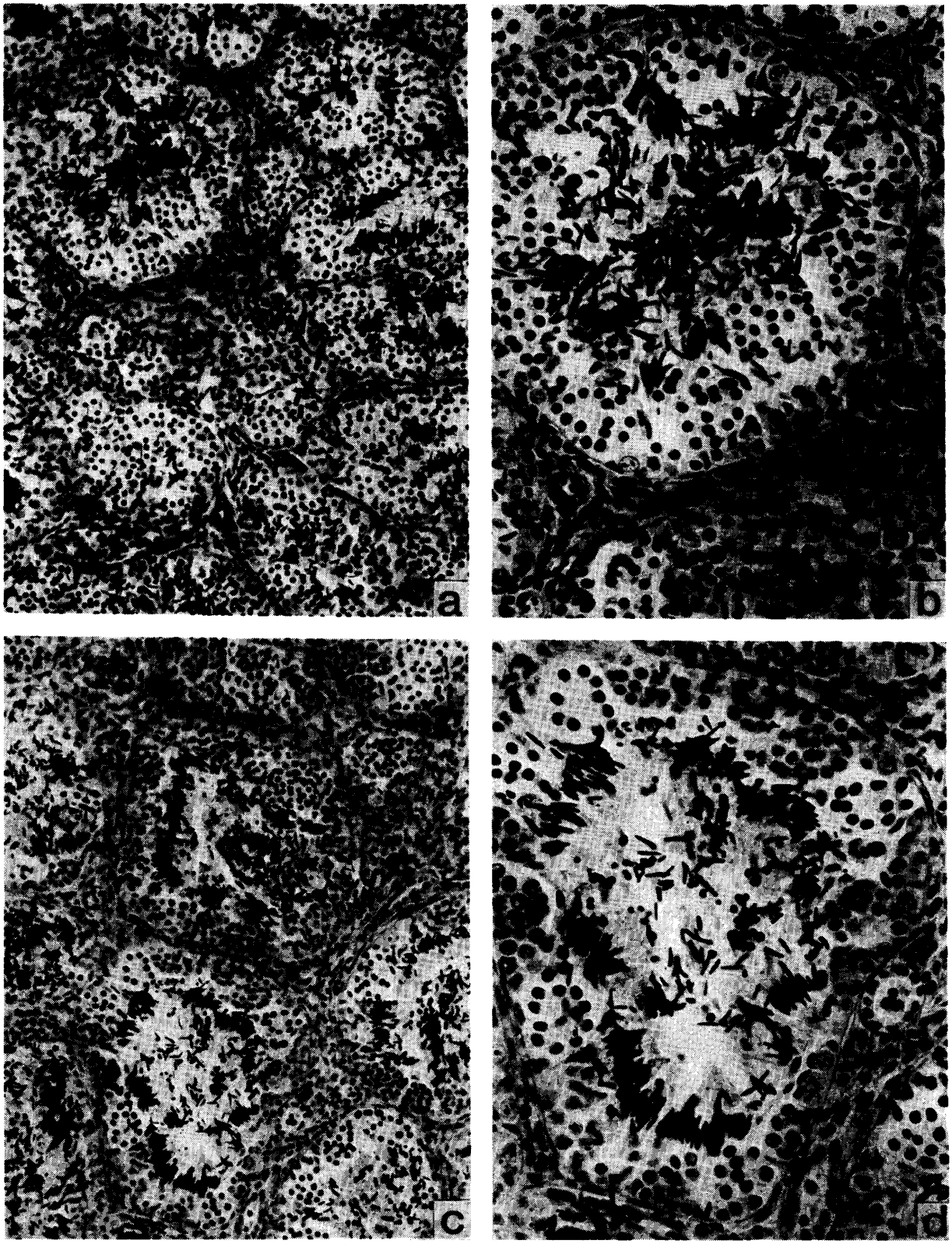

Fig. 28. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana ridibunda* from Turkey and a male *Rana esculenta* from West Germany.

a. Hybrid ♂, No. 4 (RL-type) produced from *rid* T♀, No. 1 × *esc* G♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 5 (RL-type) produced from *rid* T♀, No. 1 × *esc* G♂, No. 1. × 150
d. The same as (c). × 300

remaining male hybrid (No. 5) which was of the RL-type in external appearance and of the $R^T \cdot L^G$-type in electrophoretic patterns, the testis was more abnormal than that of male hybrid No. 4. Normal spermatozoa were sparsely distributed, while abnormal spermatozoa of various sizes and pycnotic nuclei or masses of degenerating germ cells were abundantly found (Fig. 28c, d).

4. Hybrids between a female *Rana ridibunda* from Soviet Union and five kinds of males

a. Controls, *rid* S♀ × *rid* S♂

The testes of three 1-year-old mature males obtained in 1977 from a mating, *rid* S.W76♀, No. 1 × *rid* S.W76♂, No. 1, were observed. These males were 57.0～61.0 mm, 58.5 mm on the average, in body length. Their left testes were 3.0～4.0 mm, 3.7 mm on the average, in length and 2.5 mm in width. The right testes were 3.5～4.0 mm, 3.8 mm on the average, in length and 2.5～3.5 mm, 2.8 mm on the average, in width.

While one testis of each of the three males was used in mating experiments, the other was cut into cross-sections. It was found that all the testes were normal in inner structure. The central lumen of each seminiferous tubule was filled with many compact bundles of normal spermatozoa.

b. Intraspecific hybrids, *rid* S♀ × *rid* F♂

The testes of five 1-year-old mature males (Nos. 1～5) obtained in 1977 from a mating, *rid* S.W76♀, No. 1 × *rid* F.W74♂, No. 3, were observed. These males were 49.5～66.0 mm, 59.9 mm on the average, in body length. Their left testes were 2.5～4.5 mm, 3.6 mm on the average, in length and 2.5～3.0 mm, 2.6 mm on the average, in width. 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.

While one testis of each of these five males was used in mating experiments, the other was cut into cross-sections. The results showed that the testes of three males (Nos. 2～4) contained bundles of normal spermatozoa, although the spermatozoa were considerably fewer than those of the control males. Some pycnotic nuclei and masses of degenerating germ cells were found here and there in the central lumens of seminiferous tubules. In the areas surrounding each central lumen, there were abundant masses of first spermatocytes and secondary spermatogonia. A few primary spermatogonia were situated along the wall of each seminiferous tubule (Fig. 29a, b). The testes of the remaining two males (Nos. 1 and 5) also contained normal spermatozoa which were somewhat fewer than those of the control males. They had no masses of degenerating germ cells. (Fig. 29c, d).

c. Intraspecific hybrids, *rid* S♀ × *rid* T♂

The testes of five 1-year-old mature males (Nos. 1～5) obtained in 1977 from a mating, *rid* S.W76♀, No. 1 × *rid* T.W76♂, No. 2, were observed. These males were 56.0～59.0 mm, 58.0 mm on the average, in body length. Their left

testes were 5.0～5.5 mm, 5.1 mm on the average, in length and 3.0 mm in width. The right testes were 4.0～5.0 mm, 4.8 mm on the average, in length and 2.5～3.5 mm, 2.9 mm on the average, in width.

While one testis of each of these males was used in mating experiments, the other was cut into cross-sections. The results showed that the testes of two males (Nos. 2 and 4) were completely normal in inner structure. The central lumen of each seminiferous tubule was filled with compact bundles of normal spermatozoa. The areas surrounding the central lumens were mostly occupied by first spermatocytes. Along the wall of each seminiferous tubule, there were some secondary and a few primary spermatogonia (Fig. 30a, b). The testis of another male (No. 3) was somewhat underdeveloped. Although there were some bundles of normal spermatozoa, they were fewer than those of the foregoing two males. The spermatozoa were also fewer than those of these males. There were some cross-sections of seminiferous tubules which contained only abnormal spermatozoa and pycnotic nuclei. The areas surrounding each lumen were occupied by abundant first spermatocytes and secondary spermatogonia. There were comparatively numerous primary spermatogonia along the wall of each seminiferous tubule (Fig. 30c, d). The testes of the remaining two males (Nos. 1 and 5) were very abnormal in inner structure and contained no normal spermatozoa. The central lumen of each seminiferous tubule was filled with abundant pycnotic nuclei and a few abnormal spermatozoa. The areas surrounding each lumen were mostly occupied by first spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule (Fig. 31a～d).

d. Interspecific hybrids, *rid* S♀ × *les* L♂

The testes of six 1-year-old mature male hybrids (Nos. 1～6) obtained in 1977 from a mating, *rid* S.W76♀, No. 1 × *les* L.75♂, No. 3, were examined. These male hybrids were 65.0～70.5 mm, 67.5 mm on the average, in body length. Their left testes were 3.0～5.0 mm, 4.1 mm on the average, in length and 3.0～3.5 mm, 3.2 mm on the average, in width. The right testes were 2.5～4.0 mm, 3.2 mm on the average, in length and 2.0～3.5 mm, 2.8 mm on the average, in width.

While one testis of each of three males (Nos. 1～3) was used in mating experiments, the other testis was cut into cross-sections together with the testes of the remaining three male hybrids. It was found that germ cells had almost completely degenerated in the testes of three male hybrids (Nos. 1, 4 and 5). While there were numerous interstitial cells, spermatozoa and pycnotic nuclei could be found nowhere (Fig. 32a, b). The testes of two other male hybrids (Nos. 3 and 6) were also very abnormal, although they contained a few normal spermatozoa together with some abnormally shaped spermatozoa and pycnotic nuclei. As the normal spermatozoa were extremely scarce, they were not found in most of the cross-sections of seminiferous tubules. The areas surrounding each central lumen were occupied by first spermatocytes and primary and secondary sper-

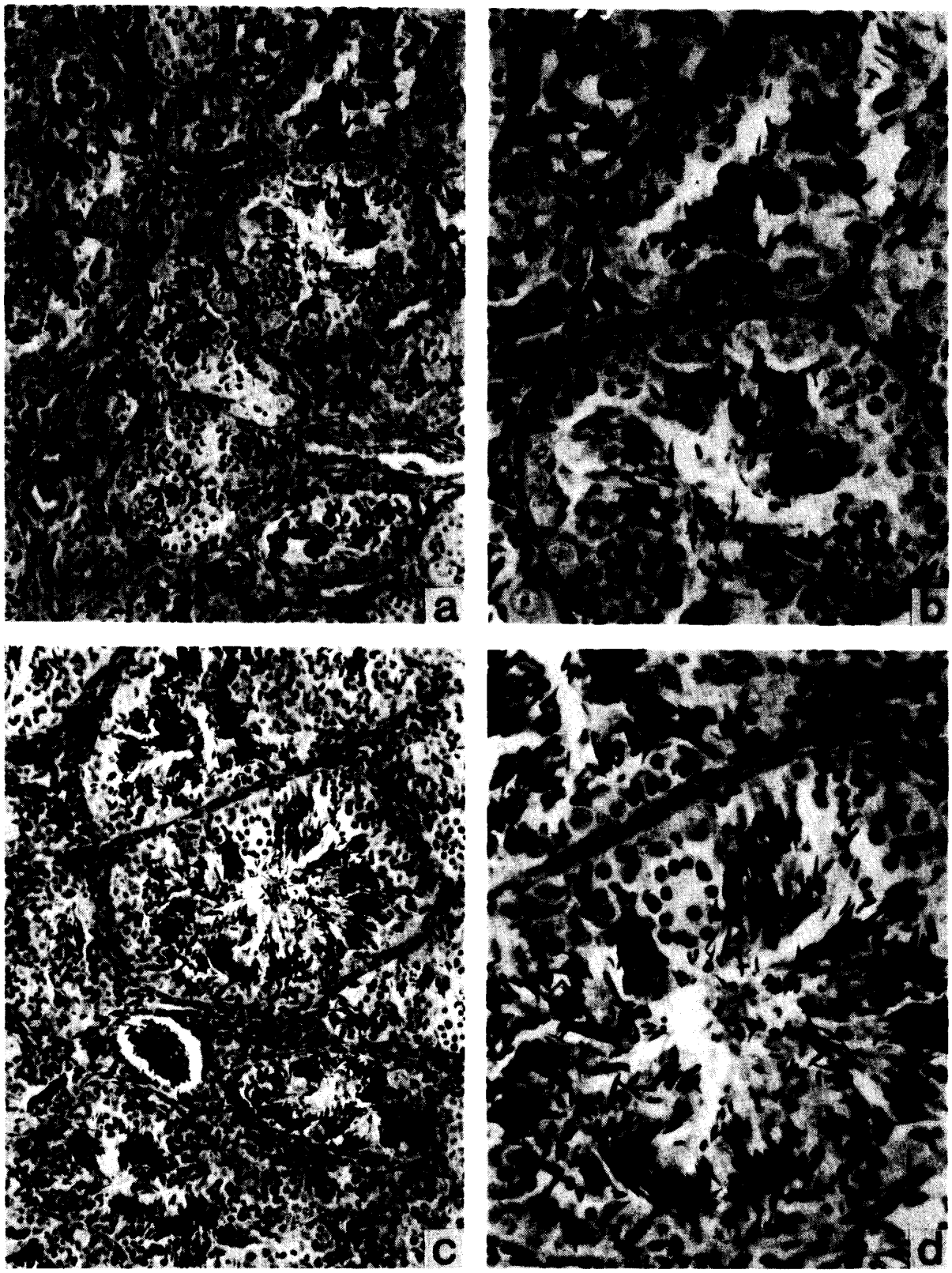

Fig. 29. Cross-sections of the testes of 1-year-old male intraspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and a male *Rana ridibunda* from France.

a. Hybrid ♂, No. 2 produced from *rid* S♀, No. 1 × *rid* F♂, No. 3. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 5 produced from *rid* S♀, No. 1 × *rid* F♂, No. 3. × 150
d. The same as (c). × 300

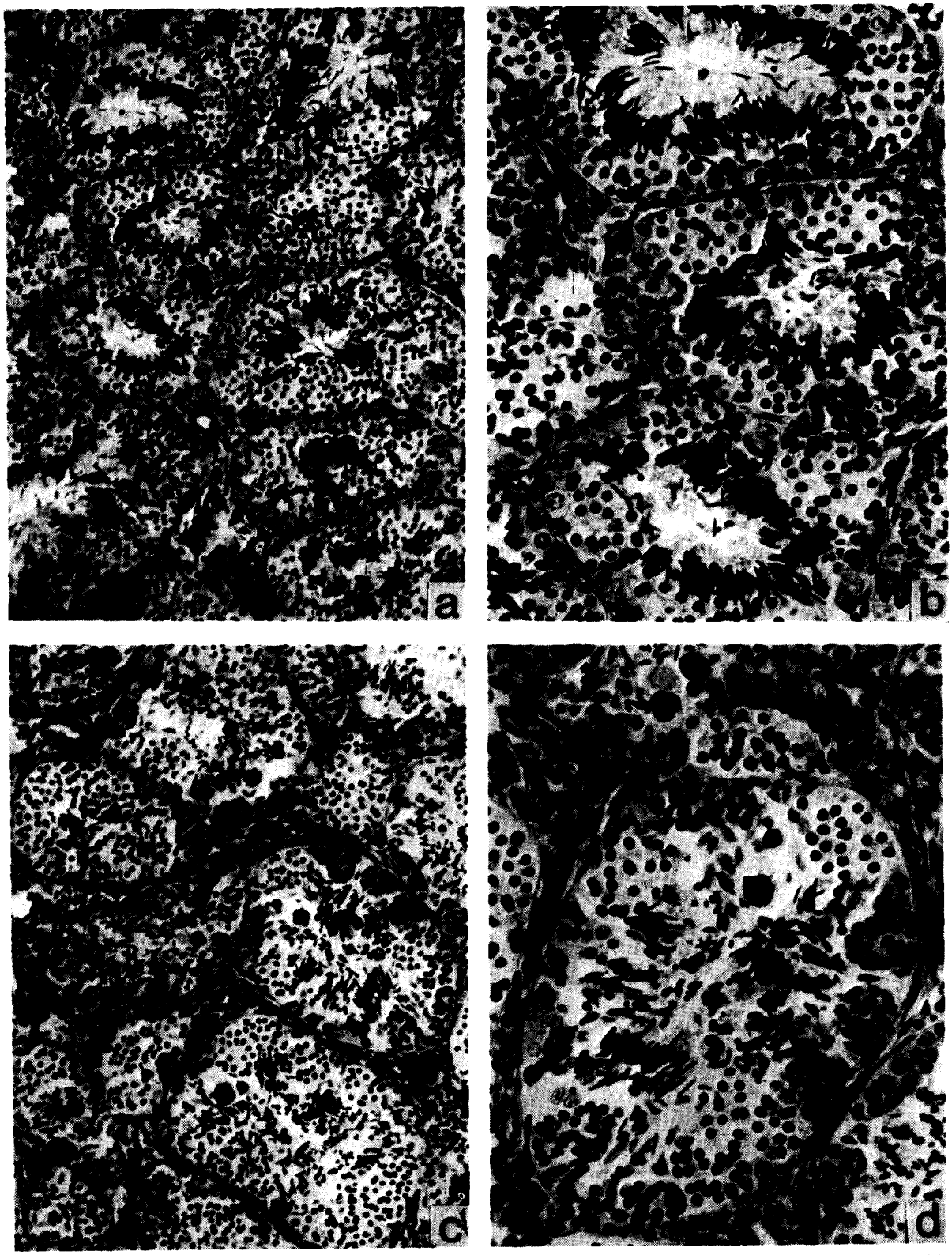

Fig. 30. Cross-sections of the testes of 1-year-old male intraspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and a male *Rana ridibunda* from Turkey.

a. Hybrid ♂, No. 2 produced from *rid* S♀, No. 1 × *rid* T♂, No. 2. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 3 produced from *rid* S♀, No. 1 × *rid* T♂, No. 2. × 150
d. The same as (c). × 300

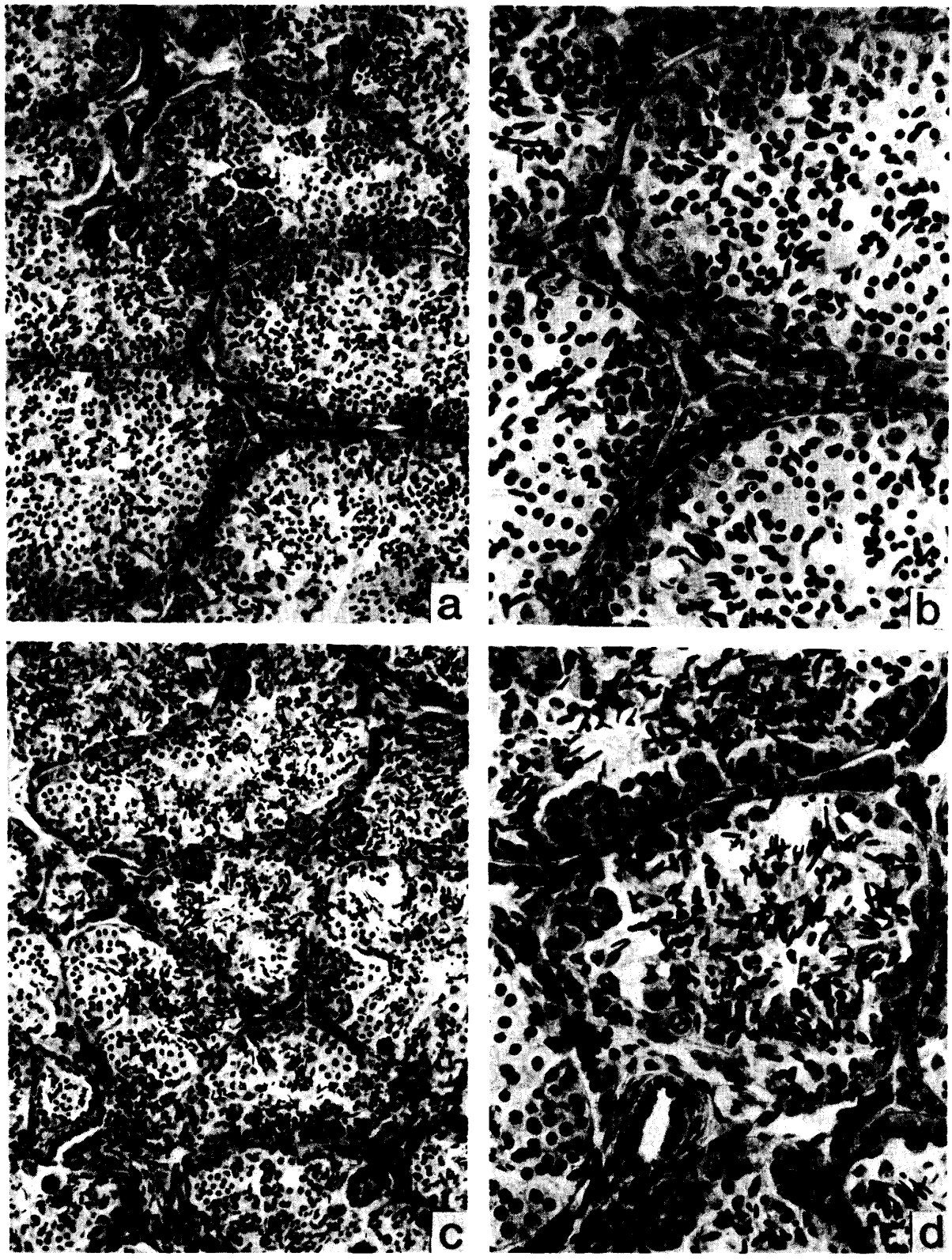

Fig. 31. Cross-sections of the testes of 1-year-old male intraspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and a male *Rana ridibunda* from Turkey.

a. Hybrid ♂, No. 1 produced from *rid* S ♀, No. 1 × *rid* T ♂, No. 2. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 5 produced from *rid* S ♀, No. 1 × *rid* T ♂, No. 2. × 150
d. The same as (c). × 300

matogonia. In the remaining male hybrid (No. 2), however, many bundles of normal spermatozoa were found in the cross-sections of a few seminiferous tubules, while the other seminiferous tubules were very similar to those of the foregoing two males (Nos. 3 and 6) in structure (Fig. 32c, d).

e. Interspecific hybrids, *rid* S♀ × *les* I♂

The testes of five 1-year-old mature male hybrids obtained in 1977 from a mating, *rid* S.W76♀, No. 1 × *les* I.W77♂, No. 1, were observed. These male hybrids were 64.5～66.0 mm, 65.1 mm on the average, in body length. Their left testes were 3.5 mm～5.5 mm, 4.6 mm on the average, in length and 2.5～4.0 mm, 3.3 mm on the average, in width. The right testes were 3.0～5.0 mm, 4.5 mm on the average, in length and 2.5～3.5 mm, 3.0 mm on the average, in width.

While one testis of each of these male hybrids was used in mating experiments, the other was cut into cross-sections. The results showed that the testes of all the male hybrids were abnormal in inner structure and contained no normal spermatozoa. In two male hybrids (Nos. 3 and 4), some abnormal spermatozoa and pycnotic nuclei were found in the central lumens of seminiferous tubules. In the areas surrounding each central lumen, there were first spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule. Another male hybrid (No. 1) contained numerous bundles of abnormally large spermatozoa in the seminiferous tubules (Fig. 33a, b), while in the testes of the remaining two (Nos. 2 and 5), germ cells were scarcely found everywhere (Fig. 33c, d).

f. Interspecific hybrids, *rid* S♀ × *esc* G♂

The testes of four 1-year-old mature male hybrids (Nos. 1～4) obtained in 1977 from a mating, *rid* S.W76♀, No. 1 × *esc* G.W76♂, No. 1, were observed. These male hybrids were 59.5～61.5 mm, 60.3 mm on the average, in body length. Their left testes were 3.0～5.5 mm, 3.8 mm on the average, in length and 3.0～4.0 mm, 3.3 mm on the average, in width. The right testes were 3.0～5.0 mm, 3.5 mm on the average, in length and 2.5～4.0 mm, 3.1 mm on the average, in width.

While one testis of each of these male hybrids was used in mating experiments, the other was cut into cross-sections. It was found that the testes of three male hybrids were abnormal in inner structure and contained no normal spermatozoa. In the seminiferous tubules of the testis of male hybrid No. 1 which was of the RR-type in external appearance and of the $R^S \cdot R^G$-type in electrophoretic patterns, some abnormal spermatozoa, pycnotic nuclei and masses of degenerated germ cells were sparsely distributed in the central lumens. In the areas surrounding the central lumen, there were first spermatocytes and primary and secondary spermatogonia (Fig. 34a, b). In the testes of male hybrids Nos. 2 and 4 which were of the RL-type in external appearance and of the $R^S \cdot L^G$-type in electrophoretic patterns, abnormal spermatozoa and pycnotic nuclei were more numerous than

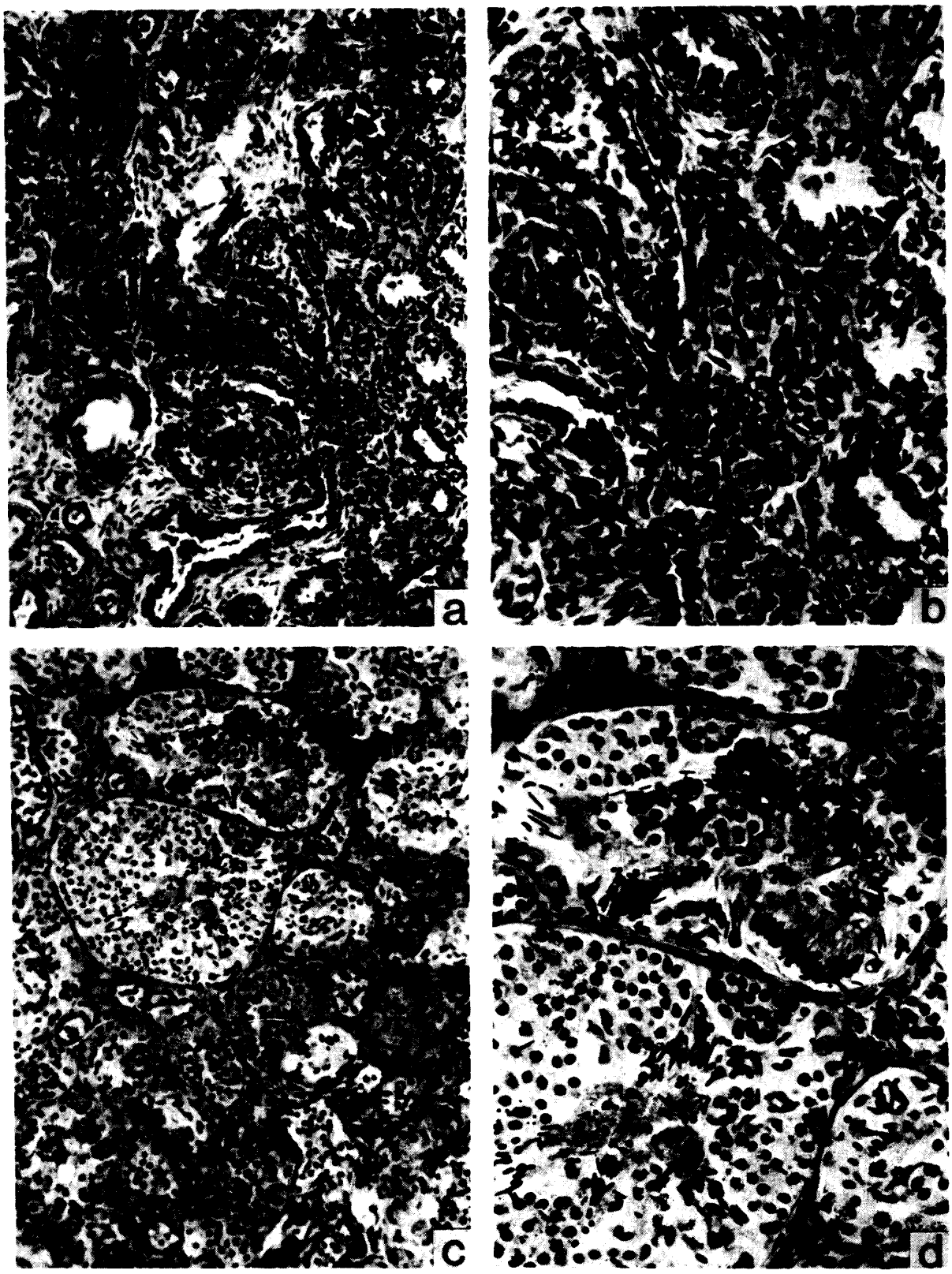

Fig. 32. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and a male *Rana lessonae* from Luxembourg.

a. Hybrid ♂, No. 1 produced from *rid* S ♀, No. 1 × *les* L ♂, No. 3. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 2 produced from *rid* S ♀, No. 1 × *les* L ♂, No. 3. × 150
d. The same as (c). × 300

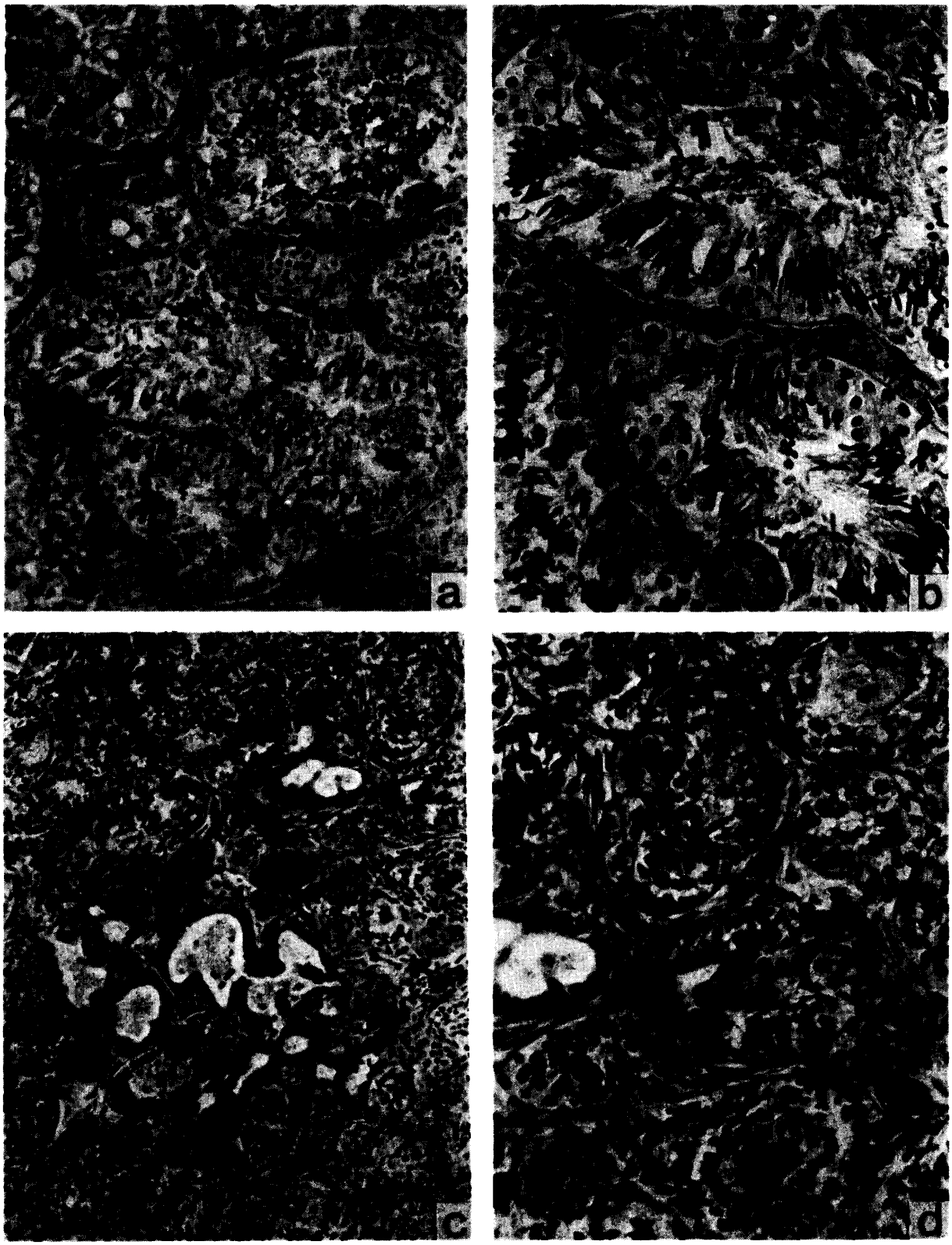

Fig. 33. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and a male *Rana lessonae* from Italy.

a. Hybrid ♂, No. 1 produced from *rid* S♀, No. 1 × *les* I♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 2 produced from *rid* S♀, No. 1 × *les* I♂, No. 1. × 150
d. The same as (c). × 300

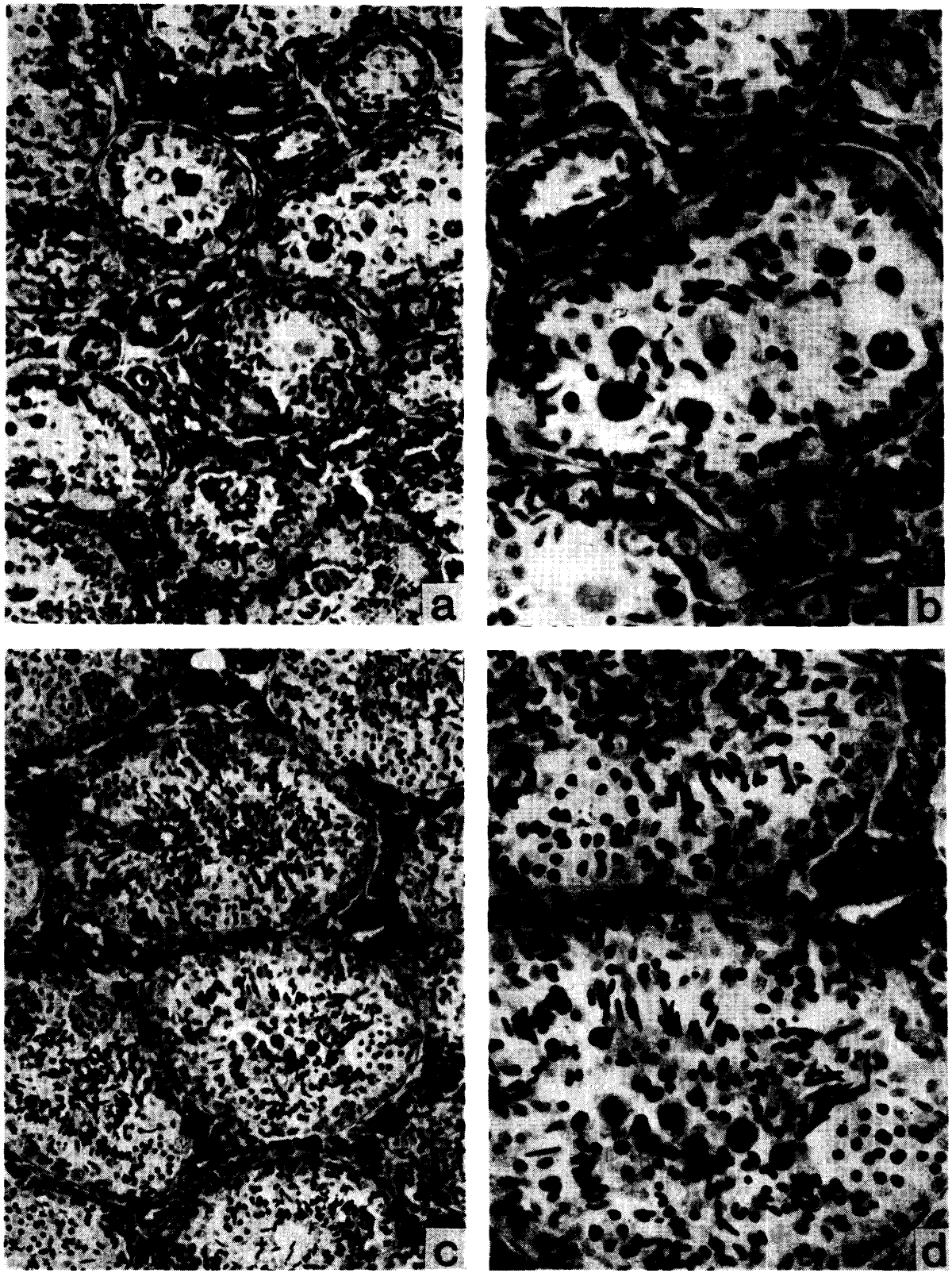

Fig. 34. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and a male *Rana esculenta* from West Germany.

a. Hybrid ♂, No. 1 (RR-type) produced from *rid* S♀, No. 1 × *esc* G♂, No. 1. × 150
b. The same as (a). × 300
c. Hybrid ♂, No. 2 (RL-type) produced from *rid* S♀, No. 1 × *esc* G♂, No. 1. × 150
d. The same as (c). × 300

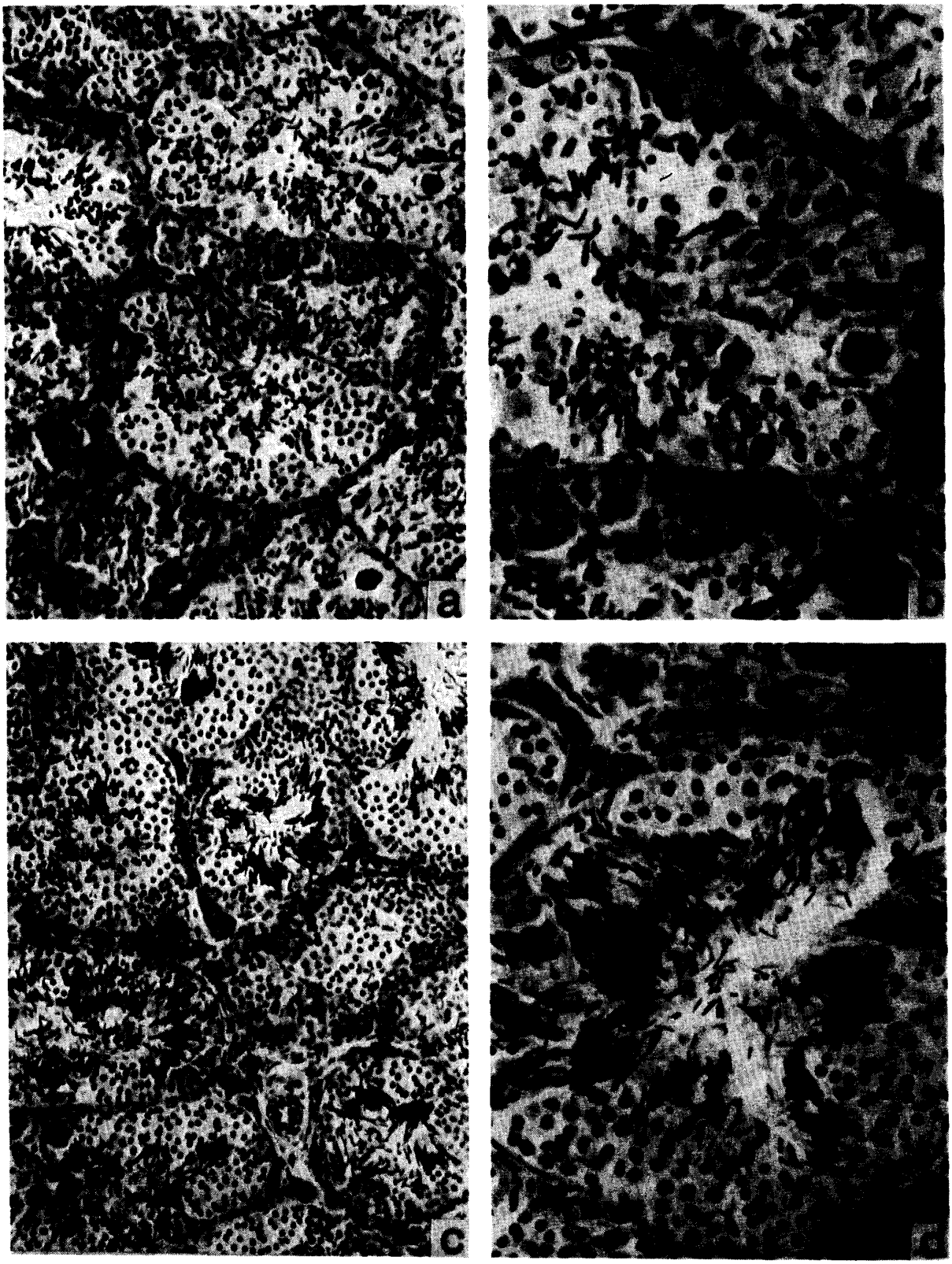

Fig. 35. Cross-sections of the testes of 1-year-old male interspecific hybrids produced in 1977 between a female *Rana ridibunda* from Soviet Union and a male *Rana esculenta* from West Germany.

a. Hybrid ♂, No. 4 (RL-type) produced from *rid* S♀, No. 1 × *esc* G♂, No. 1. ×150
b. The same as (a). ×300
c. Hybrid ♂, No. 3 (RR-type) produced from *rid* S♀, No. 1 × *esc* G♂, No. 1. ×150
d. The same as (c). ×300

those of male hybrid No. 1 (Figs. 34c, d and 35a, b). The areas surrounding the central lumens were occupied by first spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule. The testis of the remaining male hybrid (No. 3) which was of the RR-type in external appearance and of the $R^S \cdot R^G$-type in electrophoretic patterns was normal in inner structure. The central lumen of each seminiferous tubule was filled with many compact bundles of normal spermatozoa (Fig. 35c, d). The areas surrounding the central lumens were occupied by numerous first spermatocytes and secondary spermatogonia. A few primary spermatogonia were found along the wall of each seminiferous tubule.

VI. Reproductive capacity of male hybrids

1. Male hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

a. Controls, *les* L♀ × *les* L♂

In 1977, four matings were made between two 2-year-old females (Nos. 1 and 2) and four 2-year-old males (Nos. 1～4) obtained in 1975 from a mating, *les* L♀, No. 1 × *les* L♂, No. 1. In 1978, 14 matings were made between 10 females including three 3-year-old females (Nos. 3～5) obtained in 1975 from a mating, *les* L♀, No. 1 × *les* L♂, No. 1, and seven 2-year-old females (Nos. 6～12) and 14 males including seven 2-year-old males (Nos. 5～11) obtained in 1976 from matings, *les* L♀, Nos. 2 and 3 × *les* L♂, No. 2, and seven 1-year-old males (Nos. 12～18) obtained in 1977 from matings, *les* L♀, Nos. 4 and 5 × *les* L♂, Nos. 3 and 4. In 1980, three matings were made between three 3-year-old females (Nos. 13～15) obtained in 1977 from a mating, *les* L♀, No. 4 × *les* L♂, No. 3 and three 3-year-old males (Nos. 19～21) obtained in 1977 from a mating, *les* L♀, No. 5 × *les* L♂, No. 4.

From the foregoing 21 matings in total, 44.0～97.0% of the respective number of eggs, 78.5% of 2873 eggs in total, cleaved normally and 31 eggs (1.1%) cleaved abnormally. Thereafter, 40.3～93.8%, 70.3% of the total number of eggs, became normal tail-bud embryos, 35.1～91.7%, 63.4%, hatched normally, and 27.0～80.0%, 56.2%, began to eat normally. Eventually, 19.6～75.9%, 48.6% of the total number of eggs attained completion of metamorphosis and became normal froglets. This percentage of metamorphosed frogs corresponds to 62.0% of the normally cleaved eggs (Table 16).

b. Male intraspecific hybrids, *les* L♀ × *les* I♂

In 1978, six males including three 1-year-old males (Nos. 1～3) obtained in 1977 from a mating, *les* L♀, No. 4 × *les* I♂, No. 1, and three 1-year-old males (Nos. 6～8) obtained in 1977 from a mating, *les* L♀, No. 5 × *les* I♂, No. 2, were mated with six females including three 3-year-old females (Nos. 3～5) obtained in 1975 from a mating, *les* L♀, No. 1 × *les* L♂, No. 1, and three 2-year-old females (Nos. 6～8) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. It

TABLE 16

Reproductive capacity of the control offspring between female and male *Rana lessonae* from Luxembourg

Year	Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male						
1977	75 (*les* $L_1 \times$ *les* L_1) No. 1	75 (*les* $L_1 \times$ *les* L_1) No. 1	184	81 (44.0%)	76 (41.3%)	75 (40.8%)	70 (38.0%)	61 (33.2%)
		75 (*les* $L_1 \times$ *les* L_1) No. 2	197	90 (45.7%)	83 (42.1%)	79 (40.1%)	75 (38.1%)	73 (37.1%)
	75 (*les* $L_1 \times$ *les* L_1) No. 2	75 (*les* $L_1 \times$ *les* L_1) No. 3	105	96 (91.4%)	92 (87.6%)	90 (85.7%)	84 (80.0%)	58 (55.2%)
		75 (*les* $L_1 \times$ *les* L_1) No. 4	112	103 (92.0%)	96 (85.7%)	92 (82.1%)	87 (77.7%)	85 (75.9%)
1978	75 (*les* $L_1 \times$ *les* L_1) No. 3	76 (*les* $L_2 \times$ *les* L_2) No. 5	114	109 (95.6%)	103 (90.4%)	103 (90.4%)	86 (75.4%)	86 (75.4%)
		76 (*les* $L_2 \times$ *les* L_2) No. 6	195	87 (44.6%)	84 (43.1%)	84 (43.1%)	59 (30.3%)	52 (26.7%)
	75 (*les* $L_1 \times$ *les* L_1) No. 4	76 (*les* $L_2 \times$ *les* L_2) No. 7	144	137 (95.1%)	135 (93.8%)	132 (91.7%)	113 (78.5%)	99 (68.8%)
		76 (*les* $L_2 \times$ *les* L_2) No. 8	148	95 (64.2%)	89 (60.1%)	52 (35.1%)	40 (27.0%)	29 (19.6%)
	75 (*les* $L_1 \times$ *les* L_1) No. 5	76 (*les* $L_3 \times$ *les* L_2) No. 9	105	83 (79.0%)	81 (77.1%)	76 (72.4%)	67 (63.8%)	64 (61.0%)
		76 (*les* $L_3 \times$ *les* L_2) No. 10	100	86 (86.0%)	82 (82.0%)	75 (75.0%)	60 (60.0%)	58 (58.0%)
		76 (*les* $L_3 \times$ *les* L_2) No. 11	104	92 (88.5%)	90 (86.5%)	78 (75.0%)	65 (62.5%)	56 (53.8%)
	76 (*les* $L_3 \times$ *les* L_2) No. 6	77 (*les* $L_4 \times$ *les* L_3) No. 12	132	125 (94.7%)	113 (85.6%)	95 (72.0%)	81 (61.4%)	59 (44.7%)
	76 (*les* $L_3 \times$ *les* L_2) No. 7	77 (*les* $L_4 \times$ *les* L_3) No. 13	133	129 (97.0%)	124 (93.2%)	112 (84.2%)	105 (78.9%)	89 (66.9%)
	76 (*les* $L_3 \times$ *les* L_2) No. 8	77 (*les* $L_4 \times$ *les* L_3) No. 14	120	112 (93.3%)	96 (80.0%)	93 (77.5%)	89 (74.2%)	78 (65.0%)
	76 (*les* $L_3 \times$ *les* L_2) No. 9	77 (*les* $L_4 \times$ *les* L_3) No. 15	165	131 (79.4%)	69 (41.8%)	61 (37.0%)	56 (33.9%)	51 (30.9%)
	76 (*les* $L_3 \times$ *les* L_2) No. 10	77 (*les* $L_4 \times$ *les* L_3) No. 16	129	93 (72.1%)	52 (40.3%)	48 (37.2%)	43 (33.3%)	33 (25.6%)
	76 (*les* $L_3 \times$ *les* L_2) No. 11	77 (*les* $L_5 \times$ *les* L_4) No. 17	175	153 (87.4%)	127 (72.6%)	99 (56.6%)	90 (51.4%)	65 (37.1%)
	76 (*les* $L_3 \times$ *les* L_2) No. 12	77 (*les* $L_5 \times$ *les* L_4) No. 18	159	150 (94.3%)	143 (89.9%)	127 (79.9%)	114 (71.7%)	90 (56.6%)
1980	77 (*les* $L_4 \times$ *les* L_3) No. 13	77 (*les* $L_5 \times$ *les* L_4) No. 19	136	127 (93.4%)	119 (87.5%)	92 (67.6%)	85 (62.5%)	74 (54.4%)
	77 (*les* $L_4 \times$ *les* L_3) No. 14	77 (*les* $L_5 \times$ *les* L_4) No. 20	102	90 (88.2%)	82 (80.4%)	75 (73.5%)	69 (67.6%)	65 (63.7%)
	77 (*les* $L_4 \times$ *les* L_3) No. 15	77 (*les* $L_5 \times$ *les* L_4) No. 21	114	86 (75.4%)	84 (73.7%)	83 (72.8%)	77 (67.5%)	72 (63.2%)
Total			2873	2255 (78.5%)	2020 (70.3%)	1821 (63.4%)	1615 (56.2%)	1397 (48.6%)

was found that 19.6~91.3% of the respective number of eggs, 64.7% of 805 eggs in total, cleaved normally and 98 eggs (12.2%) cleaved abnormally. Thereafter, 13.3~75.4%, 55.5% of the total number of eggs, became normal tail-bud embryos, 9.5~67.5%, 47.1%, hatched normally, and 7.6~60.9%, 40.1%, began to eat normally. Eventually, 6.3~56.4%, 36.1%, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 55.9% of the normally cleaved eggs (Table 17).

c. Male interspecific hybrids, *les* L♀ × *rid* F♂

In 1977, five 2-year-old males (Nos. 1~5) obtained in 1975 from a mating,

TABLE 17

Reproductive capacity of male hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

Year	Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male						
1978	75 (*les* $L_1 \times$ *les* L_1) No. 3	77 (*les* $L_4 \times$ *les* I_1) No. 1	158	31 (19.6%)	21 (13.3%)	15 (9.5%)	12 (7.6%)	10 (6.3%)
	75 (*les* $L_1 \times$ *les* L_1) No. 4	77 (*les* $L_4 \times$ *les* I_1) No. 2	154	99 (64.3%)	78 (50.6%)	54 (35.1%)	33 (21.4%)	30 (19.5%)
	75 (*les* $L_1 \times$ *les* L_1) No. 5	77 (*les* $L_4 \times$ *les* I_1) No. 3	126	115 (91.3%)	95 (75.4%)	85 (67.5%)	71 (56.3%)	61 (48.4%)
	76 (*les* $L_3 \times$ *les* L_2) No. 6	77 (*les* $L_5 \times$ *les* I_2) No. 6	162	124 (76.5%)	110 (67.9%)	99 (61.1%)	91 (56.2%)	83 (51.2%)
	76 (*les* $L_3 \times$ *les* L_2) No. 7	77 (*les* $L_5 \times$ *les* I_2) No. 7	133	103 (77.4%)	97 (72.9%)	87 (65.4%)	81 (60.9%)	75 (56.4%)
	76 (*les* $L_3 \times$ *les* L_2) No. 8	77 (*les* $L_5 \times$ *les* I_2) No. 8	72	49 (68.1%)	46 (63.9%)	39 (54.2%)	35 (48.6%)	32 (44.4%)
1977	75 (*les* $L_1 \times$ *les* L_1) Nos. 1, 2	75 (*les* $L_1 \times$ *rid* F_1) Nos. 1～5	2034	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 3～5	76 (*les* $L_2 \times$ *rid* F_2) Nos. 6～10	934	0	0	0	0	0
		76 (*les* $L_3 \times$ *rid* F_2) Nos. 11～15	968	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 3～5	76 (*les* $L_2 \times$ *rid* T_1) Nos. 1～5	1191	0	0	0	0	0
		76 (*les* $L_3 \times$ *rid* T_1) Nos. 6～10	1206	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) No. 9	77 (*les* $L_4 \times$ *esc* G_1) No. 1	223	156 (70.0%)	139 (62.3%)	124 (55.6%)	114 (51.1%)	92 (41.3%)
	76 (*les* $L_3 \times$ *les* L_2) No. 10	77 (*les* $L_4 \times$ *esc* G_1) No. 2	163	153 (93.9%)	120 (73.6%)	95 (58.3%)	78 (47.9%)	68 (41.7%)
	76 (*les* $L_3 \times$ *les* L_2) No. 11	77 (*les* $L_4 \times$ *esc* G_1) No. 3	164	95 (57.9%)	75 (45.7%)	54 (32.9%)	40 (24.4%)	39 (23.8%)
	76 (*les* $L_3 \times$ *les* L_2) No. 12	77 (*les* $L_4 \times$ *esc* G_1) No. 4	150	141 (94.0%)	111 (74.0%)	89 (59.3%)	85 (56.7%)	79 (52.7%)
		77 (*les* $L_4 \times$ *esc* G_1) No. 5	177	73 (41.2%)	66 (37.3%)	54 (30.5%)	46 (26.0%)	37 (20.9%)
1980	77 (*les* $L_4 \times$ *les* L_3) No. 13	77 (*les* $L_4 \times$ *esc* G_1) No. 6	172	165 (95.9%)	121 (70.3%)	73 (42.4%)	68 (39.5%)	63 (36.6%)
	78 (*rid* $T_2 \times$ *rid* T_4) No. 1	77 (*les* $L_4 \times$ *esc* G_1) No. 6	194	126 (64.9%)	122 (62.9%)	113 (58.2%)	95 (49.0%)	90 (46.4%)
	77 (*les* $L_4 \times$ *les* L_3) No. 14	77 (*les* $L_4 \times$ *esc* G_1) No. 7	166	88 (53.0%)	86 (51.8%)	76 (45.8%)	74 (44.6%)	62 (37.3%)
	77 (*les* $I_2 \times$ *les* I_1) No. 11	77 (*les* $L_4 \times$ *esc* G_1) No. 7	159	116 (73.0%)	97 (61.0%)	91 (57.2%)	77 (48.4%)	75 (47.2%)
	78 (*rid* $T_2 \times$ *rid* T_4) No. 1	77 (*les* $L_4 \times$ *esc* G_1) No. 7	218	189 (86.7%)	184 (84.4%)	170 (78.0%)	167 (76.6%)	140 (64.2%)
	77 (*les* $L_4 \times$ *les* L_3) No. 15	77 (*les* $L_4 \times$ *esc* G_1) No. 8	146	64 (43.8%)	61 (41.8%)	58 (39.7%)	53 (36.3%)	49 (33.6%)
	77 (*les* $I_2 \times$ *les* I_1) No. 11	77 (*les* $L_4 \times$ *esc* G_1) No. 8	143	115 (80.4%)	94 (65.7%)	82 (57.3%)	74 (51.7%)	67 (46.9%)
	78 (*rid* $T_2 \times$ *rid* T_4) No. 1	77 (*les* $L_4 \times$ *esc* G_1) No. 8	214	182 (85.0%)	177 (82.7%)	168 (78.5%)	153 (71.5%)	121 (56.5%)

les L♀, No. 1 × *rid* F♂, No. 1, were mated with two 2-year-old females (Nos. 1 and 2) obtained in 1975 from a mating, *les* L♀, No. 1 × *les* L♂, No. 1. The results showed that none of 2034 eggs in total cleaved normally and only 29 (1.4%) cleaved abnormally. All these abnormally cleaved eggs died during the cleavage stage (Table 17).

In 1978, a total of ten 2-year-old males including five (Nos. 6～10) obtained in 1976 from a mating, *les* L♀, No. 2 × *rid* F♂, No. 2, and five (Nos. 11～15)

obtained in 1976 from a mating, *les* L♀, No. 3×*rid* F♂, No. 2, were mated with three 2-year-old females (Nos. 3~5) obtained in 1976 from a mating, *les* L♀, No. 3×*les* L♂, No. 2. The results also showed that none of 1902 eggs in total cleaved normally and only 40 eggs (2.1%) did so abnormally. All these abnormally cleaved eggs died during the cleavage stage (Table 17).

d. Male interspecific hybrids, *les* L♀×*rid* T♂

In 1978, a total of ten 2-year-old males including five males (Nos. 1~5) obtained in 1976 from a mating, *les* L♀, No. 2×*rid* T♂, No. 1, and five males (Nos. 6~10) obtained in 1976 from a mating, *les* L♀, No. 3×*rid* T♂, No. 1, were mated with three females (Nos. 3~5) obtained from a mating, *les* L♀, No. 3×*les* L♂, No. 2. The results showed that none of 2397 eggs in total cleaved normally and only seven eggs (0.3%) cleaved abnormally. All these abnormally cleaved eggs died during the cleavage stage (Table 17).

e. Male interspecific hybrids, *les* L♀×*esc* G♂

In 1978, five 1-year-old LL-type male hybrids (Nos. 1~5) obtained in 1977 from a mating, *les* L♀, No. 4×*esc* G♂, No. 1, were mated with four 2-year-old females (Nos. 9~12) obtained from a mating, *les* L♀, No. 3×*les* L♂, No. 2. It was found that 41.2~94.0% of the respective number of eggs, 70.5% of 877 eggs in total, cleaved normally and 67 eggs (7.6%) cleaved abnormally. Thereafter, 37.3~74.0%, 58.3% of the total number of eggs, became normal tail-bud embryos, 30.5~59.3%, 47.4%, hatched normally and 24.4~56.7%, 41.4%, began to eat normally. Eventually, 20.9~52.7%, 35.9% of the total number of eggs, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 51.0% of the normally cleaved eggs (Table 17).

In 1980, two 3-year-old LR-type male hybrids (Nos. 6 and 7) obtained in 1977 from a mating, *les* L♀, No. 4×*esc* G♂, No. 1, were mated with two female *Rana lessonae* from Luxembourg (Nos. 13 and 14) obtained in 1977 from a mating, *les* L♀, No. 4×*les* L♂, No. 3. It was found that 74.9% of 338 eggs in total cleaved normally, 61.2% became normal tail-bud embryos, and 44.1% hatched normally. Thereafter, 42.0% began to eat normally, and 37.0% attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 49.4% of the normally cleaved eggs (Table 17).

The foregoing two males (Nos. 6 and 7) were mated with a 2-year-old female *Rana ridibunda* from Turkey obtained in 1978 from a mating, *rid* T♀, No. 2×*rid* T♂, No. 4. The results showed that 76.5% of 412 eggs in total cleaved normally, 74.3% became normal tail-bud embryos, 68.7% hatched normally, and 63.6% began to eat normally. Eventually, 55.8% attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 73.0% of the normally cleaved eggs. On the other hand, one (No. 7) of the above two males was mated with a female *Rana lessonae* from Italy (No. 11) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1. The results showed that 73.0% of 159 eggs cleaved normally, 61.0% became normal tail-bud embryos, 57.2%

hatched normally and 48.4% began to eat normally. Eventually, 47.2% attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 64.7% of the normally cleaved eggs (Table 17).

In 1980, a 3-year-old LL-type male hybrid (No. 8) obtained in 1977 from a mating, *les* L♀, No. 4×*esc* G♂, No. 1, were mated with a total of three females including a 3-year-old female (No. 15) obtained in 1977 from a mating, *les* L♀, No. 4×*les* L♂, No. 3, a 3-year-old female (No. 11) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1, and a 2-year-old female (No. 1) obtained in 1978 from a mating, *rid* T♀, No. 2×*rid* T♂, No. 4. It was found that 43.8%, 80.4% and 85.0% of 146, 143 and 214 eggs, respectively, cleaved normally. Thereafter, 41.8%, 65.7% and 82.7% became normal tail-bud embryos, 39.7%, 57.3% and 78.5% hatched normally and 36.3%, 51.7% and 71.5% began to eat normally, and 33.6%, 46.9% and 56.5% attained completion of metamorphosis, respectively. These percentages correspond to 76.6%, 58.3% and 66.5% of the normally cleaved eggs, respectively (Table 17).

2. Male hybrids between female *Rana lessonae* from Italy and five kinds of males

a. Controls, *les* I♀×*les* I♂

In 1978 and 1980, 12 matings were made between six 1-year-old females (Nos. 1~6) and four 1-year-old males (Nos. 1~4) obtained in 1977 from a mating, *les* I♀, No. 1×*les* I♂, No. 1, between four 1-year-old females (Nos. 7~10) and two 1-year-old males (Nos. 5 and 6) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1, and between two 3-year-old females (Nos. 11 and 12) and two 3-year-old males (Nos. 7 and 8) obtained in 1977 from the above mating, *les* I♀, No. 2×*les* I♂, No. 1. The results showed that 76.3~97.0% of the respective number of eggs, 84.4% of 872 eggs in total, cleaved normally and 45 eggs (5.2%) cleaved abnormally. Thereafter, 60.9~89.9%, 75.1% of the total number of eggs, became normal tail-bud embryos, 59.7~88.9%, 72.2%, hatched normally and 47.4~86.4%, 63.3%, began to eat normally. Eventually, 44.3~74.2%, 57.0% of the total number of eggs, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 67.5% of the normally cleaved eggs (Table 18).

b. Male intraspecific hybrids, *les* I♀×*les* L♂

In 1978, a total of 10 males including five 1-year-old males (Nos. 1~5) obtained from a mating, *les* I♀, No. 1×*les* L♂, No. 3, and five 1-year-old males (Nos. 6~10) obtained from a mating, *les* I♀, No. 2×*les* L♂, No. 3, were mated with six 1-year-old female *Rana lessonae* from Italy including three females (Nos. 1~3) obtained from a mating, *les* I♀, No. 1×*les* I♂, No. 1, and three females (Nos. 7~9) obtained from a mating, *les* I♀, No. 2×*les* I♂, No. 1. It was found that 64.5~98.0% of the respective number of eggs, 85.6% of 1533 eggs in total, cleaved normally and 103 (6.7%) cleaved abnormally. Thereafter, 55.0~96.7%, 80.0% of the total number of eggs, became normal tail-bud embryos, 50.0~92.7%,

TABLE 18

Reproductive capacity of male hybrids between female *Rana lessonae* from Italy and five kinds of males and of the controls

Year	Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male						
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 1~3	77 (*les* $I_1 \times$ *les* I_1) Nos. 1, 2	198	192 (97.0%)	178 (89.9%)	176 (88.9%)	171 (86.4%)	147 (74.2%)
	77 (*les* $I_1 \times$ *les* I_1) Nos. 4~6	77 (*les* $I_1 \times$ *les* I_1) Nos. 3, 4	181	164 (90.6%)	142 (78.5%)	130 (71.8%)	103 (56.9%)	88 (48.6%)
	77 (*les* $I_2 \times$ *les* I_1) Nos. 7~10	77 (*les* $I_2 \times$ *les* I_1) Nos. 5, 6	253	193 (76.3%)	154 (60.9%)	151 (59.7%)	120 (47.4%)	112 (44.3%)
1980	77 (*les* $I_2 \times$ *les* I_1) Nos. 11, 12	77 (*les* $I_2 \times$ *les* I_1) Nos. 7, 8	240	187 (77.9%)	181 (75.4%)	173 (72.1%)	158 (65.8%)	150 (62.5%)
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 1~3	77 (*les* $I_1 \times$ *les* L_3) No. 1	153	150 (98.0%)	148 (96.7%)	109 (71.2%)	84 (54.9%)	75 (49.0%)
		77 (*les* $I_1 \times$ *les* L_3) No. 2	125	120 (96.0%)	113 (90.4%)	95 (76.0%)	75 (60.0%)	70 (56.0%)
		77 (*les* $I_1 \times$ *les* L_3) No. 3	131	96 (73.3%)	94 (71.8%)	82 (62.6%)	79 (60.3%)	47 (35.9%)
		77 (*les* $I_1 \times$ *les* L_3) No. 4	102	99 (97.1%)	74 (72.5%)	71 (69.6%)	67 (65.7%)	43 (42.2%)
		77 (*les* $I_1 \times$ *les* L_3) No. 5	200	129 (64.5%)	110 (55.0%)	100 (50.0%)	95 (47.5%)	79 (39.5%)
	77 (*les* $I_2 \times$ *les* I_1) Nos. 7~9	77 (*les* $I_2 \times$ *les* L_3) No. 6	149	132 (88.6%)	123 (82.6%)	101 (67.8%)	55 (36.9%)	55 (36.9%)
		77 (*les* $I_2 \times$ *les* L_3) No. 7	165	151 (91.5%)	141 (85.5%)	136 (82.4%)	132 (80.0%)	110 (66.7%)
		77 (*les* $I_2 \times$ *les* L_3) No. 8	191	184 (96.3%)	178 (93.2%)	177 (92.7%)	129 (67.5%)	102 (53.4%)
		77 (*les* $I_2 \times$ *les* L_3) No. 9	161	125 (77.6%)	121 (75.2%)	120 (74.5%)	116 (72.0%)	97 (60.2%)
		77 (*les* $I_2 \times$ *les* L_3) No. 10	156	127 (81.4%)	124 (79.5%)	115 (73.7%)	98 (62.8%)	91 (58.3%)
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 4~6	77 (*les* $I_1 \times$ *rid* F_3) Nos. 1~5	924	5	0	0	0	0
	77 (*les* $I_1 \times$ *les* I_1) Nos. 1~3	77 (*les* $I_2 \times$ *rid* F_4) Nos. 6~10	1276	5	2	0	0	0
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 1~3	77 (*les* $I_1 \times$ *rid* T_2) Nos. 1~5	1063	1	1	0	0	0
	77 (*les* $I_2 \times$ *les* I_1) Nos. 7~9	77 (*les* $I_2 \times$ *rid* T_3) Nos. 6~10	1091	4	1	0	0	0
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 1~3	77 (*les* $I_2 \times$ *rid* S_1) No. 1	204	12 (5.9%)	11 (5.4%)	9 (4.4%)	9 (4.4%)	8 (3.9%)
		77 (*les* $I_2 \times$ *rid* S_1) Nos. 2~5	571	0	0	0	0	0
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 4~6	77 (*les* $I_1 \times$ *esc* G_1) No. 1	144	137 (95.1%)	127 (88.2%)	120 (83.3%)	83 (57.6%)	74 (51.4%)
		77 (*les* $I_1 \times$ *esc* G_1) No. 2	160	157 (98.1%)	149 (93.1%)	143 (89.4%)	92 (57.5%)	67 (41.9%)
		77 (*les* $I_1 \times$ *esc* G_1) No. 3	114	107 (93.9%)	93 (81.6%)	92 (80.7%)	81 (71.1%)	72 (63.2%)
		77 (*les* $I_1 \times$ *esc* G_1) No. 4	174	102 (58.6%)	84 (48.3%)	82 (47.1%)	76 (43.7%)	74 (42.5%)
	77 (*les* $I_2 \times$ *les* I_1) Nos. 7~9	77 (*les* $I_2 \times$ *esc* G_1) No. 6	164	151 (92.1%)	146 (89.0%)	140 (85.4%)	114 (69.5%)	99 (60.4%)
		77 (*les* $I_2 \times$ *esc* G_1) No. 7	235	138 (58.7%)	135 (57.4%)	131 (55.7%)	117 (49.8%)	103 (43.8%)
		77 (*les* $I_2 \times$ *esc* G_1) No. 8	181	152 (84.0%)	141 (77.9%)	139 (76.8%)	115 (63.5%)	100 (55.2%)
		77 (*les* $I_2 \times$ *esc* G_1) No. 9	208	206 (99.0%)	188 (90.4%)	152 (73.1%)	121 (58.2%)	88 (42.3%)
		77 (*les* $I_2 \times$ *esc* G_1) No. 10	220	0	0	0	0	0
	77 (*les* $I_1 \times$ *les* I_1) Nos. 4~6	77 (*les* $I_3 \times$ *esc* G_1) No. 16	114	87 (76.3%)	82 (71.9%)	80 (70.2%)	75 (65.8%)	70 (61.4%)

		77 (*les* $I_3 \times esc$ G_1) No. 17	109	90 (82.6%)	86 (78.9%)	82 (75.2%)	73 (67.0%)	67 (61.5%)
		77 (*les* $I_3 \times esc$ G_1) No. 18	117	92 (78.6%)	83 (70.9%)	76 (65.0%)	61 (52.1%)	60 (51.3%)
		77 (*les* $I_3 \times esc$ G_1) No. 19	135	74 (54.8%)	70 (51.9%)	69 (51.1%)	62 (45.9%)	53 (39.3%)
		77 (*les* $I_3 \times esc$ G_1) No. 20	104	93 (89.4%)	87 (83.7%)	74 (71.2%)	68 (65.4%)	62 (59.6%)
1980	77 (*les* $I_2 \times les$ I_1) Nos. 11, 12	77 (*les* $I_2 \times esc$ G_1) No. 21	106	73 (68.9%)	68 (64.2%)	57 (53.8%)	55 (51.9%)	47 (44.3%)
		77 (*les* $I_2 \times esc$ G_1) No. 22	132	106 (80.3%)	84 (63.6%)	70 (53.0%)	65 (49.2%)	52 (39.4%)
		77 (*les* $I_2 \times esc$ G_1) No. 23	156	142 (91.0%)	134 (85.9%)	128 (82.1%)	122 (78.2%)	108 (69.2%)
	78 (*rid* $T_2 \times rid$ T_4) No. 2	77 (*les* $I_3 \times esc$ G_1) No. 24	105	95 (90.5%)	87 (82.9%)	85 (81.0%)	84 (80.0%)	79 (75.2%)
		77 (*les* $I_3 \times esc$ G_1) No. 25	142	110 (77.5%)	91 (64.1%)	90 (63.4%)	86 (60.6%)	82 (57.7%)
		77 (*les* $I_3 \times esc$ G_1) No. 26	149	76 (51.0%)	52 (34.9%)	43 (28.9%)	40 (26.8%)	36 (24.2%)

72.1%, hatched normally and 36.9~80.0%, 60.7%, began to eat normally. Eventually, 35.9~66.7%, 50.2% of the total number of eggs, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 58.6% of the normally cleaved eggs (Table 18).

c. Male interspecific hybrids, *les* I♀ × *rid* F♂

In 1978, a total of 10 male hybrids including five 1-year-old males (Nos. 1~5) obtained from a mating, *les* I♀, No. 1 × *rid* F♂, No. 3, and five 1-year-old males (Nos. 6~10) obtained from a mating, *les* I♀, No. 2 × *rid* F♂, No. 4, were mated with six 1-year-old female *Rana lessonae* from Italy (Nos. 1~6) obtained from a mating, *les* I♀, No. 1 × *les* I♂, No. 1. The results showed that only 10 (0.5%) of 2200 eggs in total cleaved normally. Of these eggs, three, two, three and two were obtained from the matings with males Nos. 1, 2, 7 and 8, respectively. All these eggs became abnormal and died by the hatching stage. Although there were 149 (6.8%) abnormally cleaved eggs, all of them died by the blastula stage. Of these abnormally cleaved eggs, 132 were obtained from the matings with seven males (Nos. 1, 2, 6~10), while 17 eggs were from the matings with three males (Nos. 3~5) (Table 18).

d. Male interspecific hybrids, *les* I♀ × *rid* T♂

In 1978, a total of 10 males including five 1-year-old males (Nos. 1~5) obtained from a mating, *les* I♀, No. 1 × *rid* T♂, No. 2, and five 1-year-old males (Nos. 6~10) obtained from a mating, *les* I♀, No. 2 × *rid* T♂, No. 3, were mated with six female *Rana lessonae* from Italy including three 1-year-old females (Nos. 1~3) obtained from a mating, *les* I♀, No. 1 × *les* I♂, No. 1, and three 1-year-old females (Nos. 7~9) obtained from a mating, *les* I♀, No. 2 × *les* I♂, No. 1. The results showed that only five (0.2%) of 2154 eggs in total cleaved normally. All these normally cleaved eggs became abnormal and died by the hatching stage. Although there were 224 (10.4%) abnormally cleaved eggs, all of them died during the cleavage stage (Table 18).

e. Male interspecific hybrids, *les* I♀ × *rid* S♂

In 1978, five 1-year-old males (Nos. 1～5) obtained from a mating, *les* I♀, No. 2 × *rid* S♂, No. 1, were mated with three 1-year-old female *Rana lessonae* from Italy (Nos. 1～3) obtained from a mating, *les* I♀, No. 1 × *les* I♂, No. 1. Of 204 eggs of a female mated with male No. 1, 12 (5.9%) cleaved normally and 37 (18.1%) did abnormally. Of the normally cleaved eggs, one, two and one died of edema at the tail-bud, the hatching and the tadpole stage, respectively. The remaining eight tadpoles (3.9%) completed metamorphosis. This number of metamorphosed frogs corresponds to 66.7% of the normally cleaved eggs. None of 571 eggs of females mated with males Nos. 2～5 cleaved normally, while 66 eggs (11.6%) cleaved abnormally. All these abnormally cleaved eggs died during the cleavage stage (Table 18).

f. Male interspecific hybrids, *les* I♀ × *esc* G♂

In 1978, a total of 14 male hybrids including three 1-year-old LL-type males (Nos. 1～3) and one 1-year-old LR-type male (No. 4) obtained from a mating, *les* I♀, No. 1 × *esc* G♂, No. 1, four 1-year-old LL-type males (Nos. 6～9) and a 1-year-old LR-type male (No. 10) obtained from a mating, *les* I♀, No. 2 × *esc* G♂, No. 1, and five 1-year-old LL-type males (Nos. 16～20) obtained from a mating, *les* I♀, No. 3 × *esc* G♂, No. 1, were mated with a total of six female *Rana lessonae* from Italy including three 1-year-old females (Nos. 4～6) obtained from a mating, *les* I♀, No. 1 × *les* I♂, No. 1, and three 1-year-old females (Nos. 7～9) obtained from a mating, *les* I♀, No. 2 × *les* I♂, No. 1. It was found that 54.8～99.0% of the respective number of eggs, 83.1% of 1785 eggs in total produced from females mated with 12 LL-type males (Nos. 1～3, 6～9, 16～20), cleaved normally, while 69 eggs (3.9%) cleaved abnormally and all of them died by the gastrula stage. Thereafter, 51.9～93.1%, 77.7% of the total number of eggs, became normal tail-bud embryos, 51.1～89.4%, 72.7%, hatched normally and 45.9～71.1%, 59.5%, began to eat normally. Eventually, 39.3～63.2%, 51.3%, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 61.7% of the normally cleaved eggs. Of 174 eggs of females mated with a LR-type male (No. 4), 58.6% cleaved normally, 48.3% became normal tail-bud embryos, 47.1% hatched normally, 43.7% began to eat normally, and 42.5% attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 72.5% of the normally cleaved eggs. None of 220 eggs of females mated with a LR-type male (No. 10) cleaved normally, while three eggs (1.4%) cleaved abnormally. All these eggs died during the cleavage stage (Table 18).

In 1980, three 3-year-old LR-type male hybrids (Nos. 21～23) obtained from a mating, *les* I♀, No. 2 × *esc* G♂, No. 1, were mated with two 3-year-old female *Rana lessonae* from Italy (Nos. 11 and 12) obtained from a mating, *les* I♀, No. 2 × *les* I♂, No. 1. The results showed that 68.9～91.0% of the respective number of eggs, 81.5% of 394 eggs in total, cleaved normally, while only five eggs (1.3%) cleaved abnormally. Thereafter, 63.6～85.9%, 72.6% of the total number of

eggs, became normal tail-bud embryos, 53.0~82.1%, 64.7%, hatched normally, and 49.2~78.2%, 61.4%, began to eat normally. Eventually, 39.4~69.2%, 52.5% of the total number of eggs, completed metamorphosis. This percentage of normally metamorphosed frogs corresponds to 64.5% of the normally cleaved eggs (Table 18).

In 1980, three 3-year-old LR-type male hybrids (Nos. 24~26) obtained from a mating, *les* I♀, No. 3×*esc* G♂, No. 1, were mated with one 2-year-old female *Rana ridibunda* from Turkey (No. 2) obtained from a mating, *rid* T♀, No. 2×*rid* T♂, No. 4. The results showed that 51.0~90.5% of the respective number of eggs, 71.0% of 396 eggs in total, cleaved normally, while 26 (6.6%) cleaved abnormally. Thereafter, 34.9~82.9%, 58.1% of the total number of eggs, became normal tail-bud embryos, 28.9~81.0%, 55.1%, hatched normally, and 26.8~80.0%, 53.0%, began to eat normally. Eventually, 24.2~75.2%, 49.7% of the total number of eggs, completed metamorphosis. This percentage of metamorphosed frogs corresponds to 70.1% of the normally cleaved eggs (Table 18).

3. Male hybrids between a female *Rana ridibunda* from Turkey and four kinds of males

a. Controls, *rid* T♀×*rid* T♂

In 1978, a 1-year-old male (No. 4) obtained from a mating, *rid* T♀, No. 1×*rid* T♂, No. 2, was mated with a female (No. 2) collected from Turkey (Table 3). The results showed that 98.5% of 530 eggs cleaved normally and 78.9% attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 80.1% of the normally cleaved eggs.

b. Male intraspecific hybrids, *rid* T♀×*rid* F♂

In 1978, four 1-year-old males (Nos. 1~4) obtained from a mating, *rid* T♀, No. 1×*rid* F♂, No. 3, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 6 and 7) obtained from a mating, *les* L♀, No. 3×*les* L♂, No. 2. The results showed that none of 194 eggs of females mated with male No. 4 cleaved normally or abnormally. In contrast, 74.9~89.2% of respective number of eggs, 82.4% of 618 eggs in total produced from females mated with males Nos. 1~3, cleaved normally, 67.0~75.4%, 71.2% of the total number of eggs, became normal tail-bud embryos, 52.7~66.0%, 60.2%, hatched normally, and 42.4~66.0%, 56.1%, began to eat normally. Eventually, 36.0~58.6%, 49.2% of the total number of eggs, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 59.7% of the normally cleaved eggs (Table 19).

c. Male interspecific hybrids, *rid* T♀×*les* L♂

In 1978, five 1-year-old male hybrids (Nos. 1~5) obtained from a mating, *rid* T♀, No. 1×*les* L♂, No. 3, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 10 and 11) obtained from a mating, *les* L♀,

TABLE 19
Reproductive capacity of male hybrids between a female *Rana ridibunda* from Turkey and four kinds of males

Year	Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male						
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 6, 7	77 (*rid* $T_1 \times$ *rid* F_3) No. 1	203	181 (89.2%)	153 (75.4%)	107 (52.7%)	86 (42.4%)	73 (36.0%)
		77 (*rid* $T_1 \times$ *rid* F_3) No. 2	215	161 (74.9%)	153 (71.2%)	142 (66.0%)	142 (66.0%)	126 (58.6%)
		77 (*rid* $T_1 \times$ *rid* F_3) No. 3	200	167 (83.5%)	134 (67.0%)	123 (61.5%)	119 (59.5%)	105 (52.5%)
		77 (*rid* $T_1 \times$ *rid* F_3) No. 4	194	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 10, 11	77 (*rid* $T_1 \times$ *les* L_3) Nos. 1～5	1178	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 10, 11	77 (*rid* $T_1 \times$ *les* I_1) Nos. 1～3	890	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 8, 9	77 (*rid* $T_1 \times$ *esc* G_1) No. 1	185	161 (87.0%)	89 (48.1%)	61 (33.0%)	54 (29.2%)	50 (27.0%)
		77 (*rid* $T_1 \times$ *esc* G_1) No. 2	215	152 (70.7%)	82 (38.1%)	63 (29.3%)	52 (24.2%)	49 (22.8%)
		77 (*rid* $T_1 \times$ *esc* G_1) No. 3	207	108 (52.2%)	73 (35.3%)	70 (33.8%)	56 (27.1%)	46 (22.2%)
		77 (*rid* $T_1 \times$ *esc* G_1) No. 4	156	102 (65.4%)	80 (51.3%)	40 (25.6%)	19 (12.2%)	15 (9.6%)
		77 (*rid* $T_1 \times$ *esc* G_1) No. 5	177	12 (6.8%)	10 (5.6%)	6 (3.4%)	6 (3.4%)	4 (2.3%)

No. 3 × *les* L♂, No. 2. The results showed that none of 1178 eggs in total cleaved normally or abnormally (Table 19).

d. Male interspecific hybrids, *rid* T♀ × *les* I♂

In 1978, three 1-year-old male hybrids (Nos. 1～3) obtained from a mating, *rid* T♀, No. 1 × *les* I♂, No. 1, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 10 and 11) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. The results showed that none of 890 eggs in total cleaved normally or abnormally (Table 19).

e. Male interspecific hybrids, *rid* T♀ × *esc* G♂

In 1978, a total of five 1-year-old male hybrids including three RR-type males (Nos. 1～3) and two RL-type male hybrids (Nos. 4 and 5) obtained from a mating, *rid* T♀, No. 1 × *esc* G♂, No. 1, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 8 and 9) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. It was found that 52.2～87.0% of the respective number of eggs, 69.4% of 607 eggs in total produced from the females mated with the three RR-type males, cleaved normally, while 61 eggs (10.0%) cleaved abnormally. Thereafter, 35.3～48.1%, 40.2% of the total number of eggs, became normal tail-bud embryos, 29.3～33.8%, 32.0%, hatched normally and 24.2～29.2%, 26.7%, began to eat normally. Eventually, 22.2～27.0%, 23.9% of the total number of eggs, attained completion of metamorphosis. This percentage of normally metamorphosed frogs corresponds to 34.4% of the normally cleaved eggs.

In the two matings with the two RL-type male hybrids (Nos. 4 and 5), 34.2% of 333 eggs in total, cleaved normally, while 72 eggs (21.6%) cleaved abnormally. Thereafter, 27.0% of the total number of eggs became normal tail-bud embryos, 13.8% hatched normally, 7.5% began to eat normally, and 5.7% attained completion of metamorphosis. This percentage of normally metamorphosed frogs corresponds to 16.7% of the normally cleaved eggs (Table 19).

4. Male hybrids between a female *Rana ridibunda* from Soviet Union and five kinds of males

a. Controls, *rid* S♀ × *rid* S♂

In 1978, a 1-year-old male (No. 2) obtained from a mating, *rid* S♀, No. 1 × *rid* S♂, No. 1, was mated with a female *Rana ridibunda* from Turkey, *rid* T.W76♀, No. 2. The results showed that 89.0% of 264 eggs cleaved normally, 80.7% hatched normally and 76.9% attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 86.4% of the normally cleaved eggs (Table 3).

b. Male intraspecific hybrids, *rid* S♀ × *rid* F♂

In 1978, five 1-year-old males (Nos. 1～5) obtained from a mating, *rid* S♀, No. 1 × *rid* F♂, No. 3, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 6 and 7) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. It was found that in three matings with three males (Nos. 1～3), 12.4～20.9% of the respective number of eggs, 18.3% of 761 eggs in total, cleaved normally, while 285 eggs (37.5%) cleaved abnormally. Thereafter, 9.4～19.1%, 13.9% of the total number of eggs, became normal tail-bud embryos, 9.0～17.7%, 12.9%, hatched normally and 9.0～17.7%, 12.4%, began to eat normally. Eventually, 5.6～15.7%, 10.1% of the total number of eggs, attained completion of metamorphosis. This percentage of normally metamorphosed frogs corresponds to 55.4% of the normally cleaved eggs. In two matings with the remaining two males (Nos. 4 and 5), 7.1% of 522 eggs in total, cleaved normally, while 41 eggs (7.9%) cleaved abnormally. All the normally cleaved eggs died by the gastrula stage. The abnormally cleaved eggs all died during the cleavage stage (Table 20).

c. Male intraspecific hybrids, *rid* S♀ × *rid* T♂

In 1978, five 1-year-old males (Nos. 1～5) obtained from a mating, *rid* S♀, No. 1 × *rid* T♂, No. 2, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 8 and 9) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. It was found that in three matings with three males (Nos. 2～4), 19.1～80.3% of the respective number of eggs, 43.8% of 564 eggs in total, cleaved normally, while 55 eggs (9.8%) cleaved abnormally. Thereafter, 19.1～72.8%, 41.3% of the total number of eggs, became normal tail-bud embryos, 18.3～70.5%, 40.1%, hatched normally, 16.3～65.3%, 37.4%, began to eat normally, and 14.4～61.3%, 35.3%, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 80.6% of the normally cleaved

TABLE 20

Reproductive capacity of male hybrids between a female *Rana ridibunda* from Soviet Union and five kinds of males

Year	Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male						
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 6, 7	77 (*rid* $S_1 \times$ *rid* F_3) No. 1	234	49 (20.9%)	28 (12.0%)	25 (10.7%)	21 (9.0%)	13 (5.6%)
		77 (*rid* $S_1 \times$ *rid* F_3) No. 2	234	29 (12.4%)	22 (9.4%)	21 (9.0%)	21 (9.0%)	18 (7.7%)
		77 (*rid* $S_1 \times$ *rid* F_3) No. 3	293	61 (20.8%)	56 (19.1%)	52 (17.7%)	52 (17.7%)	46 (15.7%)
		77 (*rid* $S_1 \times$ *rid* F_3) No. 4	267	20 (7.5%)	0	0	0	0
		77 (*rid* $S_1 \times$ *rid* F_3) No. 5	255	17 (6.7%)	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 8, 9	77 (*rid* $S_1 \times$ *rid* T_2) No. 2	134	59 (44.0%)	58 (43.3%)	57 (42.5%)	56 (41.8%)	56 (41.8%)
		77 (*rid* $S_1 \times$ *rid* T_2) No. 3	257	49 (19.1%)	49 (19.1%)	47 (18.3%)	42 (16.3%)	37 (14.4%)
		77 (*rid* $S_1 \times$ *rid* T_2) No. 4	173	139 (80.3%)	126 (72.8%)	122 (70.5%)	113 (65.3%)	106 (61.3%)
		77 (*rid* $S_1 \times$ *rid* T_2) Nos. 1, 5	416	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) No. 10	77 (*rid* $S_1 \times$ *les* L_3) No. 2	262	78 (29.8%)	55 (21.0%)	54 (20.6%)	54 (20.6%)	51 (19.5%)
		77 (*rid* $S_1 \times$ *les* L_3) Nos. 1, 3	403	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 9, 10	77 (*rid* $S_1 \times$ *les* I_1) Nos. 1～5	1069	0	0	0	0	0
1978	76 (*les* $L_3 \times$ *les* L_2) Nos. 11, 12	77 (*rid* $S_1 \times$ *esc* G_1) No. 1	259	0	0	0	0	0
		77 (*rid* $S_1 \times$ *esc* G_1) No. 2	281	0	0	0	0	0
		77 (*rid* $S_1 \times$ *esc* G_1) No. 3	216	130 (60.2%)	110 (50.9%)	101 (46.8%)	95 (44.0%)	88 (40.7%)
		77 (*rid* $S_1 \times$ *esc* G_1) No. 4	237	0	0	0	0	0

eggs. In two matings with the remaining two males (Nos. 1 and 5), none of 416 eggs in total, cleaved normally (Table 20).

d. Male interspecific hybrids, *rid* S♀ × *les* L♂

In 1978, three 1-year-old male hybrids (Nos. 1～3) obtained from a mating, *rid* S♀, No. 1 × *les* L♂, No. 3, were mated with a 2-year-old female *Rana lessonae* from Luxembourg (No. 10) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. It was found that none of 403 eggs cleaved normally in two matings with two males (Nos. 1 and 3), while 43.2% cleaved abnormally. All the abnormally cleaved eggs died during the cleavage stage. In another mating with male No. 2, 29.8% of 262 eggs cleaved normally, and 61 eggs (23.3%) cleaved abnormally. While all the abnormally cleaved eggs died during the cleavage stage, most of the normally cleaved eggs developed normally and 21.0% became normal tail-bud embryos. Thereafter, 20.6% hatched normally and 19.5% attained completion of metamorphosis. This percentage of normally metamorphosed frogs corresponds to 65.4% of the normally cleaved eggs (Table 20).

e. Male interspecific hybrids, *rid* S♀ × *les* I♂

In 1978, five 1-year-old male hybrids (Nos. 1～5) obtained from a mating, *rid* S♀, No. 1 × *les* I♂, No. 1, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 9 and 10) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. The results showed that none of 1069 eggs in total cleaved normally. Although 19 (1.8%) eggs cleaved abnormally in three matings with three males (Nos. 1, 3 and 4), all these eggs died during the cleavage stage (Table 20).

f. Male interspecific hybrids, *rid* S♀ × *esc* G♂

In 1978, four 1-year-old male hybrids (Nos. 1～4) obtained from a mating, *rid* S♀, No. 1 × *esc* G♂, No. 1, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 11 and 12) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. Of the four males, two (Nos. 1 and 3) were of the RR-type and the other two (Nos. 2 and 4) were of the RL-type. It was found that in two matings with two RL-type males (Nos. 2 and 4), none of 518 eggs cleaved normally, while 51 eggs (9.8%) cleaved abnormally and died during the cleavage stage. In another mating with one (No. 1) of the RR-type males, none of 259 eggs cleaved normally, while 66 eggs (25.5%) cleaved abnormally and died during the cleavage stage. In the mating with the remaining RR-type male (No. 3), 60.2% of 216 eggs cleaved normally and 25 eggs (11.6%) cleaved abnormally. All of the latter died during the cleavage stage. Of the normally cleaved eggs, 9.3% died by the tail-bud stage, 4.2% died at the hatching stage, 2.8% died without taking food, and 3.2% died by the stage of completion of metamorphosis. Of the total eggs, 50.9%, 46.8%, 44.0% and 40.7% became normal tail-bud embryos, hatched tadpoles, feeding tadpoles and metamorphosed frogs, respectively. The percentage of metamorphosed frogs corresponds to 67.7% of the normally cleaved eggs (Table 20).

VII. Reproductive capacity of female hybrids

1. Female interspecific hybrids, *les* L♀ × *rid* F♂

In 1977, when seven 2-year-old female hybrids obtained from a mating, *les* L♀, No. 1 × *rid* F♂, No. 1, were injected with bullfrog pituitaries, normal ovulation occurred in five (Nos. 1～5) of them. All the eggs obtained from these five females were normal and uniform in size.

In 1978, when five 3-year-old female hybrids obtained from the foregoing mating were injected with bullfrog pituitaries, normal ovulation occurred in four (Nos. 6～9) of the hybrids. While three females (Nos. 6, 8 and 9) laid eggs which were normal and uniform in size, female No. 7 laid a mixture of large and normal-size eggs. The large eggs occupied about 6% of the total number of eggs. When eight 2-year-old females obtained from a mating, *les* L♀, No. 2 × *rid* F♂, No. 2, were injected with bullfrog pituitaries, normal ovulation occurred in four females (Nos. 10～13). While three of them laid normal-size eggs alone, female No. 13 laid a mixture of large and normal-size eggs, although the large eggs occupied only

TABLE 21

Reproductive capacity of female hybrids between female *Rana lessonae* from Luxembourg and male *Rana ridibunda* from France or Turkey

Year	Parents		Egg size	No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male							
1977	75 (*les* $L_1 \times$ *rid* F_1) No. 1	75 (*les* $L_1 \times$ *les* L_1) No. 1	Normal	264	212 (80.3%)	194 (73.5%)	180 (68.2%)	172 (65.2%)	141 (53.4%)
	75 (*les* $L_1 \times$ *rid* F_1) No. 2	75 (*les* $L_1 \times$ *les* L_1) No. 2	Normal	325	245 (75.4%)	211 (64.9%)	196 (60.3%)	184 (56.6%)	135 (41.5%)
	75 (*les* $L_1 \times$ *rid* F_1) No. 3	75 (*les* $L_1 \times$ *les* L_1) No. 3	Normal	299	147 (49.2%)	132 (44.1%)	127 (42.5%)	113 (37.8%)	102 (34.1%)
	75 (*les* $L_1 \times$ *rid* F_1) No. 4	75 (*les* $L_1 \times$ *les* L_1) No. 4	Normal	286	219 (76.6%)	176 (61.5%)	162 (56.6%)	147 (51.4%)	134 (46.9%)
	75 (*les* $L_1 \times$ *rid* F_1) No. 5		Normal	320	266 (83.1%)	214 (66.9%)	199 (62.2%)	172 (53.8%)	158 (49.4%)
1978	75 (*les* $L_1 \times$ *rid* F_1) No. 6	76 (*les* $L_2 \times$ *les* L_2) No. 5	Normal	375	370 (98.7%)	357 (95.2%)	317 (84.5%)	269 (71.7%)	228 (60.8%)
	75 (*les* $L_1 \times$ *rid* F_1) No. 7		Normal	420	412 (98.1%)	395 (94.0%)	318 (75.7%)	270 (64.3%)	206 (49.0%)
			Large	26	26 (100%)	24 (92.3%)	13 (50.0%)	11 (42.3%)	11 (42.3%)
	75 (*les* $L_1 \times$ *rid* F_1) No. 8	76 (*les* $L_2 \times$ *les* L_2) No. 6	Normal	277	184 (66.4%)	179 (64.6%)	172 (62.1%)	157 (56.7%)	149 (53.8%)
	75 (*les* $L_1 \times$ *rid* F_1) No. 9		Normal	354	342 (96.6%)	331 (93.5%)	236 (66.7%)	160 (45.2%)	139 (39.3%)
	76 (*les* $L_2 \times$ *rid* F_2) No. 10	76 (*les* $L_2 \times$ *les* L_2) No. 7	Normal	338	158 (46.7%)	136 (40.2%)	108 (32.0%)	84 (24.9%)	73 (21.6%)
	76 (*les* $L_2 \times$ *rid* F_2) No. 11		Normal	447	103 (23.0%)	83 (18.6%)	71 (15.9%)	31 (6.9%)	31 (6.9%)
	76 (*les* $L_2 \times$ *rid* F_2) No. 12	76 (*les* $L_2 \times$ *les* L_2) No. 8	Normal	413	392 (94.9%)	376 (91.0%)	161 (39.0%)	70 (16.9%)	66 (16.0%)
	76 (*les* $L_2 \times$ *rid* F_2) No. 13		Normal	462	408 (88.3%)	380 (82.3%)	290 (62.8%)	230 (49.8%)	167 (36.1%)
			Large	4	4 (100%)	3 (75.0%)	3 (75.0%)	3 (75.0%)	2 (50.0%)
	76 (*les* $L_3 \times$ *rid* F_2) No. 14	76 (*les* $L_3 \times$ *les* L_2) No. 9	Normal	404	401 (99.3%)	366 (90.6%)	346 (85.6%)	315 (78.0%)	281 (69.6%)
	76 (*les* $L_3 \times$ *rid* F_2) No. 15		Normal	276	124 (44.9%)	115 (41.7%)	39 (14.1%)	17 (6.2%)	14 (5.1%)
			Large	84	50 (59.5%)	45 (53.6%)	18 (21.4%)	13 (15.5%)	11 (13.1%)
	76 (*les* $L_3 \times$ *rid* F_2) No. 16		Normal	424	371 (87.5%)	321 (75.7%)	210 (49.5%)	106 (25.0%)	77 (18.2%)
			Large	22	22 (100%)	22 (100%)	16 (72.7%)	13 (59.1%)	13 (59.1%)
	76 (*les* $L_3 \times$ *rid* F_2) No. 17	76 (*les* $L_3 \times$ *les* L_2) No. 10	Normal	251	127 (50.6%)	111 (44.2%)	105 (41.8%)	104 (41.4%)	103 (41.0%)
			Large	65	23 (35.4%)	23 (35.4%)	21 (32.3%)	20 (30.8%)	20 (30.8%)
	76 (*les* $L_3 \times$ *rid* F_2) No. 18		Normal	398	224 (56.3%)	222 (55.8%)	181 (45.5%)	144 (36.2%)	131 (32.9%)
			Large	41	33 (80.5%)	27 (65.9%)	24 (58.5%)	24 (58.5%)	24 (58.5%)
	76 (*les* $L_3 \times$ *rid* F_2) No. 19		Normal	304	212 (69.7%)	148 (48.7%)	131 (43.1%)	120 (39.5%)	91 (29.9%)
			Large	34	26 (76.5%)	17 (50.0%)	15 (44.1%)	12 (35.3%)	12 (35.3%)
1978	76 (*les* $L_2 \times$ *rid* T_1) No. 1	76 (*les* $L_3 \times$ *les* I_2) No. 11	Normal	352	37 (10.5%)	23 (6.5%)	17 (4.8%)	15 (4.3%)	13 (3.7%)
			Large	105	14 (13.3%)	14 (13.3%)	12 (11.4%)	11 (10.5%)	9 (8.6%)
	76 (*les* $L_3 \times$ *rid* T_1) No. 2		Normal	373	134 (35.9%)	124 (33.2%)	93 (24.9%)	42 (11.3%)	36 (9.7%)
			Large	143	75 (52.4%)	36 (25.2%)	31 (21.7%)	25 (17.5%)	25 (17.5%)
	76 (*les* $L_3 \times$ *rid* T_1) No. 3		Normal	294	152 (51.7%)	112 (38.1%)	97 (33.0%)	71 (24.1%)	38 (12.9%)
			Large	172	127 (73.8%)	67 (39.0%)	65 (37.8%)	44 (25.6%)	40 (23.3%)

about 1% of the total number of eggs. When eight 2-year-old females obtained from a mating, *les* L♀, No. 3×*rid* F♂, No. 2, were injected with bullfrog pituitaries, normal ovulation occurred in six (Nos. 14~19) of them. While female No. 14 laid normal-size eggs alone, the other five (Nos. 15~19) laid a mixture of large and normal-size eggs. The large eggs occupied about 5~23% of the respective number of eggs. In total, 19 females (Nos. 1~19) laid 6637 (96%) normal-size eggs, while seven of them (Nos. 7, 13, 15~19) laid 276 (4%) large eggs in addition.

These 19 females were mated with a total of 10 male *Rana lessonae* including four 2-year-old males (Nos. 1~4) obtained in 1975 from a mating, *les* L♀, No. 1× *les* L♂, No. 1, and six 2-year-old males obtained in 1976 from matings, *les* L♀, Nos. 2 and 3×*les* L♂, No. 2. It was found that 74.1% of the normal-size eggs, 23.0~99.3% of the respective number of eggs, cleaved normally. While 3.0% and 4.1% died by the neurula and the tail-bud stage, respectively, 18.6~95.2% of the respective number of eggs, 67.0% of the total number of eggs, became normal tail-bud embryos, and 14.1~85.6%, 53.5%, hatched normally. Thereafter, 6.2~78.0%, 43.2% of the total number of eggs, began to eat normally, and 5.1~69.6%, 36.6%, completed metamorphosis, while 10.3% died of edema or underdevelopment without taking food and 6.6% died by the stage of completion of metamorphosis. The percentage of metamorphosed frogs corresponds to 49.3% of the normally cleaved eggs (Table 21).

Of the 276 large eggs produced by the seven females, 35.4~100%, 66.7% of the total number of eggs, cleaved normally, while 46 eggs (16.7%) cleaved abnormally. While eight and 15 of the normally cleaved eggs died of abnormalities by the neurula and the tail-bud stage, respectively, 35.4~100%, 58.3% of the total number of eggs, became normal tail-bud embryos, 21.4~75.0%, 39.9%, hatched normally, and 15.5~75.0%, 34.8%, began to eat normally. At the hatching stage, 51 embryos became abnormal and died. Of the normally hatched tadpoles, 14 died without taking food. Eventually, 13.1~59.1%, 33.7% of the total number of eggs, attained completion of metamorphosis, and three tadpoles died by this stage. The percentage of normally metamorphosed frogs corresponds to 50.5% of the normally cleaved eggs (Table 21).

2. Female interspecific hybrids, *les* L♀×*rid* T♂

In 1978, when five 2-year-old females obtained from a mating, *les* L♀, No. 2× *rid* T♂, No. 1, were injected with bullfrog pituitaries, normal ovulation occurred in one (No. 1) of them. This female laid a mixture of large and normal-size eggs. The large eggs occupied about 30% of the total number of eggs. It was confirmed by laparotomy that the other four females possessed degenerative ovaries. In these ovaries, only a few eggs were found. When ten 2-year-old females obtained from a mating, *les* L♀, No. 3×*rid* T♂, No. 1, were injected with bullfrog pituitaries, ovulation occurred in two (Nos. 2 and 3) of them. The other eight females revealed by laparotomy that the ovaries of five females were degenerated, while those of the remaining three females contained several tens of ill-developed eggs.

Females Nos. 2 and 3 laid a mixture of large and normal-size eggs. In Nos. 2 and 3, the large eggs occupied about 30% and 40% of the total number of eggs, respectively.

The normal-size and the large eggs of females Nos. 1~3 were inseminated with sperm of a 2-year-old male (No. 11) obtained from a mating, *les* L♀, No. 3× *les* L♂, No. 2. The results showed that 10.5~51.7% of the respective number of normal-size eggs, 31.7% of 1019 eggs in total, cleaved normally. While 223 eggs (21.9%) cleaved abnormally and died during the cleavage stage. Thereafter, 6.5~38.1%, 25.4% of the total number of eggs, became normal tail-bud embryos, and 4.8~33.0%, 20.3%, hatched normally. Of the normally cleaved eggs, 40 died of abnormalities by the neurula stage, and 24 and 52 died of edema or some other abnormalities at the tail-bud and the hatching stage, respectively. Thereafter, 4.3~24.1%, 12.6%, began to eat normally, and eventually, 3.7~12.9%, 8.5% of the total number of eggs, attained completion of metamorphosis, while 4.0% died of underdevelopment or some other abnormalities by the stage of completion of metamorphosis. The percentage of metamorphosed frogs corresponds to 26.9% of the normally cleaved eggs. Of 420 large eggs, 51.4% cleaved normally, 27.9% became normal tail-bud embryos, 25.7% hatched normally and 19.0% began to eat normally. Eventually, 17.6% attained completion of metamorphosis. This percentage corresponds to 34.3% of the normally cleaved eggs (Table 21).

3. Female intraspecific hybrids, *les* L♀ × *les* I♂

In 1978, six 1-year-old females, including three (Nos. 1~3) obtained from a mating, *les* L♀, No. 4× *les* I♂, No. 1, and three (Nos. 4~6) obtained from a mating, *les* L♀, No. 5× *les* I♂, No. 2, were injected with bullfrog pituitaries. The results showed that ovulation occurred in all the six females. When these six females were mated with four 1-year-old males (Nos. 12~15) obtained from a mating, *les* L♀, No. 4× *les* L♂, No. 3, 2.8~94.4% of the respective number of eggs, 57.2% of 1409 eggs in total, cleaved normally, and 282 eggs (20.0%) cleaved abnormally. All of the latter died during the cleavage stage. Four and 23 of the normally cleaved eggs died by the neurula and the tail-bud stage, respectively. Of the respective number of eggs, 1.9~92.4%, 55.3% of the total number of eggs, became normal tail-bud embryos, and 1.9~90.8%, 54.2%, hatched normally, while 1.1% became abnormal at the hatching stage. Thereafter, 1.9~85.9%, 51.6%, began to eat normally, and 1.9~82.7%, 49.4% of the total number of eggs, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 86.4% of the normally cleaved eggs (Table 22).

In the mating of female No. 2, only 2.8% of 363 eggs cleaved normally, and 51.2% cleaved abnormally. This paucity of normally cleaved eggs was considered to be attributable to overripeness of eggs.

4. Female interspecific hybrids, *les* L♀ × *esc* G♂

In 1978, three 1-year-old female hybrids (Nos. 1~3) obtained from a mating,

TABLE 22

Reproductive capacity of female hybrids between female *Rana lessonae* from Luxembourg or Italy and three kinds of males

Year	Parents		No. of eggs	No. of normal cleavages	No. of normal tail-bud embryos	No. of normally hatched tadpoles	No. of normally feeding tadpoles	No. of metamorphosed frogs
	Female	Male						
1978	77 (*les* $L_4 \times$ *les* I_1) No. 1	77 (*les* $L_4 \times$ *les* L_3) Nos. 12, 13	249	235 (94.4%)	230 (92.4%)	226 (90.8%)	214 (85.9%)	206 (82.7%)
	77 (*les* $L_4 \times$ *les* I_1) No. 2		363	10 (2.8%)	7 (1.9%)	7 (1.9%)	7 (1.9%)	7 (1.9%)
	77 (*les* $L_4 \times$ *les* I_1) No. 3		308	156 (50.6%)	152 (49.4%)	151 (49.0%)	139 (45.1%)	129 (41.9%)
	77 (*les* $L_5 \times$ *les* I_2) No. 4	77 (*les* $L_4 \times$ *les* L_3) Nos. 14, 15	116	103 (88.8%)	97 (83.6%)	96 (82.8%)	94 (81.0%)	90 (77.6%)
	77 (*les* $L_5 \times$ *les* I_2) No. 5		199	165 (82.9%)	159 (79.9%)	154 (77.4%)	152 (76.4%)	148 (74.4%)
	77 (*les* $L_5 \times$ *les* I_2) No. 6		174	137 (78.7%)	134 (77.0%)	129 (74.1%)	121 (69.5%)	116 (66.7%)
1978	77 (*les* $L_4 \times$ *esc* G_1) No. 1	77 (*les* $L_4 \times$ *les* L_3) No. 16	317	160 (50.5%)	131 (41.3%)	112 (35.3%)	76 (24.0%)	54 (17.0%)
	77 (*les* $L_4 \times$ *esc* G_1) No. 2		330	151 (45.8%)	103 (31.2%)	81 (24.5%)	62 (18.8%)	42 (12.7%)
1978	77 (*les* $I_1 \times$ *les* L_3) No. 1	77 (*les* $L_4 \times$ *les* L_3) Nos. 12, 13	267	204 (76.4%)	192 (71.9%)	187 (70.0%)	141 (52.8%)	133 (49.8%)
	77 (*les* $I_1 \times$ *les* L_3) No. 2		254	189 (74.4%)	177 (69.7%)	152 (59.8%)	143 (56.3%)	121 (47.6%)
	77 (*les* $I_2 \times$ *les* L_3) No. 3	77 (*les* $L_4 \times$ *les* L_3) Nos. 14, 15	218	121 (55.5%)	84 (38.5%)	70 (32.1%)	62 (28.4%)	55 (25.2%)
	77 (*les* $I_2 \times$ *les* L_3) No. 4		135	121 (89.6%)	116 (85.9%)	107 (79.3%)	105 (77.8%)	103 (76.3%)
	77 (*les* $I_2 \times$ *les* L_3) No. 5		126	97 (77.0%)	95 (75.4%)	93 (73.8%)	90 (71.4%)	87 (69.0%)
1978	77 (*les* $I_1 \times$ *esc* G_1) No. 1	77 (*les* $L_5 \times$ *les* L_4) No. 17	464	162 (34.9%)	147 (31.7%)	140 (30.2%)	128 (27.6%)	125 (26.9%)
	77 (*les* $I_1 \times$ *esc* G_1) No. 2		328	73 (22.3%)	50 (15.2%)	42 (12.8%)	36 (11.0%)	22 (6.7%)
	77 (*les* $I_1 \times$ *esc* G_1) No. 3		486	371 (76.3%)	356 (73.3%)	302 (62.1%)	274 (56.4%)	253 (52.1%)
	77 (*les* $I_2 \times$ *esc* G_1) No. 4	77 (*les* $L_5 \times$ *les* L_4) No. 18	110	99 (90.0%)	97 (88.2%)	96 (87.3%)	84 (76.4%)	68 (61.8%)
	77 (*les* $I_2 \times$ *esc* G_1) No. 5		326	150 (46.0%)	121 (37.1%)	114 (35.0%)	98 (30.1%)	94 (28.8%)
	77 (*les* $I_2 \times$ *esc* G_1) No. 6		233	112 (48.1%)	93 (39.9%)	78 (33.5%)	74 (31.8%)	67 (28.8%)

les L♀, No. 4 × *esc* G♂, No. 1, were injected with bullfrog pituitaries. The results showed that normal ovulation occurred in two (Nos. 1 and 2) of them. The eggs of these two females were small and uniform in size in contrast to those of females obtained from matings between female *Rana lessonae* from Luxembourg and male *Rana ridibunda* from France or Turkey. The two female hybrids were mated with a 1-year-old male *Rana lessonae* (No. 16) obtained from a mating, *les* L♀, No. 4 × *les* L♂, No. 3. It was found that 48.1% of 647 eggs in total cleaved normally. While 22.7% of 317 eggs from female No. 1 and 39.4% of 330 eggs from female No. 2 cleaved abnormally, all these abnormally cleaved eggs died by the gastrula stage. Of the normally cleaved eggs, 28, 49 and 41 died of abnormalities by the neurula, the tail-bud and the hatching stage, respectively. Of the total number of eggs, 36.2% became normal tail-bud embryos and 29.8% hatched normally. While 8.5% died without taking food and 6.5% died during

metamorphosis, 21.3% began to eat normally and 14.8% attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 30.9% of the normally cleaved eggs (Table 22).

5. Female intraspecific hybrids, *les* I♀ × *les* L♂

In 1978, three 1-year-old females obtained from a mating, *les* I♀, No. 1 × *les* L♂, No. 3, were injected with bullfrog pituitaries. The results showed that normal ovulation occurred in two (Nos. 1 and 2) of them. When three other 1-year-old females (Nos. 3~5) obtained from a mating, *les* I ♀, No. 2 × *les* L♂, No. 3, were injected with bullfrog pituitaries, ovulation occurred in all the females. These five females were mated with four 1-year-old male *Rana lessonae* (Nos. 12~15) obtained from a mating, *les* L♀, No. 4 × *les* L♂, No. 3. It was found that 55.5~89.6% of the respective number of eggs, 73.2% of 1000 eggs in total, cleaved normally, while 3.4% cleaved abnormally and almost died during the cleavage stage. Of the respective number of eggs, 38.5~85.9%, 66.4% of the total number of eggs, became normal tail-bud embryos, and 32.1~79.3%, 60.9%, hatched normally. While 5.5% died at the hatching stage, 6.8% died without taking food, and 4.2% died during metamorphosis, 28.4~77.8%, 54.1%, began to eat normally, and eventually, 25.2~76.3%, 49.9% of the total number of eggs, attained completion of metamorphosis. This percentage of metamorphosed frogs corresponds to 68.2% of the normally cleaved eggs (Table 22).

6. Female interspecific hybrids, *les* I♀ × *esc* G♂

In 1978, 24 one-year-old female hybrids were produced from a mating, *les* I♀, No. 1 × *esc* G♂, No. 1. When the best grown eight of these females were injected with bullfrog pituitaries, normal ovulation occurred in three (Nos. 1~3) females. While one of the other five females laid several ten eggs, no ovulation occurred in the remaining four. The latter four revealed by laparotomy that one of them had ovaries with numerous normal eggs and three had degenerative ovaries, although there were well-developed oviducts. When the best grown 10 of 36 1-year-old females obtained from a mating, *les* I♀, No. 2 × *esc* G♂, No. 1, were injected with bullfrog pituitaries, normal ovulation occurred in three (Nos. 4~6) of them, while it did not occur in the other seven. It was found by laparotomy that five of the latter seven had somewhat underdeveloped ovaries with normal-size eggs and the remaining two had almost degenerative ovaries.

The six females (Nos. 1~6) in which normal ovulation occurred were mated with two male *Rana lessonae* from Luxembourg (Nos. 17 and 18) obtained from a mating, *les* L♀, No. 5 × *les* L♂, No. 4. The results showed that 22.3~90.0% of the respective number of eggs, 49.7% of 1947 eggs in total, cleaved normally, and 326 eggs (16.7%) cleaved abnormally. The abnormally cleaved eggs all died by the blastula stage. Of the normally cleaved eggs, 1.7% and 3.6% died of abnormalities at the gastrula or neurula stage and the tail-bud stage, respectively. In the six matings, 15.2~88.2% of the respective number of eggs, 44.4% of the total number of eggs, became normal tail-bud embryos and 12.8~87.3%, 39.7%,

hatched normally, while 4.7% became abnormal at the hatching stage. Thereafter, 11.0~76.4%, 35.6%, began to eat normally and eventually, 6.7~61.8%, 32.3% of the total number of eggs, attained completion of metamorphosis, while 4.0% died without taking food and 3.3% died by the stage of completion of metamorphosis. The percentage of metamorphosed frogs corresponds to 65.0% of the normally cleaved eggs (Table 22).

VIII. Sex of the offspring of male hybrids

1. Male hybrids between female *Rana lessonae* from Luxembourg and two kinds of males

a. Controls, *les* L♀ × *les* L♂

As stated in Chapter VI, 21 control matings in total were made in 1977, 1978 and 1980 by using 15 females (Nos. 1~15) and 21 males (Nos. 1~21). From these matings, 1397 frogs were produced. Sex was not determined in 233 of these frogs, owing to their postmortem changes. Of the remaining 1164 frogs, 318 died within one year, mostly within three months after metamorphosis. They consisted of 161 females and 157 (49.4%) males. Of 846 frogs which lived longer than one year, 419 were females and 427 (50.5%) were males. In total, 580 of 1164 frogs were females and 584 (50.2%) were males. The smallest rate of males was 41.8% in the mating with male No. 21, while the largest rate was 55.4% in the mating with male No. 4 (Table 23).

b. Offspring of male intraspecific hybrids, *les* L♀ × *les* I♂

In 1978, six matings were made between six females (Nos. 3~8) obtained from matings, *les* L♀, Nos. 1 and 3 × *les* L♂, Nos. 1 and 2, and six males (Nos. 1~3, 6~8) obtained from matings, *les* L♀, Nos. 4 and 5 × *les* L♂, Nos. 1 and 2, as described in Chapter VI. From three matings with males Nos. 1, 2 and 7, 115 frogs were produced. When chromosomes were counted at the tadpole stage in 55 of them, it was found that these frogs were all diploids. Sex was examined in 111 frogs. The results showed that 81 of 83 frogs which died within six months after metamorphosis were females and two (2.4%) were males. Of 28 mature frogs which lived longer than one year, 21 were females and seven (25.0%) were males. In total, 102 of the 111 frogs were females and 9 (8.1%) were males (Table 24). Thus, it is assumed that the three male parents were probably sex-reversed genetic females.

From the other three matings with males Nos. 3, 6 and 8, 176 frogs were produced. When chromosomes were counted at the tadpole stage in 60 of them, it was found that all of them were diploids. When sex was examined in 168 frogs, 61.0%, 49.4% and 53.3% of the respective number of frogs in the three matings were males. In total, 77 were females and 91 (54.2%) were males (Table 24).

c. Offspring of male interspecific hybrids, *les* L♀ × *esc* G♂

In 1978, five matings were made between four females (Nos. 9~12) obtained

TABLE 23
Sex and external appearance of the control offspring between female and male *Rana lessonae* from Luxembourg

Year	Parents		No. of metamorphosed frogs	Sex of immature frogs		Sex of mature frogs		Sex of all frogs examined			External appearance (Type)
	Female	Male		♀	♂	♀	♂	No. of frogs	♀	♂ (%)	
1977	75 (*les* $L_1 \times$ *les* L_1) No. 1	75 (*les* $L_1 \times$ *les* L_1) No. 1	61	2	1	19	24	46	21	25 (54.3)	LL
		75 (*les* $L_1 \times$ *les* L_1) No. 2	73	0	3	26	22	51	26	25 (49.0)	LL
	75 (*les* $L_1 \times$ *les* L_1) No. 2	75 (*les* $L_1 \times$ *les* L_1) No. 3	58	1	1	20	23	45	21	24 (53.3)	LL
		75 (*les* $L_1 \times$ *les* L_1) No. 4	85	1	0	32	41	74	33	41 (55.4)	LL
1978	75 (*les* $L_1 \times$ *les* L_1) No. 3	76 (*les* $L_2 \times$ *les* L_2) No. 5	86	1	3	34	36	74	35	39 (52.7)	LL
		76 (*les* $L_2 \times$ *les* L_2) No. 6	52	22	20	0	0	42	22	20 (47.6)	LL
	75 (*les* $L_1 \times$ *les* L_1) No. 4	76 (*les* $L_2 \times$ *les* L_2) No. 7	99	0	0	43	40	83	43	40 (48.2)	LL
		76 (*les* $L_2 \times$ *les* L_2) No. 8	29	12	13	0	0	25	12	13 (52.0)	LL
	75 (*les* $L_1 \times$ *les* L_1) No. 5	76 (*les* $L_3 \times$ *les* L_2) No. 9	64	0	0	30	32	62	30	32 (51.6)	LL
		76 (*les* $L_3 \times$ *les* L_2) No. 10	58	28	27	0	0	55	28	27 (49.1)	LL
		76 (*les* $L_3 \times$ *les* L_2) No. 11	56	19	18	0	0	37	19	18 (48.6)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 6	77 (*les* $L_4 \times$ *les* L_3) No. 12	59	12	10	0	0	22	12	10 (45.5)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 7	77 (*les* $L_4 \times$ *les* L_3) No. 13	89	4	2	33	37	76	37	39 (51.3)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 8	77 (*les* $L_4 \times$ *les* L_3) No. 14	78	5	3	31	34	73	36	37 (50.7)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 9	77 (*les* $L_4 \times$ *les* L_3) No. 15	51	25	26	0	0	51	25	26 (51.0)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 10	77 (*les* $L_4 \times$ *les* L_3) No. 16	33	0	1	17	13	31	17	14 (45.2)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 11	77 (*les* $L_5 \times$ *les* L_4) No. 17	65	0	0	33	29	62	33	29 (46.8)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 12	77 (*les* $L_5 \times$ *les* L_4) No. 18	90	9	11	26	27	73	35	38 (52.1)	LL
1980	77 (*les* $L_4 \times$ *les* L_3) No. 13	77 (*les* $L_5 \times$ *les* L_4) No. 19	74	7	11	23	20	61	30	31 (50.8)	LL
	77 (*les* $L_4 \times$ *les* L_3) No. 14	77 (*les* $L_5 \times$ *les* L_4) No. 20	65	1	2	25	26	54	26	28 (51.9)	LL
	77 (*les* $L_4 \times$ *les* L_3) No. 15	77 (*les* $L_5 \times$ *les* L_4) No. 21	72	12	5	27	23	67	39	28 (41.8)	LL
Total			1397	161	157	419	427	1164	580	584 (50.2)	

from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, and five LL-type males (Nos. 1~5) obtained from a mating, *les* L♀, No. 4 × *esc* G♂, No. 1, as described in Chapter VI. Chromosomes were counted at the tadpole stage in 100 of 315 metamorphosed frogs, and all of them were diploids. Sex was examined in 288 frogs. The results showed that 19 of 36 frogs which died within three months after metamorphosis were females and 17 (47.2%) were males. Of 252 mature frogs which were all of the LL-type and lived longer than one year, 105 were females and 147 (58.3%) were males. In the five matings, 51.7~65.7% of the respective number of frogs were males. In total, 124 of the 288 frogs were females and 164 (56.9%) were males (Table 24).

In 1980, three 3-year-old males including two LR-type males (Nos. 6 and 7) and one LL-type male (No. 8) obtained in 1977 from a mating, *les* L♀, No. 4 ×

TABLE 24

Sex and external appearance of the offspring of male hybrids between female *Rana lessonae* from Luxembourg and two kinds of males

Year	Parents		No. of metamorphosed frogs	Sex of immature frogs		Sex of mature frogs		Sex of all frogs examined			External appearance (Type)
	Female	Male		♀	♂	♀	♂	No. of frogs	♀	♂ (%)	
1978	75 (*les* $L_1 \times$ *les* L_1) No. 3	77 (*les* $L_4 \times$ *les* I_1) No. 1	10	10	0	0	0	10	10	0	LL
	75 (*les* $L_1 \times$ *les* L_1) No. 4	77 (*les* $L_4 \times$ *les* I_1) No. 2	30	0	0	21	7	28	21	7 (25.0)	LL
	75 (*les* $L_1 \times$ *les* L_1) No. 5	77 (*les* $L_4 \times$ *les* I_1) No. 3	61	1	2	22	34	59	23	36 (61.0)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 6	77 (*les* $L_5 \times$ *les* I_2) No. 6	83	3	4	37	35	79	40	39 (49.4)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 7	77 (*les* $L_5 \times$ *les* I_2) No. 7	75	71	2	0	0	73	71	2 (2.7)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 8	77 (*les* $L_5 \times$ *les* I_2) No. 8	32	14	16	0	0	30	14	16 (53.3)	LL
1978	76 (*les* $L_3 \times$ *les* L_2) No. 9	77 (*les* $L_4 \times$ *esc* G_1) No. 1	92	3	3	39	42	87	42	45 (51.7)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 10	77 (*les* $L_4 \times$ *esc* G_1) No. 2	68	2	1	23	36	62	25	37 (59.7)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 11	77 (*les* $L_4 \times$ *esc* G_1) No. 3	39	0	0	12	23	35	12	23 (65.7)	LL
	76 (*les* $L_3 \times$ *les* L_2) No. 12	77 (*les* $L_4 \times$ *esc* G_1) No. 4	79	14	13	17	27	71	31	40 (56.3)	LL
		77 (*les* $L_4 \times$ *esc* G_1) No. 5	37	0	0	14	19	33	14	19 (57.6)	LL
1980	77 (*les* $L_4 \times$ *les* L_3) No. 13	77 (*les* $L_4 \times$ *esc* G_1) No. 6	63	24	1	31	5	61	55	6 (9.8)	LR
	78 (*rid* $T_2 \times$ *rid* T_4) No. 1	77 (*les* $L_4 \times$ *esc* G_1) No. 6	90	18	1	63	7	89	81	8 (9.0)	RR
	77 (*les* $L_4 \times$ *les* L_3) No. 14	77 (*les* $L_4 \times$ *esc* G_1) No. 7	62	17	0	34	10	61	51	10 (16.4)	LR
	77 (*les* $I_2 \times$ *les* I_1) No. 11	77 (*les* $L_4 \times$ *esc* G_1) No. 7	75	26	2	30	12	70	56	14 (20.0)	LR
	78 (*rid* $T_2 \times$ *rid* T_4) No. 1	77 (*les* $L_4 \times$ *esc* G_1) No. 7	140	35	2	72	13	122	107	15 (12.3)	RR
	77 (*les* $L_4 \times$ *les* L_3) No. 15	77 (*les* $L_4 \times$ *esc* G_1) No. 8	49	0	0	18	26	44	18	26 (59.1)	LL
	77 (*les* $I_2 \times$ *les* I_1) No. 11	77 (*les* $L_4 \times$ *esc* G_1) No. 8	67	7	3	21	32	63	28	35 (55.6)	LL
	78 (*rid* $T_2 \times$ *rid* T_4) No. 1	77 (*les* $L_4 \times$ *esc* G_1) No. 8	121	10	3	37	48	98	47	51 (52.0)	RL

esc G♂, No. 1, were mated with female *Rana lessonae* from Luxembourg and Italy and female *Rana ridibunda* from Turkey. From two matings between LR-type male No. 6 and two females including a female (No. 13) obtained from a mating, *les* L♀, No. 4 × *les* L♂, No. 3, and a female (No. 1) obtained from a mating, *rid* T♀, No. 2 × *rid* T♂, No. 4, 153 metamorphosed frogs were produced. When chromosomes were counted at the tadpole stage, it was found that all these frogs were diploids. Of 44 frogs which died within six months after metamorphosis, 42 were females and two (4.5%) were males. Of 106 mature frogs which lived longer than one year, 94 were females, 12 (11.3%) were males and the sex of the remaining three was undetermined owing to postmortem changes. In total, 136 of the 150 frogs were females and 14 (9.3%) were males (Table 24).

From three matings between male No. 7 of the LR-type and three females

including one 3-year-old female (No. 14) obtained in 1977 from a mating, *les* L♀, No. 4×*les* L♂, No. 3, one 3-year-old female (No. 11) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1, and one 2-year-old female (No. 1) obtained in 1978 from a mating, *rid* T♀, No. 2×*rid* T♂, No. 4, 277 metamorphosed frogs were produced. When chromosomes were counted at the tadpole stage, all these frogs were diploids. Of 82 frogs which died within six months after metamorphosis, 78 were females and four (4.9%) were males. Of 195 mature frogs which lived longer than one year, 136 were females and 35 (20.5%) were males. The sex of the remaining 24 frogs was not determined owing to postmortem changes. In total, 214 of the 253 frogs were females and 39 (15.4%) were males. It was remarkable that the mature frogs produced from the two LR-type males by mating with female *Rana lessonae* were all of the LR-type, while the mature frogs produced by mating with a female *Rana ridibunda* were all of the RR-type. Thus, it was evident that the two LR-type males (Nos. 6 and 7) were sex-reversed genetic females and produced spermatozoa with the *Rana ridibunda*-genome.

From three matings between LL-type male No. 8 and three females including female No. 15 produced from a mating, *les* L♀, No. 4×*les* L♂, No. 3, female No. 11 obtained from a mating, *les* I♀, No. 2×*les* I♂, No. 1, and female No. 1 obtained from a mating, *rid* T♀, No. 2×*rid* T♂, No. 4, 237 frogs were produced. These frogs were diploids, as far as their chromosomes were counted. Of 205 of them, 93 were females and 112 (54.6%) were males (Table 24). The sex of the remaining 32 frogs was unknown, owing to postmortem changes. All the frogs produced by mating with female *Rana lessonae* were of the LL-type, while those produced by mating with a female *Rana ridibunda* were of the RL-type.

2. Male hybrids between female *Rana lessonae* from Italy and three kinds of males

a. Controls, *les* I♀×*les* I♂

In 1978 and 1980, 12 matings were made between 12 females (Nos. 1～12) and eight males (Nos. 1～8), as stated in Chapter VI. It was found that of 155 of 497 metamorphosed frogs which died or were killed within six months after metamorphosis, 75 were females and 80 (51.6%) were males. Of 295 mature frogs which lived longer than one year, 140 were females and 155 (52.5%) were males. In total, 215 of 450 frogs were females and 235 (52.2%) were males. The sex of the remaining 47 frogs was unknown owing to postmortem changes (Table 25).

b. Offspring of male intraspecific hybrids, *les* I♀×*les* L♂

In 1978, 10 matings were made between six females (Nos. 1～3, 7～9) obtained from matings, *les* I♀, Nos. 1 and 2×*les* I♂, No. 1, and 10 males (Nos. 1～10) obtained from matings, *les* I♀, Nos. 1 and 2×*les* L♂, No. 3, as stated in Chapter VI.

In three matings with males Nos. 2, 5 and 7 of the LL-type, 184 of 259 metamorphosed frogs which were diploids as far as the chromosomes were counted died or were killed within six months after metamorphosis. When their sex was

TABLE 25

Sex and external appearance of the offspring of male hybrids between female *Rana lessonae* from Italy and three kinds of males and the controls

Year	Parents		No. of metamorphosed frogs	Sex of immature frogs		Sex of mature frogs		Sex of all frogs examined			External appearance (Type)
	Female	Male		♀	♂	♀	♂	No. of frogs	♀	♂ (%)	
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 1～3	77 (*les* $I_1 \times$ *les* I_1) Nos. 1, 2	147	3	2	53	59	117	56	61 (52.1)	LL
	77 (*les* $I_1 \times$ *les* I_1) Nos. 4～6	77 (*les* $I_1 \times$ *les* I_1) Nos. 3, 4	88	7	10	30	34	81	37	44 (54.3)	LL
	77 (*les* $I_2 \times$ *les* I_1) Nos. 7～10	77 (*les* $I_2 \times$ *les* I_1) Nos. 5, 6	112	52	56	0	0	108	52	56 (51.9)	LL
1980	77 (*les* $I_2 \times$ *les* I_1) Nos. 11, 12	77 (*les* $I_2 \times$ *les* I_1) Nos. 7, 8	150	13	12	57	62	144	70	74 (51.4)	LL
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 1～3	77 (*les* $I_1 \times$ *les* L_3) No. 1	75	4	1	32	36	73	36	37 (50.7)	LL
		77 (*les* $I_1 \times$ *les* L_3) No. 2	70	5	0	61	3	69	66	3 (4.3)	LL
		77 (*les* $I_1 \times$ *les* L_3) No. 3	47	5	7	17	15	44	22	22 (50.0)	LL
		77 (*les* $I_1 \times$ *les* L_3) No. 4	43	19	21	0	0	40	19	21 (52.5)	LL
		77 (*les* $I_1 \times$ *les* L_3) No. 5	79	76	0	0	0	76	76	0	LL
	77 (*les* $I_2 \times$ *les* I_1) Nos. 7～9	77 (*les* $I_2 \times$ *les* L_3) No. 6	55	3	3	21	20	47	24	23 (48.9)	LL
		77 (*les* $I_2 \times$ *les* L_3) No. 7	110	102	1	0	0	103	102	1 (1.0)	LL
		77 (*les* $I_2 \times$ *les* L_3) No. 8	102	49	53	0	0	102	49	53 (52.0)	LL
		77 (*les* $I_2 \times$ *les* L_3) No. 9	97	34	36	15	11	96	49	47 (49.0)	LL
		77 (*les* $I_2 \times$ *les* L_3) No. 10	91	43	40	0	0	83	43	40 (48.2)	LL
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 1～3	77 (*les* $I_2 \times$ *rid* S_1) No. 1	8	0	0	0	4	4	0	4	LR
1978	77 (*les* $I_1 \times$ *les* I_1) Nos. 4～6	77 (*les* $I_1 \times$ *esc* G_1) No. 1	74	9	5	23	29	66	32	34 (51.5)	LL
		77 (*les* $I_1 \times$ *esc* G_1) No. 2	67	10	11	16	20	57	26	31 (54.4)	LL
		77 (*les* $I_1 \times$ *esc* G_1) No. 3	72	30	32	0	0	62	30	32 (51.6)	LL
		77 (*les* $I_1 \times$ *esc* G_1) No. 4	74	63	0	0	0	63	63	0	LR
	77 (*les* $I_2 \times$ *les* I_1) Nos. 7～9	77 (*les* $I_2 \times$ *esc* G_1) No. 6	99	7	10	46	31	94	53	41 (43.6)	LL
		77 (*les* $I_2 \times$ *esc* G_1) No. 7	103	22	26	32	20	100	54	46 (46.0)	LL
		77 (*les* $I_2 \times$ *esc* G_1) No. 8	100	29	31	19	16	95	48	47 (49.5)	LL
		77 (*les* $I_2 \times$ *esc* G_1) No. 9	88	18	17	25	23	83	43	40 (48.2)	LL
	77 (*les* $I_1 \times$ *les* I_1) Nos. 4～6	77 (*les* $I_3 \times$ *esc* G_1) No. 16	70	12	11	19	23	65	31	34 (52.3)	LL
		77 (*les* $I_3 \times$ *esc* G_1) No. 17	67	14	18	15	13	60	29	31 (51.7)	LL
		77 (*les* $I_3 \times$ *esc* G_1) No. 18	60	5	4	22	20	51	27	24 (47.1)	LL
		77 (*les* $I_3 \times$ *esc* G_1) No. 19	53	23	26	0	0	49	23	26 (53.1)	LL
		77 (*les* $I_3 \times$ *esc* G_1) No. 20	62	27	31	0	0	58	27	31 (53.4)	LL
1980	77 (*les* $I_2 \times$ *les* I_1) Nos. 11, 12	77 (*les* $I_2 \times$ *esc* G_1) No. 21	47	42	1	0	0	43	42	1 (2.3)	LR
		77 (*les* $I_2 \times$ *esc* G_1) No. 22	52	6	0	35	11	52	41	11 (21.2)	LR
		77 (*les* $I_2 \times$ *esc* G_1) No. 23	108	26	1	64	12	103	90	13 (12.6)	LR
	78 (*rid* $T_2 \times$ *rid* T_4) No. 2	77 (*les* $I_3 \times$ *esc* G_1) No. 24	79	32	0	33	2	67	65	2 (3.0)	RR
		77 (*les* $I_3 \times$ *esc* G_1) No. 25	82	26	2	48	4	80	74	6 (7.5)	RR
		77 (*les* $I_3 \times$ *esc* G_1) No. 26	36	35	0	0	0	35	35	0	RR

examined, 183 were females and only one (0.5%) was a male. Of 64 mature frogs which lived longer than one year, 61 were females and three (4.7%) were males. In total, 244 of 248 frogs were females and four (1.6%) were males. The three male parents (Nos. 2, 5 and 7) as well as the four male offspring were considered to be sex-reversed genetic females.

In seven matings with seven males, Nos. 1, 3, 4, 6, 8, 9 and 10, 510 metamorphosed frogs were produced. These frogs were all diploids as far as their chromosomes were counted. When the sex of 318 frogs which died or were killed within six months after metamorphosis was examined, it was found that 157 were females and 161 (50.6%) were males. Of 167 mature frogs which lived longer than one year, 85 were females and 82 (49.1%) were males. In total, 242 of 485

frogs were females and 243 (50.1%) were males (Table 25).

c. Offspring of male interspecific hybrids, *les* I♀ × *rid* S♂

In 1978, three matings were made between three females (Nos. 1~3) obtained from a mating, *les* I♀, No. 1 × *les* I♂, No. 1, and one male (No. 1) obtained from a mating, *les* I♀, No. 2 × *rid* S♂, No. 1. Eight frogs produced from these matings were all diploids. Four of them were LR-type males. The other four died immediately after metamorphosis and their sex was not determined owing to their postmortem changes (Table 25).

d. Offspring of male interspecific hybrids, *les* I♀ × *esc* G♂

In 1978, 12 LL-type males (Nos. 1~3, 6~9 and 16~20) obtained from matings, *les* I♀, Nos. 1~3 × *esc* G♂, No. 1, were mated with six LL-type females (Nos. 4~9) obtained from matings, *les* I♀, Nos. 1 and 2 × *les* I♂, No. 1. When chromosomes were counted at the tadpole stage in 120 of 915 frogs produced from these matings, it was found that all of them were diploids. Of 428 frogs which died or were killed within six months after metamorphosis, 206 were females and 222 (51.9%) were males. Of 412 mature frogs which lived longer than one year, 217 were females and 195 (47.3%) were males. In total, 423 of 840 frogs were females and 417 (50.2%) were males. The sex of the remaining 75 frogs could not be determined owing to postmortem changes (Table 25).

In 1978 and 1980, seven LR-type males (Nos. 4, 21~26) obtained from matings, *les* I♀, Nos. 1~3 × *esc* G♂, No. 1, were mated with five LL-type females (Nos. 4~6, 11 and 12) obtained from matings, *les* I♀, Nos. 1 and 2 × *les* I♂, No. 1 and one RR-type female (No. 2) obtained from a mating, *rid* T♀, No. 2 × *rid* T♂, No. 4, as described in Chapter VI. When chromosomes were counted at the tadpole stage in 210 of 478 frogs, all of them were diploids. Of 234 frogs which died or were killed within six months after metamorphosis, 230 were females and only four (1.7%) were males. Of 209 mature frogs which lived longer than one year, 180 were females and 29 (13.9%) were males. In total, 410 of 443 frogs were females and 33 (7.4%) were males. It is assumed that the seven LR-type male parents as well as the 33 male offspring were sex-reversed genetic females (Table 25).

On the other hand, matings between LR-type males and LL-type females always produced LR-type offspring alone, while matings between LR-type males and RR-type females always produced RR-type offspring alone. Thus, the LR-type males were considered to produce spermatozoa which had only the R-genome with the X-chromosome.

3. Male hybrids between a female *Rana ridibunda* from Turkey and two kinds of males

a. Offspring of male intraspecific hybrids, *rid* T♀ × *rid* F♂

In 1978, three males (Nos. 1~3) obtained from a mating, *rid* T♀, No. 1 × *rid* F♂, No. 3, were mated with two females (Nos. 6 and 7) obtained from a mating,

les L♀, No. 3 × *les* L♂, No. 2. Of 199 metamorphosed frogs produced from two matings with two males (Nos. 1 and 2), 90 were all diploids when their chromosomes were counted at the tadpole stage. Sex was examined in 115 frogs which died or were killed within six months after metamorphosis. The results showed that 59 of them were females and 56 (48.7%) were males. Of 70 mature frogs which lived longer than one year, 32 were females and 38 (54.3%) were males. In total, 91 of 185 frogs were females and 94 (50.8%) were males. The sex of the remaining 14 was unknown owing to postmortem changes (Table 26).

Of 105 metamorphosed frogs produced from a mating with male No. 3, 20 were all diploids when their chromosomes were counted. Of 99 frogs whose sex was examined, 91 were females and eight (8.1%) were males. Thus, the male parent (No. 3) was considered to be a sex-reversed genetic female (Table 26).

b. Offspring of male interspecific hybrids, *rid* T♀ × *esc* G♂

In 1978, five males including three RR-type (Nos. 1~3) and two RL-type ones (Nos. 4 and 5) obtained from a mating, *rid* T♀, No. 1 × *esc* G♂, No. 1, were mated with two females (Nos. 8 and 9) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, as stated in Chapter VI. Of 145 metamorphosed frogs, produced from matings with males Nos. 1~3, 60 were diploids when their chromosomes were counted at the tadpole stage. Of 47 frogs which died within six months after metamorphosis, 45 were females and two (4.3%) were males. Of 76 mature frogs which lived longer than one year, 63 were females and 13 (17.1%) were males. In total, 108 of 123 were females and 15 (12.2%) were males. The sex of the remaining 22 was not determined owing to postmortem changes. All the mature frogs were of the LR-type. Thus, the three male parents (Nos. 1~3) of the RR-type were considered to be sex-reversed genetic females.

All 19 metamorphosed frogs produced from matings with the two RL-type males (Nos. 4 and 5) were diploids when their chromosomes were counted. They died within six months after metamorphosis. When the sex of 16 of them was examined, all of them were males. These frogs were of the LL-type (Table 26).

TABLE 26

Sex and external appearance of the offspring of male hybrids between a female *Rana ridibunda* from Turkey and two kinds of males

Year	Parents		No. of metamorphosed frogs	Sex of immature frogs		Sex of mature frogs		Sex of all frogs examined			External appearance (Type)
	Female	Male		♀	♂	♀	♂	No. of frogs	♀	♂ (%)	
1978	76 (*les* L_3 × *les* L_2) Nos. 6, 7	77 (*rid* T_1 × *rid* F_3) No. 1	73	7	6	19	27	59	26	33 (55.9)	LR
		77 (*rid* T_1 × *rid* F_3) No. 2	126	52	50	13	11	126	65	61 (48.4)	LR
		77 (*rid* T_1 × *rid* F_3) No. 3	105	37	2	54	6	99	91	8 (8.1)	LR
1978	76 (*les* L_3 × *les* L_2) Nos. 8, 9	77 (*rid* T_1 × *esc* G_1) No. 1	50	9	0	31	2	42	40	2 (4.8)	LR
		77 (*rid* T_1 × *esc* G_1) No. 2	49	22	2	9	2	35	31	4 (11.4)	LR
		77 (*rid* T_1 × *esc* G_1) No. 3	46	14	0	23	9	46	37	9 (19.6)	LR
		77 (*rid* T_1 × *esc* G_1) No. 4	15	0	12	0	0	12	0	12 (100)	LL
		77 (*rid* T_1 × *esc* G_1) No. 5	4	0	4	0	0	4	0	4 (100)	LL

4. Male hybrids between a female *Rana ridibunda* from Soviet Union and four kinds of males

a. Offspring of male intraspecific hybrids, *rid* S♀ × *rid* F♂

In 1978, three males (Nos. 1~3) obtained from a mating, *rid* S♀, No. 1 × *rid* F♂, No. 3, were mated with two females (Nos. 6 and 7) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, as stated in Chapter VI. All 13 metamorphosed frogs produced from a mating with male No. 1 were diploids when their chromosomes were counted at the tadpole stage. Of these frogs, 11 lived longer than one year and sexually matured. Five of them were females and six (54.5%) were males. The sex of the remaining two frogs was unknown owing to postmortem changes. From two matings with the other two males (Nos. 2 and 3), 64 metamorphosed frogs were produced. Of these frogs, 38 were diploids when their chromosomes were counted at the tadpole stage. Of the 64 frogs, 21 died within six months after metamorphosis. When their sex was examined, it was found that all of them were females. Of 32 mature frogs which lived longer than one year, 29 were females and three (9.4%) were males. In total, 50 of 53 frogs were females, and three (5.7%) were males. The sex of the remaining 11 frogs was unknown owing to postmortem changes. Thus, it is assumed that the two male parents (Nos. 2 and 3) were sex-reversed genetic females (Table 27).

b. Offspring of male intraspecific hybrids, *rid* S♀ × *rid* T♂

In 1978, three males (Nos. 2~4) obtained from a mating, *rid* S♀, No. 1 × *rid* T♂, No. 2, were mated with two females (Nos. 8 and 9) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, as stated in Chapter VI. Of 93 metamorphosed frogs produced from two matings with two males (Nos. 2 and 3), 40 were diploids when their chromosomes were counted at the tadpole stage. Three frogs which died within three months after metamorphosis were all females. Of 86 mature frogs which lived longer than one year, 66 were females and 20

TABLE 27

Sex and external appearance of the offspring of male hybrids between a female *Rana ridibunda* from Soviet Union and four kinds of males

Year	Parents		No. of metamorphosed frogs	Sex of immature frogs		Sex of mature frogs		Sex of all frogs examined			External appearance (Type)
	Female	Male		♀	♂	♀	♂	No. of frogs	♀	♂ (%)	
1978	76 (*les* L_3 × *les* L_2) Nos. 6, 7	77 (*rid* S_1 × *rid* F_3) No. 1	13	0	0	5	6	11	5	6 (54.5)	LR
		77 (*rid* S_1 × *rid* F_3) No. 2	18	1	0	14	2	17	15	2 (11.8)	LR
		77 (*rid* S_1 × *rid* F_3) No. 3	46	20	0	15	1	36	35	1 (2.8)	LR
1978	76 (*les* L_3 × *les* L_2) Nos. 8, 9	77 (*rid* S_1 × *rid* T_2) No. 2	56	0	0	44	12	56	44	12 (21.4)	LR
		77 (*rid* S_1 × *rid* T_2) No. 3	37	3	0	22	8	33	25	8 (24.2)	LR
		77 (*rid* S_1 × *rid* T_2) No. 4	106	9	10	44	41	104	53	51 (49.0)	LR
1978	76 (*les* L_3 × *les* L_2) No. 10	77 (*rid* S_1 × *les* L_3) No. 2	51	1	0	43	2	46	44	2 (4.3)	LR
1978	76 (*les* L_3 × *les* L_2) Nos. 11, 12	77 (*rid* S_1 × *esc* G_1) No. 3	88	7	1	45	18	71	52	19 (26.8)	LR

(23.3%) were males. In total, 69 of the 89 frogs were females and 20 (22.5%) were males. The sex of the remaining four frogs could not be determined owing to postmortem changes (Table 27).

Of 106 frogs produced from a mating with male No. 4, 25 were diploids when their chromosomes were counted at the tadpole stage. Of 19 frogs which died within six months after metamorphosis, nine were females and 10 (52.6%) were males. Of 85 mature frogs which lived longer than one year, 44 were females and 41 (48.2%) were males. In total, 53 of 104 frogs were females and 51 (49.0%) were males. The sex of the remaining two frogs was unknown owing to postmortem changes (Table 27). Thus, it is assumed that the two male parents (Nos. 2 and 3) might be sex-reversed genetic females.

c. Offspring of a male interspecific hybrid, *rid* S♀ × *les* L♂

In 1978, one male (No. 2) produced from a mating, *rid* S♀, No. 1 × *les* L♂, No. 3, was mated with a female (No. 10) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, as stated in Chapter VI. Of 51 metamorphosed frogs produced from this mating, 25 were diploids when their chromosomes were counted at the tadpole stage. One frog which died about three months after metamorphosis was a female. Of 45 mature frogs which lived longer than one year, 43 were females and only two (4.4%) were males. In total, 44 of the 46 frogs were females and two (4.3%) were males. The sex of the remaining five frogs could not be determined owing to postmortem changes. On the other hand, as all the 45 mature frogs were of the LR-type, the spermatozoa of the male parent (No. 2) were considered to have only the R-genome with the X-chromosome (Table 27).

d. Offspring of a male interspecific hybrid, *rid* S♀ × *esc* G♂

In 1978, a RR-type male (No. 3) obtained from a mating, *rid* S♀, No. 1 × *esc* G♂, No. 1, was mated with two females (Nos. 11 and 12) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, as stated in Chapter VI. Of 88 metamorphosed frogs produced from these matings, 40 were diploids when their chromosomes were counted at the tadpole stage. Of eight frogs which died within six months after metamorphosis, seven were females and one (12.5%) was a male. Of 63 mature frogs which lived longer than one year, 45 were females and 18 (28.6%) were males. In total, 52 of the 71 frogs were females and 19 (26.8%) were males. The sex of the remaining 17 frogs was unknown owing to postmortem changes or loss. The 71 frogs were all of the LR-type (Table 27).

IX. Sex of the offspring of female hybrids

1. Female hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

a. Offspring of female interspecific hybrids, *les* L♀ × *rid* F♂

As stated in Chapter VII, two kinds of eggs which were different in size and obtained in 1977 and 1978 from 19 female interspecific hybrids (Nos. 1 ~ 19) pro-

duced from matings, *les* L♀, Nos. 1~3×*rid* F♂, Nos. 1 and 2, were inseminated with spermatozoa of 10 male *Rana lessonae* from Luxembourg. When chromosomes were counted at the tadpole stage in 573 of 2426 metamorphosed frogs raised from normal-size eggs, almost all of them were diploids, although 11 were triploids or some other ploids. Of 1269 frogs which died or were killed within six months after metamorphosis, 612 were females and 657 (51.8%) were males. Of 939 mature frogs which lived longer than one year, 444 were females and 495 (52.7%) were males. In total, 1056 of the 2208 frogs were females and 1152

TABLE 28

Sex and external appearance of the offspring of female hybrids between female *Rana lessonae* from Luxembourg and male *Rana ridibunda* from France or Turkey

Year	Parents		Egg size	No. of metamorphosed frogs	Sex of immature frogs		Sex of mature frogs		Sex of all frogs examined			External appearance (Type)
	Female	Male			♀	♂	♀	♂	No. of frogs	♀	♂ (%)	
1977	75 (*les* L_1×*rid* F_1) No. 1	75 (*les* L_1×*les* L_1) No. 1	Normal	141	40	43	18	24	125	58	67 (53.6)	
	75 (*les* L_1×*rid* F_1) No. 2	75 (*les* L_1×*les* L_1) No. 2	Normal	135	42	40	17	17	116	59	57 (49.1)	
	75 (*les* L_1×*rid* F_1) No. 3	75 (*les* L_1×*les* L_1) No. 3	Normal	102	21	22	26	24	93	47	46 (49.5)	
	75 (*les* L_1×*rid* F_1) No. 4	75 (*les* L_1×*les* L_1) No. 4	Normal	134	39	41	24	22	126	63	63 (50.0)	
	75 (*les* L_1×*rid* F_1) No. 5		Normal	158	46	44	21	26	137	67	70 (51.1)	
1978	75 (*les* L_1×*rid* F_1) No. 6	76 (*les* L_2×*les* L_2) No. 5	Normal	228	84	88	20	23	215	104	111 (51.6)	
	75 (*les* L_1×*rid* F_1) No. 7		Normal	206	72	76	22	20	190	94	96 (50.5)	
			Large	11	1	1	4	5	11	5	6 (54.5)	LLR
	75 (*les* L_1×*rid* F_1) No. 8	76 (*les* L_2×*les* L_2) No. 6	Normal	149	45	50	17	23	135	62	73 (54.1)	
	75 (*les* L_1×*rid* F_1) No. 9		Normal	139	33	41	23	23	120	56	64 (53.3)	
	76 (*les* L_2×*rid* F_2) No. 10	76 (*les* L_2×*les* L_2) No. 7	Normal	73	4	6	27	30	67	31	36 (53.7)	
	76 (*les* L_2×*rid* F_2) No. 11		Normal	31	0	0	17	14	31	17	14 (45.2)	
	76 (*les* L_2×*rid* F_2) No. 12	76 (*les* L_2×*les* L_2) No. 8	Normal	66	0	0	31	34	65	31	34 (52.3)	
	76 (*les* L_2×*rid* F_2) No. 13		Normal	167	47	45	30	36	158	77	81 (51.3)	
			Large	2	0	0	1	1	2	1	1 (50.0)	LLR
	76 (*les* L_3×*rid* F_2) No. 14	76 (*les* L_3×*les* L_2) No. 9	Normal	281	86	109	34	35	264	120	144 (54.5)	
	76 (*les* L_3×*rid* F_2) No. 15		Normal	14	0	0	5	8	13	5	8 (61.5)	
			Large	11	0	0	5	6	11	5	6 (54.5)	LLR
	76 (*les* L_3×*rid* F_2) No. 16		Normal	77	0	0	27	34	61	27	34 (55.7)	
			Large	13	1	1	7	4	13	8	5 (38.5)	LLR
	76 (*les* L_3×*rid* F_2) No. 17	76 (*les* L_3×*les* L_2) No. 10	Normal	103	2	1	43	55	101	45	56 (55.4)	
			Large	20	4	3	7	6	20	11	9 (45.0)	LLR
	76 (*les* L_3×*rid* F_2) No. 18		Normal	131	36	34	20	19	109	56	53 (48.6)	
			Large	24	2	3	11	8	24	13	11 (45.8)	LLR
	76 (*les* L_3×*rid* F_2) No. 19		Normal	91	15	17	22	28	82	37	45 (54.9)	
			Large	12	1	1	4	6	12	5	7 (58.3)	LLR
1978	76 (*les* L_2×*rid* T_1) No. 1	76 (*les* L_3×*les* L_2) No. 11	Normal	13	1	0	4	6	11	5	6 (54.5)	
			Large	9	1	1	4	3	9	5	4 (44.4)	LLR
	76 (*les* L_3×*rid* T_1) No. 2		Normal	36	3	2	12	17	34	15	19 (55.9)	
			Large	25	0	0	11	14	25	11	14 (56.0)	LLR
	76 (*les* L_3×*rid* T_1) No. 3		Normal	38	1	1	16	19	37	17	20 (54.1)	
			Large	40	3	5	14	18	40	17	23 (57.5)	LLR

(52.2%) were males. The sex of the remaining 218 could not be determined owing to postmortem changes or loss (Table 28). All 93 metamorphosed frogs raised from large eggs of females Nos. 7, 13, 15~19 were triploids when their chromosomes were counted at the tadpole stage. Of 18 frogs which died within six months after metamorphosis, nine were females and nine (50.0%) were males. Of 75 mature frogs which lived longer than one year, 39 were females and 36 (48.0%) were males. In total, 48 of the 93 frogs were females and 45 (48.4%) were males (Table 28).

b. Offspring of female interspecific hybrids, *les* L♀ × *rid* T♂

In 1978, normal-size eggs of three female interspecific hybrids (Nos. 1~3) obtained from matings, *les* L♀, Nos. 2 and 3 × *rid* T♂, No. 1, were inseminated with spermatozoa of a male (No. 11) obtained from a mating, *les* L♀, No. 3 × *les* L♂, No. 2, as stated in Chapter VII. All 87 metamorphosed frogs produced from these matings were diploids when their chromosomes were counted at the tadpole stage. Of eight frogs which died within six months after metamorphosis, five were females and three (37.5%) were males. Of 74 mature frogs which lived longer than one year, 32 were females and 42 (56.8%) were males. In total, 37 of 82 frogs were females and 45 (54.9%) were males. The sex of the remaining five frogs was unknown owing to postmortem changes or loss (Table 28).

All 74 metamorphosed frogs raised from large eggs were triploids when their chromosomes were counted at the tadpole stage. Of 10 frogs which died within six months after metamorphosis, four were females and six were males. Of 64 mature frogs which lived longer than one year, 29 were females and 35 (54.7%) were males. In total, 33 of 74 frogs were females and 41 (55.4%) were males (Table 28).

c. Offspring of female intraspecific hybrids, *les* L♀ × *les* I♂

In 1978, six female intraspecific hybrids (Nos. 1~6) obtained from matings, *les* L♀, Nos. 4 and 5 × *les* I♂, Nos. 1 and 2, were mated with four males (Nos. 12~15) obtained from a mating, *les* L♀, No. 4 × *les* L♂, No. 3, as stated in Chapter VII. Of 696 metamorphosed frogs produced from these matings, 120 were diploids when their chromosomes were counted at the tadpole stage. Of 421 frogs which died or were killed within six months after metamorphosis, 202 were females and 219 (52.0%) were males. Of 232 mature frogs which lived longer than one year, 111 were females and 121 (52.2%) were males. In total, 313 of the 653 frogs were females and 340 (52.1%) were males. The sex of the remaining 43 could not be determined owing to postmortem changes or loss (Table 29).

d. Offspring of female interspecific hybrids, *les* L♀ × *esc* G♂

In 1978, two LR-type female interspecific hybrids (Nos. 1 and 2) obtained from a mating, *les* L♀, No. 4 × *esc* G♂, No. 1, were mated with one LL-type male (No. 16) obtained from a mating, *les* L♀, No. 4 × *les* L♂, No. 3, as stated in

TABLE 29

Sex and external appearance of the offspring of female hybrids between female *Rana lessonae* from Luxembourg or Italy and three kinds of males

Year	Parents		No. of metamorphosed frogs	Sex of immature frogs		Sex of mature frogs		Sex of all frogs examined			External appearance (Type)
	Female	Male		♀	♂	♀	♂	No. of frogs	♀	♂ (%)	
1978	77 (*les* $L_4 \times$ *les* I_1) No. 1	77 (*les* $L_4 \times$ *les* L_3) Nos. 12, 13	206	50	57	35	39	181	85	96 (53.0)	LL
	77 (*les* $L_4 \times$ *les* I_1) No. 2		7	3	4	0	0	7	3	4 (57.1)	LL
	77 (*les* $L_4 \times$ *les* I_1) No. 3		129	33	36	32	25	126	65	61 (48.4)	LL
	77 (*les* $L_5 \times$ *les* I_2) No. 4	77 (*les* $L_4 \times$ *les* L_3) Nos. 14, 15	90	18	15	24	31	88	42	46 (52.3)	LL
	77 (*les* $L_5 \times$ *les* I_2) No. 5		148	66	73	0	0	139	66	73 (52.5)	LL
	77 (*les* $L_5 \times$ *les* I_2) No. 6		116	32	34	20	26	112	52	60 (53.6)	LL
1978	77 (*les* $L_4 \times$ *esc* G_1) No. 1	77 (*les* $L_4 \times$ *les* L_3) No. 16	54	2	3	25	21	51	27	24 (47.1)	RL
	77 (*les* $L_4 \times$ *esc* G_1) No. 2		42	3	4	19	12	38	22	16 (42.1)	RL
1978	77 (*les* $I_1 \times$ *les* L_3) No. 1	77 (*les* $L_4 \times$ *les* L_3) Nos. 12, 13	133	31	33	24	37	125	55	70 (56.0)	LL
	77 (*les* $I_1 \times$ *les* L_3) No. 2		121	60	57	0	0	117	60	57 (48.7)	LL
	77 (*les* $I_2 \times$ *les* L_3) No. 3	77 (*les* $L_4 \times$ *les* L_3) Nos. 14, 15	55	12	7	13	9	41	25	16 (39.0)	LL
	77 (*les* $I_2 \times$ *les* L_3) No. 4		103	14	16	30	21	81	44	37 (45.7)	LL
	77 (*les* $I_2 \times$ *les* L_3) No. 5		87	19	20	14	25	78	33	45 (57.7)	LL
1978	77 (*les* $I_1 \times$ *esc* G_1) No. 1	77 (*les* $L_5 \times$ *les* L_4) No. 17	125	9	7	46	53	115	55	60 (52.2)	RL
	77 (*les* $I_1 \times$ *esc* G_1) No. 2		22	0	0	12	7	19	12	7 (36.8)	RL
	77 (*les* $I_1 \times$ *esc* G_1) No. 3		253	82	75	39	48	244	121	123 (50.4)	RL
	77 (*les* $I_2 \times$ *esc* G_1) No. 4	77 (*les* $L_5 \times$ *les* L_4) No. 18	68	10	10	24	19	63	34	29 (46.0)	RL
	77 (*les* $I_2 \times$ *esc* G_1) No. 5		94	51	43	0	0	94	51	43 (45.7)	RL
	77 (*les* $I_2 \times$ *esc* G_1) No. 6		67	2	1	22	26	51	24	27 (52.9)	RL

Chapter VII. All 96 metamorphosed frogs produced from these matings were diploids when their chromosomes were counted at the tadpole stage. Of 12 frogs which died within six months after metamorphosis, five were females and seven were males. Of 77 mature frogs which lived longer than one year, 44 were females and 33 (42.9%) were males. In total, 49 of the 89 frogs were females and 40 (44.9%) were males. These frogs were all of the RL-type. The sex of the remaining seven frogs could not be determined owing to postmortem changes or loss (Table 29).

2. Female hybrids between female *Rana lessonae* from Italy and two kinds of males

a. Offspring of female intraspecific hybrids, *les* I♀ × *les* L♂

In 1978, five female intraspecific hybrids (Nos. 1~5) obtained from matings, *les* I♀, Nos. 1 and 2 × *les* L♂, No. 3, were mated with four males (Nos. 12~15) obtained from a mating, *les* L♀, No. 4 × *les* L♂, No. 3, as stated in Chapter VII. Of 499 metamorphosed frogs produced from these matings, 60 were diploids when their chromosomes were counted at the tadpole stage. Of 269 frogs which died or were killed within six months after metamorphosis, 136 were females and 133 (49.4%) were males. Of 173 mature frogs which lived longer than one year,

81 were females and 92 (53.2%) were males. In total, 217 of the 442 frogs were females and 225 (50.9%) were males. The sex of the remaining 57 could not be determined owing to postmortem changes or loss (Table 29).

b. Offspring of female interspecific hybrids, *les* I♀ × *esc* G♂

In 1978, six LR-type female interspecific hybrids (Nos. 1~6) obtained from matings, *les* I♀, Nos. 1 and 2 × *esc* G♂, No. 1, were mated with two LL-type males (Nos. 17 and 18) obtained from a mating, *les* L♀, No. 5 × *les* L♂, No. 4, as stated in Chapter VII. Of 629 metamorphosed frogs produced from these matings, 121 were diploids and one was a mosaic when the chromosomes of 122 frogs were counted at the tadpole stage. Of 290 frogs which died or were killed within six months after metamorphosis, 154 were females and 136 (46.9%) were males. Of 296 mature frogs which lived longer than one year, 143 were females and 153 (51.7%) were males. In total, 297 of the 586 frogs were females and 289 (49.3%) were males. These frogs were all of the RL-type. The sex of the remaining 43 could not be determined owing to postmortem changes or loss (Table 29).

X. External appearance and electrophoretic patterns of the offspring of male hybrids

1. Offspring of male hybrids between female *Rana lessonae* from Luxembourg and two kinds of males

a. Controls, (*les* L♀ × *les* L♂)♀ × (*les* L♀ × *les* L♂)♂

In the three years from 1975 to 1977, F_1 offspring were produced from matings, *les* L♀, Nos. 1~5 × *les* L♂, Nos. 1~4. The offspring were all of the LL-type in external appearance (Tables 5 and 10). Electrophoretic patterns of the following 10 kinds of blood proteins and enzymes extracted from skeletal muscles and livers, Hb, Ab, LDH-B, PGM, 6-PGD, MPI, ALD, Pep-A, GPI and AAT-B, were examined in the offspring. The results showed that these 10 blood proteins and enzymes were *dd*, *dd*, *ee*, *bb*, *bb*, *hh*, *dd*, *ee*, *dd* and *cc* in phenotype and that the offspring were all homozygous and of the $L^L \cdot L^L$-type in electrophoretic patterns (Tables 14 and 15).

In 1977, 1978 and 1980, 21 matings were made between 15 females (Nos. 1~15) and 21 males (Nos. 1~21) of the F_1 offspring (Table 16). The F_2 offspring produced from these matings were the same as the F_1 and of the LL-type in external appearance (Table 23). Electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 34 males and females, two or three frogs from each of 15 of the 21 matings. It was found that all the F_2 frogs were completely the same as the F_1 in electrophoretic pattern (Table 30).

b. Backcrosses of male intraspecific hybrids, *les* L♀ × *les* I♂

In 1978, three male intraspecific hybrids (Nos. 2, 3 and 6) obtained in 1977 from matings, *les* L♀, Nos. 4 and 5 × *les* I♂, Nos. 1 and 2, were backcrossed to three female *Rana lessonae* from Luxembourg (Nos. 4~6) obtained in 1975 and

TABLE 30

External appearance and electrophoretic patterns of the offspring of male

Parents						External appearance (Type)	No. of frogs
Female		(Type)	Male		(Type)		
les $L_{1\sim4}$ × *les* $L_{1\sim3}$,	Nos. 1~15	(LL)	*les* $L_{1\sim5}$ × *les* $L_{1\sim4}$,	Nos. 1~21	(LL)	LL	34
les $L_{1,3}$ × *les* $L_{1,2}$,	Nos. 4~6	(LL)	*les* $L_{4,5}$ × *les* $I_{1,2}$,	Nos. 2, 3, 6	(LL)	LL	18
les L_3 × *les* L_2,	Nos. 9~11	(LL)	*les* L_4 × *esc* G_1,	Nos. 1~3	(LL)	LL	41
les L_4 × *les* L_3,	Nos. 13, 14	(LL)	*les* L_4 × *esc* G_1,	Nos. 6, 7	(LR)	LR	20
rid T_2 × *rid* T_4,	No. 1	(RR)	*les* L_4 × *esc* G_1,	Nos. 6, 7	(LR)	RR	20
les I_2 × *les* I_1,	No. 11	(LL)	*les* L_4 × *esc* G_1,	No, 7	(LR)	LR	10
les L_4 × *les* L_3,	No. 15	(LL)	*les* L_4 × *esc* G_1,	No. 8	(LL)	LL	5
les I_2 × *les* I_1,	No. 11	(LL)	*les* L_4 × *esc* G_1,	No. 8	(LL)	LL	10
rid T_2 × *rid* T_4,	No. 1	(RR)	*les* L_4 × *esc* G_1,	No. 8	(LL)	RL	10
les I_1 × *les* I_1,	Nos. 1~6	(LL)	*les* I_1 × *les* I_1,	Nos. 1~4	(LL)	LL	20
les I_2 × *les* I_1,	Nos. 11, 12	(LL)	*les* I_2 × *les* I_1,	Nos. 7, 8	(LL)	LL	10
les I_1 × *les* I_1,	Nos. 1~3	(LL)	*les* I_1 × *les* L_3,	Nos. 1~3	(LL)	LL	22
les I_2 × *les* I_1,	Nos. 7~9	(LL)	*les* I_2 × *les* L_3,	Nos. 6, 9	(LL)	LL	16
les I_1 × *les* I_1,	Nos. 1~3	(LL)	*les* I_2 × *rid* S_1,	No. 1	(LR)	LR	3
les I_1 × *les* I_1,	Nos. 4~6	(LL)	*les* I_1 × *esc* G_1,	Nos. 1, 2	(LL)	LL	29
les I_2 × *les* I_1,	Nos. 7~9	(LL)	*les* I_2 × *esc* G_1,	Nos. 6~8	(LL)	LL	30
les I_1 × *les* I_1,	Nos. 4~6	(LL)	*les* I_3 × *esc* G_1,	Nos. 16~18	(LL)	LL	28
les I_2 × *les* I_1,	Nos, 11, 12	(LL)	*les* I_2 × *esc* G_1,	Nos. 21, 22	(LR)	LR	20
rid T_2 × *rid* T_4,	No. 2	(RR)	*les* I_3 × *esc* G_1,	Nos. 24, 25	(LR)	RR	19
les L_3 × *les* L_2,	Nos. 6, 7	(LL)	*rid* T_1 × *rid* F_3,	No. 1	(RR)	LR	10
			rid T_1 × *rid* F_3,	No. 2	(RR)	LR	10
			rid T_1 × *rid* F_3,	No. 3	(RR)	LR	10
les L_3 × *les* L_2,	Nos. 8, 9	(LL)	*rid* T_1 × *esc* G_1,	Nos. 1~3	(RR)	LR	24
			rid T_1 × *esc* G_1,	Nos. 4, 5	(RL)	LL	6
les L_3 × *les* L_2,	Nos. 6, 7	(LL)	*rid* S_1 × *rid* F_3,	No. 1	(RR)	LR	6
			rid S_1 × *rid* F_3,	No. 2	(RR)	LR	5
			rid S_1 × *rid* F_3,	No. 3	(RR)	LR	5
les L_3 × *les* L_2,	Nos. 8, 9	(LL)	*rid* S_1 × *rid* T_2,	Nos. 2, 3	(RR)	LR	12
			rid S_1 × *rid* T_2,	No. 4	(RR)	LR	10
les L_3 × *les* L_2,	No. 10	(LL)	*rid* S_1 × *les* L_3,	No. 2	(RL)	LR	8
les L_3 × *les* L_2,	Nos. 11, 12	(LL)	*rid* S_1 × *esc* G_1,	No. 3	(RR)	LR	8
les L_1 × *rid* F_1,	Nos. 1~9	(LR)	*les* $L_{1,2}$ × *les* $L_{1,2}$,	Nos. 1~6	(LL)	(2n)	45
les L_1 × *rid* F_1,	No. 7	(LR)	*les* L_2 × *les* L_2,	No. 5	(LL)	LLR	4
les $L_{2,3}$ × *rid* F_2,	Nos. 10~19	(LR)	*les* $L_{2,3}$ × *les* L_2,	Nos. 7~10	(LL)	(2n)	40
les $L_{2,3}$ × *rid* F_2,	Nos. 15~19	(LR)	*les* $L_{2,3}$ × *les* L_2,	Nos. 8~10	(LL)	LLR	19
les L_2 × *rid* T_1,	No. 1	(LR)	*les* L_3 × *les* L_2,	No. 11	(LL)	(2n)	4
						LLR	4
les L_3 × *rid* T_1,	Nos. 2, 3	(LR)	*les* L_3 × *les* L_2,	No. 11	(LL)	(2n)	12
						LLR	12
les $L_{4,5}$ × *les* $I_{1,2}$,	Nos. 3, 4	(LL)	*les* L_4 × *les* L_3,	Nos. 12~15	(LL)	LL	10
les L_4 × *esc* G_1,	Nos. 1, 2	(LR)	*les* L_4 × *les* L_3,	No. 16	(LL)	RL	12
les $I_{1,2}$ × *les* L_3,	Nos. 1, 4, 5	(LL)	*les* L_4 × *les* L_3,	Nos. 12~15	(LL)	LL	12
les I_2 × *les* L_3,	No. 3	(LL)	*les* L_4 × *les* L_3,	Nos. 14, 15	(LL)	LL	6
les I_1 × *esc* G_1,	Nos. 1~3	(LR)	*les* L_5 × *les* L_4,	No. 17	(LL)	RL	26
les I_2 × *esc* G_1,	Nos. 4~6	(LR)	*les* L_5 × *les* L_4,	No. 18	(LL)	RL	24

1976 from matings, *les* L♀, Nos. 1 and 3 × *les* L♂, Nos. 1 and 2. Mature males and females produced from these backcrossings were all of the LL-type in external appearance. Electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 18 backcrosses. The results showed that the phenotypes of these backcrosses did not differ from those of *Rana lessonae* from Luxembourg except the phenotype of AAT–B. The phenotype of AAT–B was *cc* or *cb*, while that of the control *Rana lessonae* from Luxembourg was always *cc*. The electrophoretic patterns of the other nine proteins and enzymes in the backcrosses were the same as those in the control *Rana lessonae* from Luxem-

or female hybrids among *Rana lessonae*, *Rana ridibunda* and *Rana esculenta*

Hb	Ab	LDH-B	PGM	6-PGD	MPI	ALD	Pep-A	GPI	AAT-B	Phenotype
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*cc*	$L^L \cdot L^L$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*cc cb*	$L^L \cdot L^{L-I}$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*cc*	$L^L \cdot L^{L-G}$
de	*dg*	*eb*	*bc*	*be*	*hf*	*dg*	*eb*	*db*	*cb*	$L^L \cdot R^G$
ee	*hg*	*db*	*cc*	*ee*	*ff cf*	*cg*	*bb ab*	*db*	*bb*	$R^T \cdot R^G$
de	*dg*	*eb*	*bc*	*be*	*hf if*	*dg*	*eb*	*db*	*bb*	$L^I \cdot R^G$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*cc*	$L^L \cdot L^{L-G}$
dd	*dd*	*ee*	*bb*	*bb*	*hh ih*	*dd*	*ee*	*dd*	*bc*	$L^I \cdot L^{L-G}$
ed	*hd*	*de*	*cb*	*eb*	*ch fh*	*cd*	*be ae*	*dd*	*bc*	$R^T \cdot L^{L-G}$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*bb*	$L^I \cdot L^I$
dd	*dd*	*ee*	*bb*	*bb*	*hh ih*	*dd*	*ee*	*dd*	*bb*	$L^I \cdot L^I$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*bb bc*	$L^I \cdot L^{I-L}$
dd	*dd*	*ee*	*bb*	*bb*	*hh ih*	*dd*	*ee*	*dd*	*bb bc*	$L^I \cdot L^{I-L}$
de	*dh*	*eb*	*bb*	*be*	*hf*	*dg*	*eb*	*dd*	*bb*	$L^I \cdot R^S$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*bb bc*	$L^I \cdot L^{I-G}$
dd	*dd*	*ee*	*bb*	*bb*	*hh ih*	*dd*	*ee*	*dd*	*bb bc*	$L^I \cdot L^{I-G}$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*bb bc*	$L^I \cdot L^{I-G}$
de	*dg*	*eb*	*bc*	*be*	*hf if*	*dg*	*eb*	*db*	*bb*	$L^I \cdot R^G$
ee	*hg*	*db*	*cc*	*ee*	*ff cf*	*cg*	*ab bb*	*db*	*bb*	$R^T \cdot R^G$
de	*dh dg*	*ed eb*	*bc*	*be*	*ha hf*	*da dc*	*eb*	*dd*	*cb*	$L^L \cdot R^{T-F}$
de	*dh df*	*ed eb*	*bc*	*be*	*ha hf*	*da dc*	*eb*	*dd*	*cb*	$L^L \cdot R^{T-F}$
de	*dh dg*	*ed*	*bc*	*be*	*hc hf*	*da dg*	*eb*	*dd*	*cb*	$L^L \cdot R^{T-F}$
de	*dh dg*	*eb ed*	*bc*	*be*	*hf*	*dg dc*	*eb*	*dd db*	*cb*	$L^L \cdot R^{T-G}$
dd	*dd*	*ee*								$L^L \cdot L^G$
de	*dg*	*eb ed*	*bc*	*be*	*hc*	*da dg*	*eb*	*dd*	*cb*	$L^L \cdot R^{S-F}$
de	*dg dh*	*eb*	*bc*	*be*	*hc ha*	*da dc*	*eb*	*db*	*cb*	$L^L \cdot R^{S-F}$
de	*dg df*	*ed*	*bc*	*be*	*hc ha*	*da dg*	*eb*	*dd db*	*cb*	$L^L \cdot R^{S-F}$
de	*dh*	*eb ed*	*bc*	*be*	*hc hb*	*dg*	*eb*	*dd*	*cb*	$L^L \cdot R^{S-T}$
de	*dh*	*ed*	*bc*	*be*	*hc hf*	*dg*	*eb*	*dd*	*cb*	$L^L \cdot R^{S-T}$
de	*dh*	*eb*	*bc*	*be*	*hc*	*dg*	*eb*	*dd*	*cb*	$L^L \cdot R^S$
de	*dh dg*	*eb*	*bc*	*be*	*hc hf*	*dg*	*eb*	*dd db*	*cb*	$L^L \cdot R^{S-G}$
dd ed	*dd gd*	*ee de*	*bb cb*	*bb eb*	*hh ch*	*dd ad*	*ee be*	*dd*	*cc bc*	$L^L\text{-}R^F \cdot L^L$
dde	*ddg*	*eed*	*bbc*	*bbe*	*hhc*	*dda*	*eeb*	*ddd*	*ccb*	$L^L \cdot L^L \cdot R^F$
dd ed	*dd fd*	*ee de*	*bb cb*	*bb eb*	*hh ch*	*dd ad*	*ee be*	*dd*	*cc*	$L^L\text{-}R^F \cdot L^L$
	dd hd						*ee ae*	*dd bd*	*cc bc*	
dde	*ddf ddh*	*eed*	*bbc*	*bbe*	*hhc*	*dda*	*eeb eea*	*ddd ddb*	*ccc ccb*	$L^L \cdot L^L \cdot R^F$
dd ed	*dd hd*	*ee de*	*bb cb*	*bb eb*	*hh bh*	*dd cd*	*ee ae*	*dd*	*cc bc*	$L^L\text{-}R^T \cdot L^L$
dde	*ddh*	*eed*	*bbc*	*bbe*	*hhb*	*ddc*	*eea*	*ddd*	*ccb*	$L^L \cdot L^L \cdot R^T$
dd ed	*dd hd*	*ee de*	*bb cb*	*bb eb*	*hh bh*	*dd gd*	*ee ae*	*dd*	*cc bc*	$L^L\text{-}R^T \cdot L^L$
dde	*ddh*	*eed*	*bbc*	*bbe*	*hhb*	*ddg*	*eea*	*ddd*	*ccb*	$L^L \cdot L^L \cdot R^T$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*cc bc*	$L^{L-I} \cdot L^L$
ed	*gd*	*be*	*cb*	*eb*	*fh*	*gd*	*be*	*bd*	*bc*	$R^G \cdot L^L$
dd	*dd*	*ee*	*bb*	*bb*	*hh*	*dd*	*ee*	*dd*	*cc bc*	$L^{I-L} \cdot L^L$
dd	*dd*	*ee*	*bb*	*bb*	*hh ih*	*dd*	*ee*	*dd*	*cc bc*	$L^{I-L} \cdot L^L$
ed	*gd*	*be*	*cb*	*eb*	*fh*	*gd*	*be*	*bd*	*bc*	$R^G \cdot L^L$
ed	*gd*	*be*	*cb*	*eb*	*fh*	*gd*	*be*	*bd*	*bc*	$R^G \cdot L^L$

bourg (Table 30). Thus, the electrophoretic patterns of these backcrosses are considered to be of the $L^L \cdot L^{L-I}$-type in contrast to the $L^L \cdot L^L$-type of the controls.

c. Backcrosses of male interspecific hybrids, *les* L♀ × *esc* G♂

i) LL-type male hybrids backcrossed in 1978

Three 1-year-old LL-type male hybrids (Nos. 1～3) obtained in 1977 from a mating, *les* L♀, No. 4 × *esc* G♂, No. 1, were backcrossed with three 2-year-old female *Rana lessonae* from Luxembourg (Nos. 9～11) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. The electrophoretic patterns of the fore-

going 10 kinds of blood proteins and enzymes in the hybrids were of the $L^L \cdot L^G$-type and did not differ from the $L^L \cdot L^L$-type (Table 15).

The backcrosses were all of the LL-type in external appearance. Electrophoretic patterns of the above 10 kinds of blood proteins and enzymes were examined in 41 male and female backcrosses. The results showed that each of them was homozygous and completely the same as that of the $L^L \cdot L^L$-type (Table 30). Thus, the phenotypes in these backcrosses are considered to be $L^L \cdot L^{L-G}$-type.

ii) LR-type male hybrids backcrossed in 1980

Two 3-year-old LR-type male hybrids (Nos. 6 and 7) obtained in 1977 from a mating, *les* L♀, No. 4×*esc* G♂, No. 1, were backcrossed with two 3-year-old female *Rana lessonae* from Luxembourg (Nos. 13 and 14) obtained in 1977 from a mating, *les* L♀, No. 4×*les* L♂, No. 3. The electrophoretic patterns of the two male hybrids were of the $L^L \cdot R^G$-type (Table 15). The backcrosses were all of the LR-type in external appearance. When the electrophoretic patterns of the above 10 kinds of blood proteins and enzymes were examined in 20 of the backcrosses, it was found that all the backcrosses were of the $L^L \cdot R^G$-type.

The same two LR-type male hybrids were backcrossed with one 2-year-old female *Rana ridibunda* (No. 1) obtained in 1978 from a mating, *rid* T♀, No. 2×*rid* T♂, No. 4. The backcrosses were all of the RR-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 20 of the backcrosses. The results showed that the phenotype of each of Ab, LDH-B, MPI, ALD, Pep-A and GPI was completely of the $R^T \cdot R^G$-type (Table 30).

One (No. 7) of the two LR-type male hybrids was backcrossed with one 3-year-old female *Rana lessonae* from Italy (No. 11) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1. The backcrosses produced from this mating were all of the LR-type in external appearance. When the electrophoretic patterns of the foregoing ten blood proteins and enzymes were examined in 10 of the backcrosses, it was found that all the frogs were of the $L^I \cdot R^G$-type (Table 30).

iii) LL-type male hybrids backcrossed in 1980

One 3-year-old LL-type male hybrid (No. 8) obtained in 1977 from a mating, *les* L♀, No. 4×*esc* G♂, No. 1, was backcrossed with a female *Rana lessonae* from Luxembourg (No. 15) obtained in 1977 from a mating, *les* L♀, No. 4×*les* L♂, No. 3. The backcrosses produced from this mating were all of the LL-type in external appearance. When the electrophoretic patterns of the foregoing 10 blood proteins and enzymes were examined in five of the backcrosses, it was found that all the phenotypes in these backcrosses were of the $L^L \cdot L^{L-G}$-type$=L^L \cdot L^L$-type (Table 30).

The same LL-type male hybrid (No. 8) was backcrossed with one 3-year-old female *Rana lessonae* from Italy (No. 11) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1. It was found that the backcrosses obtained were all of the LL-type in external appearance. When the electrophoretic patterns of the foregoing 10 blood proteins and enzymes were examined in 10 of the backcrosses,

the results showed that they were of the $L^{I} \cdot L^{L-G}$-type (Table 30). On the other hand, when this male hybrid was backcrossed with one 2-year-old female *Rana ridibunda* from Turkey (No. 1) obtained in 1978 from a mating, *rid* T♀, No. 2 × *rid* T♂, No. 4, all the backcrosses were of the RL-type in external appearance. The electrophoretic patterns of the 10 blood proteins and enzymes were examined in 10 of the backcrosses. The results showed that all of them were of the $R^{T} \cdot L^{L-G}$-type (Table 30).

It seems evident that the two LR-type male hybrids (Nos. 6 and 7) obtained from a mating, *les* L♀, No. 4 × *esc* G♂, No. 1, eliminated the L-genome and produced spermatozoa retaining the R-genome alone. On the other hand, it is evident from the data in Table 24 that male *Rana esculenta* from West Germany No. 1 (*esc* G♂, No. 1) produced two kinds of spermatozoa, one of which contained the R-genome and the other contained the L-genome. LR-type male hybrids Nos. 6 and 7 obtained by fertilization with the R-spermatozoa were sex-reversed genetic females, in contrast to LL-type male hybrid No. 8 which was obtained by fertilization with the L-spermatozoa and produced nearly an equal number of males and females. Thus, it is assumed that the R- and the L-genome included the X- and the Y-chromosome, respectively.

2. Offspring of male hybrids between female *Rana lessonae* from Italy and three kinds of males

a. Controls, (*les* I♀ × *les* I♂)♀ × (*les* I♀ × *les* I♂)♂

Rana lessonae from Italy were very similar to *Rana lessonae* from Luxembourg in external appearance. The phenotypes of two kinds of blood proteins, Hb and Ab, and eight kinds of enzymes, LDH–B, PGM, 6–GPD, MPI, ALD, Pep–A, GPI and AAT–B in *Rana lessonae* from Italy were the same as those in *Rana lessonae* from Luxembourg, except those of AAT–B and MPI. While the phenotype of AAT–B was *cc* in Luxembourg, it was *bb* in Italy. The phenotype of MPI in one female from Italy, *les* I.W77♀, No. 2, was *hi*, although it was *hh* in the other frogs from Italy. In contrast, the phenotype of MPI was *hh* in all frogs from Luxembourg.

The phenotype of MPI was always *hh* in the F_1 offspring obtained in 1977 from a mating, *les* I♀, No. 1 × *les* I♂, No. 1 (Table 14). In 20 F_2 offspring obtained in 1978 from matings between six females (Nos. 1 ~ 6) and four males (Nos. 1 ~ 4) of these F_1 offspring, the electrophoretic patterns of nine blood proteins and enzymes except AAT–B whose phenotype was *bb* were identical to those of frogs from Luxembourg. On the other hand, in the F_2 offspring between two females (Nos. 11 and 12) and two males (Nos. 7 and 8) obtained from a mating, *les* I♀, No. 2 × *les* I♂, No. 1, the phenotype of MPI was *hh* and *ih*. This dimorphism is due to the fact that the phenotype of female No. 11 was *ih*, and those of female No. 12 and males Nos. 7 and 8 were *hh*. The phenotypes of the other blood proteins and enzymes were identical to those of the F_2 offspring obtained from the foregoing mating, *les* I♀, No. 1 × *les* I♂, No. 1 (Table 30).

b. Backcrosses of male intraspecific hybrids, *les* I♀ × *les* L♂

In 1978, three 1-year-old male hybrids (Nos. 1~3) obtained in 1977 from a mating, *les* I♀, No. 1 × *les* L♂, No. 3, were backcrossed with three female *Rana lessonae* from Italy (Nos. 1~3) obtained in 1977 from a mating, *les* I♀, No. 1 × *les* I♂, No. 1. The backcrosses produced from these matings were all of the LL-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 22 male and female backcrosses. The results showed that the phenotypes of nine kinds of blood proteins and enzymes were identical to those of the $L^L \cdot L^L$- or $L^I \cdot L^I$-type, while the phenotype of AAT–B was *bb* in 10 and *bc* in 12 backcrosses. Thus, it is assumed that the phenotypes of the backcrosses were of the $L^I \cdot L^{I-L}$-type (Table 30).

Two other 1-year-old male hybrids (Nos. 6 and 9) obtained in 1977 from a mating, *les* I♀, No. 2 × *les* L♂, No. 3, were backcrossed with three 1-year-old female *Rana lessonae* from Italy (Nos. 7~9) obtained in 1977 from a mating, *les* I♀, No. 2 × *les* I♂, No. 1. All the backcrosses produced from these matings were of the LL-type in external appearance. The electrophoretic patterns of the above 10 kinds of blood proteins and enzymes were examined in 16 backcrosses. The results showed that the phenotype of MPI was *ih* in four and *hh* in 12 backcrosses, as it was *hi*, *hh* and *hh* in female parents Nos. 7, 8 and 9, respectively, and *hh* in male parents Nos. 6 and 9. The phenotype of AAT–B was *bb* in 8, and *bc* in 8 backcrosses ($L^I \cdot L^{I-L}$-type). The phenotypes of the other eight blood proteins and enzymes were all homozygous and the same as those of the $L^L \cdot L^L$- or $L^I \cdot L^I$-type in the 16 backcrosses (Table 30).

c. Backcrosses of a male interspecific hybrid, *les* I♀ × *rid* S♂

In 1978, one 1-year-old LR-type male hybrid (No. 1) obtained in 1977 from a mating, *les* I♀, No. 2 × *rid* S♂, No. 1, was backcrossed with three 1-year-old female *Rana lessonae* from Italy (Nos. 1~3) obtained in 1977 from a mating, *les* I♀, No. 1 × *les* I♂, No. 1. The backcrosses were all of the LR-type in external appearance. The electrophoretic patterns of the above 10 kinds of blood proteins and enzymes were examined in three backcrosses. It was found that the phenotypes of seven kinds, Hb, Ab, LDH–B, 6–PGD, MPI, ALD and Pep–A, were all of the $L^I \cdot R^S$-type, that is, the hybrid patterns. The phenotypes of the other three kinds, PGM, GPI and AAT–B in *Rana lessonae* from Italy were the same as those in *Rana ridibunda* (Table 30). Thus, it is considered that male parent No. 1 obtained from a mating, *les* I♀, No. 2 × *rid* S♂, No. 1, eliminated the L-genome and formed spermatozoa containing the R-genome with the Y-chromosome.

d. Backcrosses of male interspecific hybrids, *les* I♀ × *esc* G♂

i) LL-type male hybrids

In 1978, five 1-year-old LL-type male hybrids, including two males (Nos. 1 and 2) obtained in 1977 from a mating, *les* I♀, No. 1 × *esc* G♂, No. 1, and three males (Nos. 16~18) obtained in 1977 from a mating, *les* I♀, No. 3 × *esc* G♂, No. 1, were backcrossed with three 1-year-old female *Rana lessonae* from Italy (Nos. 4~6)

obtained in 1977 from a mating, *les* I♀, No. 1×*les* I♂, No. 1. The results showed that all the backcrosses were of the LL-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 57 male and female backcrosses. The phenotypes of AAT–B was *bb* ($L^I \cdot L^I$-type) in 28 and *bc* ($L^I \cdot L^G$-type) in 29 backcrosses. The phenotypes of the other nine kinds of blood proteins and enzymes of *Rana lessonae* from Luxembourg were the same as those of *Rana lessonae* from Italy. Thus, it is considered that the 57 backcrosses all showed the electrophoretic patterns of the $L^I \cdot L^{I-G}$-type.

In the same year, three other 1-year-old LL-type male hybrids (Nos. 6~8) obtained in 1977 from a mating, *les* I♀, No. 2×*esc* G♂, No. 1, were backcrossed with three female *Rana lessonae* from Italy (Nos. 7~9) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1. All the backcrosses were of the LL-type in external appearance. The electrophoretic patterns of the above 10 kinds of blood proteins and enzymes were examined in 30 of the backcrosses. The results showed that the phenotype of MPI was *ih* in six and *hh* in 24 backcrosses. The phenotype of AAT–B was *bb* in 17 and *bc* in 13 backcrosses. The phenotype of MPI of female parents Nos. 7, 8 and 9 was *hi*, *hh* and *hh*, respectively, while that of male parents Nos. 6, 7 and 8 was all *hh*. The phenotypes of the other eight kinds of blood proteins and enzymes in the 30 backcrosses were all the same as those of the $L^I \cdot L^I$- or $L^L \cdot L^L$-type. Thus, it seems evident that the electrophoretic patterns of the backcrosses were of the $L^I \cdot L^{I-G}$-type (Table 30).

ii) LR-type male hybrids

In 1980, two 3-year-old male hybrids (Nos. 21 and 22) obtained in 1977 from a mating, *les* I♀, No. 2×*esc* G♂, No. 1, were backcrossed with two 3-year-old female *Rana lessonae* from Italy (Nos. 11 and 12) obtained in 1977 from a mating, *les* I♀, No. 2×*les* I♂, No. 1. The male hybrids were of the LR-type in external appearance and of the $L^I \cdot R^G$-type in electrophoretic patterns. All the backcrosses produced from these matings were all of the LR-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 20 of the backcrosses. The results showed that all of the latter were of the $L^I \cdot R^G$-type (Table 30).

Two other 3-year-old LR-type male hybrids (Nos. 24 and 25) obtained in 1977 from a mating, *les* I♀, No. 3×*esc* G♂, No. 1, were backcrossed with a female *Rana ridibunda* (No. 2) obtained in 1978 from a mating, *rid* T♀, No. 2×*rid* T♂, No. 4. The results showed that the backcrosses were all of the RR-type in external appearance. When the electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 19 of the backcrosses, all the backcrosses were of the $R^T \cdot R^G$-type.

It seems evident that the four LR-type male hybrids (Nos. 21, 22, 24 and 25) obtained from matings, *les* I♀, ×*esc* G♂, eliminated the L-genome and produced spermatozoa retaining the R-genome alone. On the other hand, it is evident from the data in Table 25 that male *Rana esculenta* from West Germany No. 1 (*esc* G♂, No. 1) produced two kinds of spermatozoa, one of which contained the R-genome

and the other contained the L-genome. The LR-type male hybrids, Nos. 21, 22, 24 and 25, obtained by fertilization with the R-spermatozoa were sex-reversed genetic females, in contrast to the eight LL-type male hybrids, Nos. 1, 2, 6~8, 16~18, which were obtained by fertilization with the L-spermatozoa and produced nearly an equal number of males and females. Thus, it is believed that the R- and the L-genome include the X- and the Y-chromosome, respectively.

3. Offspring of male hybrids between a female *Rana ridibunda* from Turkey and two kinds of males

a. Offspring of male intraspecific hybrids, *rid* T♀ × *rid* F♂

In 1978, three 1-year-old male intraspecific hybrids (Nos. 1~3) obtained in 1977 from a mating, *rid* T♀, No. 1 × *rid* F♂, No. 3, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 6 and 7) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. The three males were of the RR-type in external appearance and of the $R^T \cdot R^F$-type in electrophoretic patterns. The offspring between these males and the female *Rana lessonae* were all of the LR-type in external appearance. The electrophoretic patterns of two blood proteins, Hb and Ab, and eight enzymes, LDH–B, PGM, 6–PGD, MPI, ALD, Pep–A, GPI and AAT–B, were examined in 30 males and females of the offspring. The results showed that all the offspring were of the $L^L \cdot R^{T-F}$-type in electrophoretic patterns (Table 30).

The phenotypes of Hb, PGM, 6–PGD, Pep–A, GPI and AAT–B were *de*, *bc*, *be*, *eb*, *dd* and *cb*, respectively. The phenotype of Ab was *dh* or *dg* in the offspring of males Nos. 1 and 3, while it was *dh* or *df* in the offspring of male No. 2. The phenotypes of LDH–B, MPI and ALD were *ed* or *eb*, *ha* or *hf*, and *da* or *dc*, respectively, in the offspring obtained from males Nos. 1 and 2, while they were *ed*, *hc* or *hf*, and *da* or *dg*, respectively, in the offspring obtained from male No. 3. Thus, the electrophoretic patterns of the offspring between the female *Rana lessonae* and the male *Rana ridibunda* were all of the $L^L \cdot R^{T-F}$-type (Table 30).

b. Offspring of male interspecific hybrids, *rid* T♀ × *esc* G♂

In 1978, five 1-year-old male hybrids (Nos. 1~5) obtained in 1977 from a mating, *rid* T♀, No. 1 × *esc* G♂, No. 1, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 8 and 9) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. Of these five male hybrids, three (Nos. 1~3) were of the RR-type in external appearance and of the $R^T \cdot R^G$-type in electrophoretic patterns, and two (Nos. 4 and 5) were of the RL-type in external appearance and of the $R^T \cdot L^G$-type in electrophoretic patterns. The results of matings showed that the offspring of the RR-type males (Nos. 1~3) were all of the LR-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 20 females and four males of the offspring. It was found that the phenotypes of six kinds were uniform, while those of the other four were not. The phenotypes of Ab, LDH–B and GPI were *dh* or *dg*, *eb* or *ed*, and *dd* or *db*, respectively. The phenotype of

ALD was always *dc* or *dg* in the offspring from males Nos. 1 and 3, while it was *dg* in the offspring from male No. 2. The electrophoretic patterns of these offspring were all of the $L^{L}\cdot R^{T-G}$-type, as expected (Table 30).

On the other hand, the offspring obtained from matings with RL-type male hybrids were all of the LL-type. When the phenotypes of Hb, Ab and LDH–B were examined in six male offspring which were comparatively rapid in growth, they were *dd*, *dd* and *ee*, respectively, and the same ($L^{L}\cdot L^{G}$-type) as those of *Rana lessonae* from Luxembourg. Thus, it is evident that the RL-type males produced spermatozoa including the L-genome alone (Table 30).

4. Offspring of male hybrids between a female *Rana ridibunda* from Soviet Union and four kinds of males

a. Offspring of male intraspecific hybrids, *rid* S♀ × *rid* F♂

In 1978, three 1-year-old male intraspecific hybrids (Nos. 1～3) obtained in 1977 from a mating, *rid* S♀, No. 1 × *rid* F♂, No. 3, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 6 and 7) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. All the offspring were of the LR-type in external appearance. The electrophoretic patterns of two kinds of blood proteins, Hb and Ab, and eight kinds of enzymes extracted from skeletal muscles and livers, LDH–B, PGM, 6–PGD, MPI, ALD, Pep–A, GPI and AAT–B, were examined in 13 females and three males of the offspring. The results showed that the phenotypes of Hb, PGM, 6–PGD, Pep–A and AAT–B were *de*, *bc*, *be*, *eb* and *cb*, respectively, in all the 16 offspring. However, the phenotype of Ab was *dg* in all six offspring of male No. 1, *dg* or *dh* in those of male No. 2 and *dg* or *df* in those of No. 3. The phenotype of LDH–B was *eb* or *ed* in the offspring of male No. 1, *eb* in those of male No. 2 and *ed* in those of male No. 3. The phenotype of MPI was *hc* in the offspring of male No. 1 and *hc* or *ha* in those of males Nos. 2 and 3. The phenotype of ALD was *da* or *dg* in the offspring of males Nos. 1 and 3, and *da* or *dc* in the offspring of male No. 2. The phenotype of GPI was *dd* and *db* in the offspring of males Nos. 1 and 2, respectively, and *dd* or *db* in the offspring of male No. 3. Thus, these electrophoretic patterns were of the $L^{L}\cdot R^{S-F}$-type (Table 30).

b. Offspring of male intraspecific hybrids, *rid* S♀ × *rid* T♂

In 1978, three 1-year-old male intraspecific hybrids (Nos. 2～4) obtained in 1977 from a mating, *rid* S♀, No. 1 × *rid* T♂, No. 2, were mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 8 and 9) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. All the offspring were of the LR-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 22 offspring including 12 males and females produced from males Nos. 2 and 3 which were *bd* and *cb* in the phenotypes of LDH–B and MPI, respectively, and 10 males and females produced from male No. 4 which was *cf* in the phenotype of MPI. The results showed that eight kinds of blood proteins and enzymes, Hb, Ab, PGM, 6–PGD, ALD, Pep–A, GPI

and AAT–B were *de*, *dh*, *bc*, *be*, *dg*, *eb*, *dd* and *cb*, respectively, in all the 22 offspring. However, the phenotypes of LDH–B and MPI were *eb* or *ed*, and *hc* or *hb*, respectively, in 12 offspring produced from males Nos. 2 and 3, and *ed* and *hc* or *hf* in 10 offspring produced from male No. 4. These electrophoretic patterns were of the $L^{L}\cdot R^{S-T}$-type (Table 30).

c. Backcrosses of a male interspecific hybrid, *rid* S♀ × *les* L♂

In 1978, a 1-year-old RL-type male (No. 2) obtained in 1977 from a mating, *rid* S♀, No. 1 × *les* L♂, No. 3, was mated with a 2-year-old female (No. 10) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. The offspring produced from this mating were all of the LR-type in external appearance and almost all of them were females. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in eight of the offspring. The results showed that all the eight offspring were of the $L^{L}\cdot R^{S}$-type. Thus, it is believed that male No. 2 obtained from the mating, *rid* S♀ × *les* L♂, produced only spermatozoa including the R-genome derived from the *Rana ridibunda* from Soviet Union (Table 30).

d. Offspring of a male interspecific hybrid, *rid* S♀ × *esc* G♂

In 1978, a 1-year-old RR-type male (No. 3) obtained in 1977 from a mating, *rid* S♀, No. 1 × *esc* G♂, No. 1, was mated with two 2-year-old female *Rana lessonae* from Luxembourg (Nos. 11 and 12) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. The male (No. 3) was of the $R^{S}\cdot R^{G}$-type in phenotypes of the 10 kinds of blood proteins and enzymes. The offspring produced from the two matings were all of the LR-type in external appearance. When the phenotypes of the foregoing 10 kinds of blood proteins and enzymes were examined in eight males and females of the offspring, all of the latter were of the $L^{L}\cdot R^{S-G}$-type (Table 30).

XI. External appearance and electrophoretic patterns of the offspring of female hybrids

1. Offspring of female hybrids between female *Rana lessonae* from Luxembourg and four kinds of males

a. Backcrosses of female interspecific hybrids, *les* L♀ × *rid* F♂

i) Experiment I

In 1977 and 1978, nine LR-type female hybrids in total including five 2-year-old females (Nos. 1~5) and four 3-year-old females (Nos. 6~9) obtained in 1975 from a mating, *les* L♀, No. 1 × *rid* F♂, No. 1, were mated with six male *Rana lessonae* from Luxembourg in total, including four 2-year-old males (Nos. 1~4) obtained in 1975 from a mating, *les* L♀, No. 1 × *les* L♂, No. 1, and two 2-year-old males (Nos. 5 and 6) obtained in 1976 from a mating, *les* L♀, No. 2 × *les* L♂, No. 2. In the offspring produced from these female hybrids, there were both diploids raised from normal-size eggs and triploids raised from large eggs. The

diploid frogs were various in external appearance from an approximate LL-type to an approximate LR-type. In contrast, the triploid frogs were uniform in external appearance and of the LLR-type, that is, being intermediate between the LL-type and the LR-type.

The electrophoretic patterns of two kinds of blood proteins, Hb and Ab, and eight kinds of enzymes extracted from skeletal muscles and livers, LDH–B, PGM, 6–PGD, MPI, ALD, Pep–A, GPI and AAT–B, were examined in three to six diploid backcrosses from each mating, 45 male and female backcrosses in total. The results showed that the phenotype of each of the 10 kinds of blood proteins and enzymes was of the $L^L \cdot L^L$- or $R^F \cdot L^L$-type. The phenotype of Hb was *dd* ($L^L \cdot L^L$-type) or *ed* ($R^F \cdot L^L$-type), Ab was *dd* ($L^L \cdot L^L$-type) or *gd* ($R^F \cdot L^L$-type), LDH–B was *ee* ($L^L \cdot L^L$-type) or *de* ($R^F \cdot L^L$-type), PGM was *bb*($L^L \cdot L^L$-type) or *cb* ($R^F \cdot L^L$-type), 6–PGD was *bb* ($L^L \cdot L^L$-type) or *eb* ($R^F \cdot L^L$-type), MPI was *hh* ($L^L \cdot L^L$-type) or *ch* ($R^F \cdot L^L$-type), ALD was *dd* ($L^L \cdot L^L$-type) or *ad* ($R^F \cdot L^L$-type), Pep–A was *ee* ($L^L \cdot L^L$-type) or *be* ($R^F \cdot L^L$-type), GPI was *dd* ($L^L \cdot L^L = R^F \cdot L^L$), and AAT–B was *cc* ($L^L \cdot L^L$-type) or *bc* ($R^F \cdot L^L$-type). Thus, the electrophoretic patterns of the 10 kinds of blood proteins and enzymes are of the $L^L \cdot L^L$- or $R^F \cdot L^L$-type. The electrophoretic pattern of the diploid offspring obtained from backcrossing, (*les* L♀ × *rid* F♂)♀ × *les* L♂, is called L^L–$R^F \cdot L^L$-type (Table 30).

On the other hand, nine mature backcrosses raised from large eggs of female No. 7 were triploids which were of the LLR-type, being intermediate between the LL-type and the LR-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in four of the triploid backcrosses. The results showed that all of them were of the $L^L \cdot L^L \cdot R^F$-type (Table 30).

ii) Experiment II

In 1978, ten 2-year-old LR-type females including four (Nos. 10~13) obtained in 1976 from a mating, *les* L♀, No. 2 × *rid* F♂, No. 2, and six (Nos. 14~19) obtained in 1976 from a mating, *les* L♀, No. 3 × *rid* F♂, No. 2, were mated with four 2-year-old male *Rana lessonae* from Luxembourg in total, including two (Nos. 7 and 8) obtained in 1976 from a mating, *les* L♀, No. 2 × *les* L♂, No. 2, and two (Nos. 9 and 10) obtained in 1976 from a mating, *les* L♀, No. 3 × *les* L♂, No. 2. The offspring raised from normal-size eggs were diploids and various in external appearance from an approximate LL-type to an approximate LR-type. The electrophoretic patterns of the foregoing 10 blood proteins and enzymes were examined in 40 males and females of the diploid offspring. It was found that the electrophoretic patterns, Hb, LDH–B, PGM, 6–PGD, MPI and ALD, were the same as those found in the diploid offspring of the females obtained from a mating, *les* L♀, No. 1 × *rid* F♂, No. 1, in experiment I, but the electrophoretic patterns of the other Ab, Pep–A, GPI and AAT–B differed from those of the latter. The phenotype of Ab was *dd* or *fd* in the backcrosses of female hybrids Nos. 10, 13, 15, 17 and 18, while it was *dd* or *hd* in those of female hybrids Nos. 11, 12, 16 and 19. The phenotype of Pep–A was *ee* or *ae* in the backcrosses of female hybrids Nos. 10, 13, 17 and 19, while it was *ee* or *be* in those of female hybrids

Nos. 11, 12, 15, 16 and 18. The phenotype of GPI was *dd* in the backcrosses of female hybrids Nos. 10, 12, 13, 16 and 17, while it was *dd* or *bd* in those of female hybrids Nos. 11, 15, 18 and 19. The phenotype of AAT–B was *cc* in the backcrosses of female hybrids Nos. 10, 11, 15, 17 and 18, while it was *cc* or *bc* in the backcrosses of female hybrids Nos. 12, 13, 16 and 19. Thus, it is evident that the phenotype of each of the four kinds of substances in the backcrosses of each female hybrid differed from that in the backcrosses of the other female hybrids. Although the electrophoretic patterns of these blood proteins and enzymes had not been examined in the backcrosses of female hybrid No. 14, the foregoing electrophoretic patterns were of the L^L–$R^F \cdot L^L$-type (Table 30).

On the other hand, the frogs raised from large eggs which were obtained from female hybrids Nos. 13, 15～19 produced from matings, *les* L♀, Nos. 2 and 3×*rid* F♂, No. 2, were all triploids. These triploids were of the LLR-type and uniform in external appearance. The electrophoretic patterns of the above 10 kinds of blood proteins and enzymes were examined in 19 male and female LLR-type offspring of female hybrids Nos. 15～19. The results showed that the phenotype of Hb was *dde*, LDH–B was *eed*, PGM was *bbc*, 6–PGD was *bbe*, MPI was *hhc*, and ALD was *dda* in all the offspring. The phenotype of Ab in the offspring of female hybrids Nos. 15, 17 and 18 was *ddf*, while that in the offspring of female hybrids Nos. 16 and 19 was *ddh*. The phenotype of Pep–A in the offspring of female hybrids Nos. 15, 16 and 18 was *eeb*, while that in the offspring of Nos. 17 and 19 was *eea*. The phenotype of GPI in the offspring of female hybrids, Nos. 15, 18 and 19, was *ddb*, while that in the offspring of Nos. 16 and 17 was *ddd*. The phenotype of AAT–B in the offspring of female hybrids Nos. 15, 17 and 18 was *ccc*, while that in the offspring of Nos. 16 and 19 was *ccb*. Thus, it seems evident that the electrophoretic patterns of the triploid backcrosses were of the $L^L \cdot L^L \cdot R^F$-type (Table 30).

b. Backcrosses of female interspecific hybrids, *les* L♀×*rid* T♂

In 1978, three 2-year-old female interspecific hybrids (Nos. 1～3) obtained in 1976 from matings, *les* L♀, Nos. 2 and 3×*rid* T♂, No. 1, were backcrossed with a 2-year-old male *Rana lessonae* from Luxembourg (No. 11) obtained in 1976 from a mating, *les* L♀, No. 3×*les* L♂, No. 2. In the backcrosses produced from these matings, there were both diploids raised from normal-size eggs and triploids raised from large eggs. The diploid backcrosses were various in external appearance from an approximate LL-type to an approximate LR-type, while all the triploids were uniform in external appearance, being of the LLR-type intermediate between the LL-type and the LR-type.

The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in a total of 16 diploid backcrosses including four, six and six produced from female hybrids Nos. 1, 2 and 3, respectively. It was found that all the electrophoretic patterns were of the L^L–$R^T \cdot L^L$-type. As the phenotype of ALD in female hybrid No. 1 was *dc* and that in female hybrids Nos. 2 and 3 was *dg*, the phenotype of ALD was *dd* or *cd* in the offspring of female hybrid No. 1

and *dd* or *gd* in the offspring of Nos. 2 and 3. Of the other nine blood proteins and enzymes, the phenotype of Hb was *dd* or *ed*, that of Ab was *dd* or *hd*, that of LDH–B was *ee* or *de*, that of PGM was *bb* or *cb*, that of 6–PGD was *bb* or *eb*, that of MPI was *hh* or *bh*, that of Pep–A was *ee* or *ae*, that of GPI was *dd* alone and that of AAT–B was *cc* or *bc* in all the offspring of female hybrids Nos. 1～3 (Table 30).

The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in a total of 16 LLR-type triploids including four, six and six produced from female hybrids Nos. 1, 2 and 3, respectively. The results showed that the phenotypes of Hb, Ab, LDH–B, PGM, 6–PGD, MPI, Pep–A, GPI and AAT–B were *dde*, *ddh*, *eed*, *bbc*, *bbe*, *hhb*, *eea*, *ddd* and *ccb*, respectively, while the phenotype of ALD was *ddc* in four offspring of female hybrid No. 1 and *ddg* in 12 offspring of Nos. 2 and 3. Thus, these electrophoretic patterns were of the $L^L \cdot L^L \cdot R^T$-type (Table 30).

c. Backcrosses of female intraspecific hybrids, *les* L♀ × *les* I♂

In 1978, two 1-year-old female intraspecific hybrids (Nos. 3 and 4) obtained in 1977 from matings, *les* L♀, Nos. 4 and 5 × *les* I♂, Nos. 1 and 2, were backcrossed with four 1-year-old male *Rana lessonae* from Luxembourg (Nos. 12～15) obtained in 1977 from a mating, *les* L♀, No. 4 × *les* L♂, No. 3. All the offspring were of the LL-type in external appearance. The electrophoretic patterns of the foregoing 10 kinds of blood proteins and enzymes were examined in 10 of the offspring. The phenotype of AAT–B was *cc* ($L^L \cdot L^L$-type) or *bc* ($L^I \cdot L^L$-type). The phenotypes of the other nine blood proteins and enzymes were all homozygous, as the $L^L \cdot L^L$ and $L^I \cdot L^I$ were not distinguished from each other. Thus, these electrophoretic patterns were of the $L^{L-I} \cdot L^L$-type (Table 30).

d. Backcrosses of female interspecific hybrids, *les* L♀ × *esc* G♂

In 1978, two 1-year-old female hybrids (Nos. 1 and 2) obtained in 1977 from a mating, *les* L♀, No. 4 × *esc* G♂, No. 1, were backcrossed with a 1-year-old male *Rana lessonae* from Luxembourg (No. 16) obtained in 1977 from a mating, *les* L♀, No. 4 × *les* L♂, No. 3. The female hybrids obtained from the former mating were all of the LR-type in external appearance. Two of them were used as the female parents to produce backcrosses. It was found that all the backcrosses were of the RL-type in external appearance. When the electrophoretic patterns of the above 10 blood proteins and enzymes were examined in 12 males and females of the backcrosses, the phenotypes of Hb, Ab, LDH–B, PGM, 6–PGD, MPI, ALD, Pep–A, GPI and AAT–B were all of the $R^G \cdot L^L$-type, that is, *ed*, *gd*, *be*, *cb*, *eb*, *fh*, *gd*, *be*, *bd* and *bc*, respectively (Table 30). Thus, it is evident that the LR-type female hybrids obtained from a mating, *les* L♀ × *esc* G♂, eliminated the *Rana lessonae* genome and produced eggs containing the *Rana ridibunda* genome alone.

2. Offspring of female hybrids between female *Rana lessonae* from Italy and two kinds of males

a. Backcrosses of female intraspecific hybrids, *les* I♀ × *les* L♂

In 1978, five 1-year-old female intraspecific hybrids (Nos. 1～5) obtained in 1977 from matings, *les* I♀, Nos. 1 and 2×*les* L♂, No. 3, were backcrossed with four 1-year-old male *Rana lessonae* from Luxembourg (Nos. 12～15) obtained in 1977 from a mating, *les* L♀, No. 4×*les* L♂, No. 3. The offspring were all of the LL-type in external appearance. The electrophoretic patterns of the above 10 blood proteins and enzymes were examined in 18 offspring of four female intraspecific hybrids (Nos. 1, 3, 4 and 5). The results showed that the phenotypes of the eight blood proteins and enzymes except MPI and AAT-B were all of the $L^L \cdot L^L$ ($=L^I \cdot L^I$)-type. The electrophoretic patterns derived from *Rana lessonae* from Italy could not be distinguished from those derived from *Rana lessonae* from Luxembourg. The phenotype of AAT-B was *cc* ($L^L \cdot L^L$-type) in eight of the 18 offspring, and *bc* ($L^I \cdot L^L$-type) in the others. The phenotype of MPI was *hh* in three and *ih* ($L^I \cdot L^L$-type) in three of six offspring of a female hybrid (No. 3) obtained from a mating, *les* I♀, No. 2×*les* L♂, No. 3, as the electrophoretic pattern of MPI in *Rana lessonae* from Italy was dimorphic (*h* and *i*) and the female hybrid (No. 3) was heterozygous (*ih*). In 12 offspring produced from the other three female hybrids (Nos. 1, 4 and 5), the phenotype of MPI was *hh*. The electrophoretic pattern of MPI derived from *Rana lessonae* from Italy and that from *Rana lessonae* from Luxembourg could not be distinguished from each other. It is considered that the backcrosses were of either the $L^I \cdot L^L$-type or the $L^L \cdot L^L$-type in electrophoretic patterns. Thus, these electrophoretic patterns were of the $L^{I-L} \cdot L^L$-type (Table 30).

b. Backcrosses of female interspecific hybrids, *les* I♀×*esc* G♂

In 1978, six 1-year-old LR-type females (Nos. 1～6) obtained in 1977 from matings, *les* I♀, Nos. 1 and 2×*esc* G♂, No. 1, were backcrossed with two 1-year-old male *Rana lessonae* from Luxembourg (Nos. 17 and 18) obtained in 1977 from a mating, *les* L♀, No. 5×*les* L♂, No. 4. These backcrosses were all of the RL-type in external appearance. The electrophoretic patterns of the above 10 kinds of blood proteins and enzymes were examined in 50 of the backcrosses. The results showed that they were all of the hybrid patterns. The phenotypes of Hb, Ab, LDH-B, PGM, 6-PGD, MPI, ALD, Pep-A, GPI and AAT-B were *ed*, *gd*, *be*, *cb*, *eb*, *fh*, *gd*, *be*, *bd* and *bc*, respectively, that is, all of them were of the $R^G \cdot L^L$-type. Thus, it is evident that the female hybrids obtained from the matings, *les* I♀, Nos. 1 and 2×*esc* G♂, No. 1, eliminated the *Rana lessonae* genome and produced only eggs retaining the *Rana ridibunda* genome derived from the male *Rana esculenta* (Table 30).

DISCUSSION

1. Historical review of *Rana esculenta*

The scientific name *Rana esculenta* of the edible frog was given by LINNÉ (1758), which is a member of the green frog or water frog complex distributed widely in

Europe. *Rana ridibunda* is another member named by PALLAS (1771). This frog is larger than *R. esculenta* and mostly found in middle and eastern Europe. PFLÜGER and SMITH (1883) have made a crossing experiment between *R. esculenta* commonly found in Germany and a population of large green frogs known as the Berlin race which corresponds to *Rana ridibunda* named by PALLAS. The results showed that eggs developed normally and became healthy tadpoles. Although metamorphosed frogs were not obtained owing to insufficient care, PFLÜGER and SMITH have considered that the Berlin race cannot be regarded as a valid species, as healthy tadpoles are produced between them. Thereafter, CAMERANO (1883) has reported *Rana esculenta* var. *lessonae* from Italy and SEOANE (1885) has described *Rana esculenta perezi* from Spain. Since 1789, many new species, new subspecies and new varieties have been reported in the green frog complex besides the foregoing four kinds of frogs, but only these four kinds survive at present as European green frogs. Moreover, it is only *Rana esculenta* that the scientific name has not been changed from the beginning, for the taxonomic situations of the other three kinds of frogs have been changed several times.

BOULENGER (1891) has believed that the green frog complex widely distributed in the Palearctic region including *Rana nigromaculata* from the East Asia belongs to a single species *Rana esculenta*, by examining minutely the specimens collected from various districts. On the basis of morphological observations, BOULENGER has divided *R. esculenta* into four forms, forma typica and three varieties including *ridibunda*, *lessonae* and *nigromaculata*. *Rana esculenta* var. *perezi* described by SEOANE is regarded as a synonym of *ridibunda*. NIKOL'SKII (1918) has divided *Rana esculenta* into *R. e. esculenta*, *R. e. ridibunda* and *R. e. lessonae*.

MERTENS(1925) has placed *ridibunda* as a valid species and *perezi* as a subspecies of *Rana ridibunda*. According to MERTENS, the common ancestor of *R. esculenta* and *R. ridibunda* was divided into western and eastern populations and differentiated into these two species during the glacial age. After this age, the two species expanded their distribution toward the central Europe with overlapping in many areas. TERENTJEV (1927) has divided *Rana ridibunda* into *R. r. ridibunda* with long hind legs and *R. r. saharica* with short hind legs, and has also divided *Rana esculenta* into *R. e. esculenta* with long hind legs and *R. e. lessonae* with short hind legs. KAURI (1954) has not be able to distinguish *R. ridibunda* from *R. esculenta* and has insisted that all the green frogs distributed in Europe and Central Middle East should be included in *Rana esculenta*. In contrast, MERTENS and WERMUTH (1960) have again distinguished *R. ridibunda* as a valid species from *R. esculenta*, and *perezi* as a subspecies of *R. ridibunda*, while they have regarded *R. lessonae* as a synonym of *R. esculenta*.

BERGER (1955) has discovered *Rana ridibunda*-like frogs in a national park near Poznań, Poland, besides *R. esculenta lessonae* which are abundantly found in this district. The results of examining many tadpoles and froglets collected from Poznań and its vicinity have shown that there are three forms, *R. esculenta ridibunda*, *R. e. esculenta* and *R. e. lessonae*. While *R. ridibunda* usually lives in lakes or rivers, the other two live in ponds. When he examined tadpoles and froglets

from two shallow ponds in Ostrów district situated southeast of Poznań, two species, *R. esculenta* and *R. ridibunda*, could be evidently distinguished from each other and there were no intermediate forms. Thereafter, he (1966) has examined the frogs collected from many lakes and ponds distributed in the suburbs of Poznań by measuring various sites of the body. The results showed that the frogs can be sorted into three groups of sizes, large, middle and small, and there are no intermediates among the three groups. As they were considered to be three independent species, *R. ridibunda*, *R. esculenta* and *R. lessonae*, he (1967) made crossing experiments among them and examined the development and viability of the embryos and tadpoles produced from these crossings. It has been found that *R. esculenta* is very inferior in reproductive capacity and presumably a hybrid between the other two species. When metamorphosed frogs obtained from various combinations among three species were observed, the following facts were confirmed. While the same species as the parents are obtained from *R. ridibunda* and *R. lessonae*, the offspring of *R. esculenta* or those between *R. esculenta* and *R. ridibunda* are almost *R. ridibunda*. The offspring between *R. lessonae* and *R. esculenta* or between *R. lessonae* and *R. ridibunda* are *R. esculenta*. On the basis of these results of crossings, BERGER (1968) has concluded that *R. esculenta* is a hybrid between *R. ridibunda* and *R. lessonae*, both of which are valid species. BERGER (1971) has reported on the sex ratios of the frogs produced in 1963～1969 from nine kinds of combinations among *R. ridibunda*, *R. esculenta* and *R. lessonae*. He (1976, 1977) has reported on many crossing experiments performed by using frogs produced by his experiments and confirmed the results obtained previously. The results of these experiments showed that the sex ratio of offspring is determined by the paternal parent. If the latter is *R. lessonae* or *R. ridibunda*, the sex ratio is always 1 : 1 regardless of the maternal parent. In contrast, when the paternal parent is *R. esculenta*, it is shifted in the direction of one sex, and only female offspring are produced in most cases. However, when paternal *R. esculenta* derived from female *R. lessonae* and male *R. ridibunda* are mated with maternal *R. esculenta*, almost all of the offspring are males.

GÜNTHER (1967, 1968) has confirmed that *R. ridibunda* and *R. esculenta* are overlapped in distribution with each other in wide areas surrounding Berlin and Leipzig, although these two species are ecologically isolated from each other. He (1970) has found seven triploids among 24 *R. esculenta* typica named by BOULENGER (1891), and considered that the appearance of many triploids indicates the inferiority of *R. esculenta* in reproductive capacity and that this meager reproductive capacity is due to its hybridism between *R. ridibunda* and *R. lessonae*. GÜNTHER (1973) has made various kinds of mating experiments among *R. ridibunda*, *R. esculenta* and *R. lessonae*, and has found that *R. esculenta* is always inferior in reproductive capacity, the matings between female and male *R. esculenta* being especially inferior in fertilization. While most of the frogs obtained from this kind of matings are of the *R. esculenta* type, there are frogs of the *R. ridibunda* type or of the intermediate type between *R. esculenta* and *R. lessonae*. Reciprocal hybrids between *R. ridibunda* and *R. lessonae* are almost all of the *esculenta* type and are remarkably inferior in reproductive capacity. By comparing the artificial hybrids between *R. ridibunda*

and *R. lessonae* with *R. esculenta* distributed in the field, GÜNTHER has assumed that *R. esculenta* is a hybrid between *R. ridibunda* and *R. lessonae*, as BERGER had already proposed. He has proposed that *R. esculenta* should be treated with quotation marks, "*Rana esculenta*", as this is not a valid species.

BLANKENHORN, HEUSSER and VOGEL (1971) have made four kinds of mating experiments among *R. ridibunda*, *R. esculenta* and *R. lessonae* collected from the neighborhood of Zürich. The results have shown that all the offspring between female and male *R. esculenta* die at the tadpole stage, while all the hybrids between female *R. esculenta* and male *R. lessonae* become frogs of the *R. esculenta* type. These results are the same as those obtained by BERGER in Polish green frogs. BLANKENHORN (1973) and BLANKENHORN, HEUSSER and NOTTER (1973) have observed the distribution of the green frog complex in the neighborhood of Zürich and have confirmed that *R. esculenta* coexists with *R. ridibunda* in the western area, while it coexists with *R. lessonae* in the eastern area. According to BLANKENHORN (1977), the tadpoles produced between female and male *R. esculenta* all die within 4~8 weeks, although this kind of matings occurs frequently. While the crossings between female *R. lessonae* and male *R. esculenta* seldom occur, the reciprocal crossings easily occur and produce female and male *R. esculenta*.

TUNNER (1970, 1972) and ENGELMANN (1972, 1973) have examined the three kinds of green frogs, *R. esculenta*, *R. ridibunda* and *R. lessonae*, distributed sympatrically in Europe by electrophoretically analyzing their serum proteins. The results have evidently demonstrated that *R. esculenta* is a hybrid between *R. ridibunda* and *R. lessonae*. TUNNER (1973) has also analyzed the serum proteins of these species collected by BERGER from the environs of Poznań as well as those of hybrids and backcrosses obtained by BERGER, and has confirmed that *R. esculenta* is undoubtedly a hybrid between *R. ridibunda* and *R. lessonae*. The finding that *R. esculenta* is a hybrid between *R. ridibunda* and *R. lessonae* has been repeatedly confirmed by many investigators, including ENGELMANN (1974), UZZELL and BERGER (1975), TUNNER and DOBROWSKY (1976), VOGEL and CHEN (1976a, b, 1977) and EBENDAL (1977) by analyzing serum proteins and several enzymes in green frogs collected from various areas of Europe.

2. Hybridogenesis

With the progress of both field observations and mating experiments, it has become gradually evident that *R. esculenta* somewhat differs from a usual interspecific hybrid. Although all the three species, *R. esculenta*, *R. ridibunda* and *R. lessonae*, exist together with one another in Poland, East Germany, Switzerland, etc., natural crossings between *R. ridibunda* and *R. lessonae* to produce *R. esculenta* seem to be observed only in Poland. In many districts of central Europe, the coexistence of two species, *R. esculenta* and *R. lessonae*, (E–L system) has been reported by many investigators. On the other hand, the coexistence of *R. esculenta* with *R. ridibunda* has been known in East and West Germany, Switzerland, etc. A solitary distribution of *R. esculenta* has also been reported in some districts in East and West Germany and Poland. It is an interesting problem to elucidate

how *R. esculenta* was produced without crossing between *R. ridibunda* and *R. lessonae*.

TUNNER (1973) has conducted mating experiments among the three green frog species sent by BERGER from Poland. From crossing between *R. lessonae* and *R. esculenta*, he has obtained only *R. esculenta* and no intermediate forms and also *R. ridibunda* from matings between female and male *R. esculenta*. These results seemed to indicate that free recombination of chromosomes does not occur in meioses of *R. esculenta*. TUNNER (1974) has confirmed these findings by observing the green frogs distributed in a district of Austria, where female and male *R. lessonae* and only female *R. esculenta* are found. As the female *R. esculenta* increases by mating with the male *R. lessonae*, it has been assumed that the eggs of *R. esculenta* should contain only the *ridibunda*-genome by elimination of the *lessonae*-genome. From this assumption, he has considered that *R. esculenta* of the L–E system reproduces by hybridogenesis. Concerning the femaleness of all the *R. esculenta*, TUNNER has assumed that this may be due to female heterogametism. However, as females and males are found at the rate of 1 : 1 in *R. esculenta* of L–E system distributed in Poland and East Germany, TUNNER and DOBROWSKY (1976) have considered that males are heterogametic in these cases. UZZELL and BERGER (1975) have also recognized that the reproduction of *R. esculenta* is due to hybridogenesis, as TUNNER proposed. In the populations of the R–E system, where *R. esculenta* exist together with *R. ridibunda*, *R. esculenta* seems to increase by hybridogenesis. In this case, their gametes may contain only the *lessonae*-genome, by elimination of the *ridibunda*-genome in contrast to *R. esculenta* in the L–E system. The hybridogenesis of *R. esculenta* has thereafter been repeatedly confirmed in populations consisting of a mixture of *R. esculenta* and *R. lessonae* or *R. ridibunda*, or of *R. esculenta* alone (UZZELL, GÜNTHER and BERGER, 1977; BERGER, 1977, 1983; TUNNER, 1978; HEPPICH, 1978; GÜNTHER, UZZELL and BERGER, 1979; UZZELL, HOTZ and BERGER, 1980; TUNNER and HEPPICH, 1981; HEPPICH, TUNNER and GREILHUBER, 1982; BINKERT, BORNER and CHEN, 1982; BERGER, UZZELL and HOTZ, 1982, etc.).

When BERGER (1967) made mating experiments between each of 35 pairs of female and male *R. esculenta*, numerous metamorphosed frogs were produced from only one pair, while only five metamorphosed frogs were obtained from four of the remaining pairs. According to him (1968, 1971, 1973), 166 of 172 metamorphosed frogs were of the *R. ridibunda* (RR)-type and the other six were of the *R. esculenta* (LR)-type. The mating experiments performed by GÜNTHER (1973) between female and male *R. esculenta* showed results somewhat differing from those obtained by BERGER, although these results agreed with the latter in that both females and males were very inferior in reproductive capacity. In the case of GÜNTHER's experiments, most of the offspring were of the *R. esculenta* (LR)-type, and the remainders were of the *R. ridibunda* (RR)- or *R. lessonae* (LL)-type. According to HEMMER (1977), no *R. ridibunda* have been found in the population of *R. esculenta*, as they are inferior in viability and cannot attain sexual maturity, even if they are produced by hybridogenesis. GÜNTHER (1975a) has observed the meiotic divisions in the testes of male diploid *R. esculenta*. Although the testes

are generally very abnormal in inner structure, normal first and second meiotic figures can be observed in almost all the males. However, no specific divisions supporting the mechanism of hybridogenesis have been found.

GRAF, KARCH and MOREILLON (1977) have discovered in south France a population which resulted from hybridization between *R. ridibunda* and *R. perezi*. This type of hybrids reproduces by hybridogenesis like *R. esculenta*. They have examined the enzyme phenotypes of oocytes I from hybrid females, and have confirmed the existence of only the *ridibunda*-type allozymes which are brought about by a premeiotic exclusion of the *perezi*-genome. The distribution of these two species in France and Spain has been elucidated by UZZELL and TUNNER (1983). UZZELL and HOTZ (1979) have described two forms of green frogs which almost certainly constitute hybridogenetic lineages in Italy. One of them is a scarcely heterozygous non-hybrid having mostly *lessonae*-like alleles, while the other is a highly heterozygous form having as a rule both *lessonae*-like and *ridibunda*-like alleles at the same loci.

In *Rana esculenta*, GRAF and MÜLLER (1979) have confirmed that the gynogenetic offspring of females are exclusively of the *ridibunda*-type. According to them, this is due to the premeiotic exclusion of the *lessonae*-genome from the germ cells of the hybrid females. No recombination has occurred between the two genomes. UZZELL, HOTZ and BERGER (1980) have also confirmed by evidence from electrophoresis of individual oocytes of female diploid *Rana esculenta* that the *lessonae*-genome is excluded premeiotically, although recombination between the parental genomes occurs at a low frequency. On the other hand, KOREF-SANTIBANEZ and GÜNTHER (1980) have reported that a small percentage of sympatric *R. lessonae* and *R. ridibunda* shows introgression of an albumin allele, while no gene introgression is found in allopatric *R. lessonae* and *R. ridibunda*. According to them, both recombination as well as introgression of the albumin and of several enzyme alleles have been found in most populations from GDR. BINKERT, BORNER and CHEN (1982) have reported that no total elimination of the *lessonae*-genome occurs in the *esculenta* germ cells, as the *lessonae*-specific alleles can be passed to the F_1 progeny from a parental female or male of the *esculenta*-phenotype. They have suggested the possibility of chromosomal recombination between *lessonae* and *ridibunda* in the hybrid *R. esculenta*. SPOLSKY and UZZELL (1984) have assumed that transfer of mit-DNA from *R. lessonae* to *R. ridibunda* probably occurs not directly but through *R. esculenta*.

The present authors (1977) reported on the isolating mechanisms between European and Far Eastern green frogs. They (1979) also reported on the results of mating experiments among European green frogs as well as between European and Far Eastern green frogs. Although the hybrids produced from crossing between European green frogs were reared until sexual maturity, their offspring were not examined. Moreover, some of the scientific names of the green frogs used in the crossing experiments were thereafter corrected principally on the basis of the results of electrophoretic analyses of blood proteins and several enzymes extracted from the skeletal muscles. It was found that *R. esculenta* from Italy is *R.*

lessonae, and *R. esculenta* from France is *R. ridibunda*. The present researches are the continuation of those reported by KAWAMURA and NISHIOKA (1979).

The green frogs used in the present studies are *R. lessonae* from Luxembourg and Italy, *R. ridibunda* from France, Turkey and Soviet Union and *R. esculenta* from West Germany. It was found that two male *R. esculenta* (Nos. 1 and 2) used in various crossings reproduce by hybridogenesis which remarkably differ from those reported previously by many investigators.

(1) One of the male *R. esculenta*, *esc* G♂, No. 1, was of the RL-type in external appearance and of the $R^G \cdot L^G$-type in electrophoretic phenotype. The results of various crossing experiments between this male and some other females presented in 12 tables (Nos. 5~8, 15, 19, 20, 24~27 and 30) do not seem to be reasonably explained by other than the following hypotheses: male *R. esculenta*, *esc* G♂, No. 1, produced two kinds of spermatozoa, L-sperm containing the *lessonae*-genome and R-sperm containing the *ridibunda*-genome. The Y-chromosome is included in the *lessonae*-genome, while the X-chromosome is in the *ridibunda*-genome.

The female hybrids produced from a mating, *les* L♀ or *les* I♀ × *esc* G♂, No. 1, were all of the LR-type ($L^L \cdot R^G$- or $L^I \cdot R^G$-type in electrophoretic pattern). The male hybrids produced from the same mating were mostly of the LL-type ($L^L \cdot L^G$- or $L^I \cdot L^G$-type). A part of the males were considered to be sex-reversed genetic females of the LR-type (Tables 5, 6 and 15). Six females produced from matings, *rid* T♀ or *rid* S♀ × *esc* G♂, No. 1, were of the RR-type ($R^T \cdot R^G$- or $R^S \cdot R^G$-type). Six males produced from the same mating were of the RL-type ($R^T \cdot L^G$- or $R^S \cdot L^G$-type). Five males of the RR-type were considered to be sex-reversed genetic females (Tables 7, 8 and 15).

The LL-type males obtained from *les* ♀ × *esc* G♂, No. 1, had testes which were completely normal in inner structure. These males produced offspring of the LL-type by mating with female *R. lessonae*, while they produced RL-type offspring by mating with a female *R. ridibunda* (Tables 24, 25 and 30). These offspring were approximately 1 : 1 in sex ratio. The LR-type males which were reversed from genetic females obtained from the same mating had testes which were various in inner structure from completely normal to abnormal. These males produced RR-type ($R^T \cdot R^G$-type) offspring by mating with female *R. ridibunda*, and nearly all of these offspring were females. It is evident that the male parents of the LR-type produced only R-sperm containing the *ridibunda*-genome by eliminating the *lessonae*-genome (Tables 24, 25 and 30). On the other hand, the LR-type females obtained from the same mating produced RL-type ($R^G \cdot L^L$- or $R^G \cdot L^I$-type) offspring by mating with male *R. lessonae*. These offspring were approximately 1 : 1 in sex ratio. It is evident that the female parents of the LR-type produced only R-eggs containing the *ridibunda*-genome by eliminating the *lessonae*-genome (Table 29).

Of two RL-type males (Nos. 4 and 5) obtained from female *R. ridibunda*, *rid* T♀, No. 1, and male *R. esculenta*, *esc* G♂, No. 1, one (No. 4) had testes which were almost normal in inner structure, while the testes of the other (No. 5) were somewhat abnormal. From these males, only LL-type male offspring were produced by mating with female *R. lessonae* from Luxembourg. Thus, it is evident

that the two RL-type males produced only L-sperm containing the *lessonae*-genome by eliminating the *ridibunda*-genome, and that the *lessonae*-genome includes the Y-chromosome (Tables 19, 26 and 30). Two RL-type males (Nos. 2 and 4) obtained from male *R. esculenta*, *esc* G♂, No. 1, by mating with a female *R. ridibunda* from Soviet Union had abnormal testes and were completely sterile.

Three RR-type males (Nos. 1~3) obtained from male *R. esculenta*, *esc* G♂, No. 1, by mating with a female *R. ridibunda* from Turkey and a RR-type male (No. 3) obtained from the same male by mating with a female *R. ridibunda* from Soviet Union had normal testes and produced R-sperm containing the *ridibunda*-genome (Tables 19, 20, 26, 27 and 30). One RR-type male (No. 1) obtained from *rid* S♀ × *esc* G♂, No. 1 had abnormal testes, containing almost degenerated spermatogonia.

(2) Another male *R. esculenta*, *esc* G♂, No. 2, was of the RL-type ($R^G \cdot L^G$-type). The hybrids obtained from this male by mating with female *R. ridibunda* (*rid* T♀, No. 2 × *esc* G♂, No. 2) were almost females of the RR-type ($R^T \cdot R^G$-type) (Tables 7 and 15). Thus, it is evident that this male produced only R-sperm containing the *ridibunda*-genome by eliminating the *lessonae*-genome, and that the R-sperm included only the X-chromosome.

It was found that the offspring of a male *R. ridibunda* from Soviet Union hybridized with a female *R. lessonae* from Italy uncommonly reproduced hybridogenetically. Twelve mature offspring of the LR-type were produced from *les* I♀, No. 2 × *rid* S♂, No. 1. All of them were males (Table 6). When the testes of 10 of these males were sectioned to examine the inner structures, only one male (No. 1) had small bundles of spermatozoa in a part of the testes, while the other males were completely sterile. Of eight backcrosses of this male mated with female *R. lessonae* from Italy, four attained sexual maturity and became males of the LR-type ($L^I \cdot R^S$-type). Thus, it is evident that the only male (No. 1) produced R-sperm containing the *ridibunda*-genome by eliminating the *lessonae*-genome. Although the backcrosses were only four in number, they seem to have Y-chromosome in the *ridibunda*-genome derived from male parent, *rid* S♂, No. 1, as all of them were males (Tables 25 and 30).

A similar case of hybridogenesis was found in the offspring of a female *R. ridibunda* from Soviet Union and a male *R. lessonae* from Luxembourg. Seven mature hybrids of RL-type were obtained from *rid* S♀, No. 1 × *les* L♂, No. 3. Of these hybrids, one was a female and six were males (Nos. 1~6). While three (Nos. 1, 4 and 5) of the males had almost completely degenerated testes, the other three (Nos. 2, 3 and 6) had testes which appeared to contain almost abnormal spermatozoa. When one (No. 2) of the six male hybrids was backcrossed with a female *R. lessonae*, 29.8% of the eggs cleaved normally and 51 eggs became metamorphosed frogs (Table 20). When the sex of 46 of these frogs was examined, it was found that 44 were females and two were males. All these frogs were of the LR-type (Table 27). Electrophoretic patterns of blood proteins and various enzymes analyzed in eight of them showed that all these frogs were of the $L^L \cdot R^S$-type. Thus, it is evident that the male hybrid (No. 2) produced only R-sperm

containing the *ridibunda*-genome by eliminating the *lessonae*-genome. As the X-chromosome is included in the *ridibunda*-genome, almost all the offspring seem to become females (Tables 27 and 30).

The hybridization between *R. lessonae* from Luxembourg or Italy and *R. ridibunda* from France, Turkey or Soviet Union always produce interspecific hybrids of the LR-type. The male hybrids are almost completely sterile except a few males obtained from two kinds of crossings, *les* I♀ × *rid* S♂ and *rid* S♀ × *les* L♂. In contrast, the female hybrids are fertile and produce female and male offspring by mating with male *R. lessonae*. By examining the electrophoretic patterns of the offspring of female hybrids between female *R. lessonae* from Luxembourg and male *R. ridibunda* from France or Turkey, it was evident that the recombination of chromosomes occurs during their oogenesis (Table 30).

In the intraspecific hybrids of *R. lessonae* as well as interspecific hybrids between female *R. lessonae* from Luxembourg or Italy and male *R. ridibunda* from France or Turkey, males are usually more numerous than females (Tables 5 and 6). The excess of males seems to be attributable to sex-reversal of females into males. The overwhelming majority of females in the offspring between female *R. ridibunda* from Turkey No. 2 and male *R. ridibunda* from Turkey No. 4 or *R. ridibunda* from Soviet Union No. 2 may be also attributable to the fact that the male was a sex-reversed genetic female (Table 7).

3. Triploids

The finding that female *R. esculenta* often lay eggs irregular in size has been reported by BERGER (1967) and GÜNTHER (1970). UZZELL, BERGER and GÜNTHER (1975) obtained a female hybrid from a crossing between a female *R. ridibunda* and a male *R. lessonae* collected from the neighborhood of Poznań, Poland, and examined the development of eggs laid by this female. They divided the eggs into large, middle and small ones. Backcrossings were made by fertilizing these three kinds of eggs with spermatozoa of *R. lessonae* or *R. ridibunda*. The results showed that all the frogs raised from small and middle eggs were diploids of the LR- or RR-type, while all the frogs raised from large eggs were triploids of the LLR- or RRL-type. These findings indicate that the small and middle eggs are haploid, containing a *R. ridibunda*-genome, while the large eggs are diploid, containing both *R. ridibunda*- and *R. lessonae*-genomes. UZZELL, BERGER and GÜNTHER (1975b) have considered that these diploid eggs are produced from first oocytes which are tetraploids.

According to UZZELL and BERGER (1975), UZZELL, BERGER and GÜNTHER (1975), GÜNTHER (1975b, 1979), GÜNTHER and HÄHNEL (1976), GÜNTHER, UZZELL and BERGER (1979), EBENDAL, BERGLUND and RYMAN (1981) and EBENDAL and UZZELL (1982), the triploids found in the populations of *R. esculenta* alone or a mixture of *R. esculenta* and *R. lessonae* are usually of the LLR-type, while those in the populations of *R. esculenta* and *R. ridibunda* are of the RRL-type. GÜNTHER (1975a) confirmed the existence of 13 chromosomes in the second meiosis and the formation of normal spermatozoa by examining the spermatogenesis in male

allotriploids, although the meioses of triploids are abnormal in most cases. According to GÜNTHER, UZZELL and BERGER (1979) and GÜNTHER (1979), the presence of the same two genomes derived from *R. lessonae* or *R. ridibunda* in male and female allotriploids is assumed to result in ready synapsis and producing haploid gametes, while the remaining genome is excluded. The triploids seem to perform an important role in the reproduction of the populations consisting of diploid and triploid *R. esculenta*.

The present authors (1978) have reported that allotriploids are produced from female reciprocal hybrids between two Japanese green frogs, *R. nigromaculata* and *R. brevipoda*, by backcrossing with males of the parental species. About one- or two-tenths of the female hybrids laid a considerable number of large eggs together with normal-size eggs. The large eggs are probably diploid ones derived from tetraploid oogonia. All these large eggs develop into triploid tadpoles by fertilization with normal spermatozoa. Numerous allotriploids have been obtained by NISHIOKA (1983) from females and males of reciprocal hybrids between *R. nigromaculata* and *R. plancyi chosenica* by backcrossing with the parental species. Females of reciprocal hybrids usually lay a few large eggs together with many normal-size ones. Almost all the large eggs as well as a few normal-size ones become triploids. Most of the eggs obtained from *R. nigromaculata* also become triploids by mating with males of reciprocal hybrids between the two species.

NISHIOKA and OHTANI (1984) have obtained a few female and male allotriploids together with abundant diploid hybrids from crossings between female *R. brevipoda* from Japan and male *R. lessonae* from Italy. They have also obtained many female and male allotriploids from the same crossings by refrigerating eggs after insemination. These allotriploids are constructed of two *brevipoda*-genomes and one *lessonae*-genome. The offspring of male allotriploids backcrossed with female *R. brevipoda* were completely of the *brevipoda*-type at the tadpole and adult stages. Almost all of them were females and the same as diploid *R. brevipoda* in the electrophoretic patterns of serum proteins, hemoglobin and various enzymes extracted from the skeletal muscles. All these findings indicate that normal haploid gametes are formed by normal meiosis between the two *brevipoda*-genomes after the single *lessonae*-genome was eliminated in the germ cells.

In the present studies, seven of 19 female hybrids between female *R. lessonae* from Luxembourg and male *R. ridibunda* from France and all of three female hybrids between female *R. lessonae* from Luxembourg and a male *R. ridibunda* from Turkey laid a few or a considerable number of large eggs together with many normal-size eggs (Table 21). All these large eggs became female and male allotriploids of the LLR-type by backcrossing with male *R. lessonae* from Luxembourg (Table 28). The genetic constitution of these allotriploids was confirmed by analyzing two blood proteins and eight enzymes obtained from each animal. It is yet unknown whether the single *ridibunda*-genome is eliminated in the germ cells of these allotriploids.

SUMMARY

1. Hybridization experiments were performed among *Rana lessonae* from Luxembourg (*les* L) and Italy (*les* I), *Rana ridibunda* from France (*rid* F), Turkey (*rid* T) and Soviet Union (*rid* S) and *Rana esculenta* from West Germany (*esc* G). There is no gametic isolation among these species and local populations. Any distinct difference in developmental capacity during the period from beginning of cleavage to completion of metamorphosis was scarcely found between interspecific or intraspecific hybrids and the controls.

2. Most of the metamorphosed frogs attained sexual maturity. In the control *les* L or I, there was nearly an equal number of males and females. In reciprocal hybrids between these two populations, males were somewhat more numerous than females. In the hybrids, *les* L♀ × *rid* F♂, and *rid* T♀ × *les* L♂ or *les* I♂, there was nearly an equal number of males and females. In the hybrids, *les* L♀ × *rid* T♂ or *esc* G♂, No. 1, and *les* I♀ × *rid* F♂, *rid* T♂ or *esc* G♂, No. 1, males were somewhat more numerous than females. Of the offspring obtained from *rid* T♀, No. 2 × *rid* T♂, No. 4, *rid* S♂, No. 2 or *esc* G♂, No. 2, an overwhelming majority was females.

3. The interspecific hybrids, *les* × *rid*, were all of the LR-type like *esc* in external appearance. In the hybrids, *les* L♀ or *les* I♀ × *esc* G♂, No. 1, there was nearly an equal number of the LL-type and LR-type frogs. Female hybrids which occupied about 40% were all of the LR-type, while of the remaining male hybrids about two-thirds or three-fourths were of the LL-type and the others were of the LR-type. The same male, *esc* G♂, No. 1, produced six female and 11 male offspring by matings with female *rid* T and *rid* S. All the female offspring were of the RR-type, while five and six of the male offspring were of the RR- and RL-type, respectively. These findings seem to show that the male, *esc* G♂, No. 1, produced two kinds of spermatozoa, one containing the *les*-genome with the Y-chromosome and the other containing the *rid*-genome with the X-chromosome by eliminating one of the two genomes. In contrast, almost all the hybrids obtained from a mating, *rid* T♀ × *esc* G♂, No. 2, were RR-type females. Thus, this male, *esc* G♂, No. 2, seems to have produced the one and only kind of spermatozoa containing the *rid*-genome with the X-chromosome by eliminating the *les*-genome with the Y-chromosome.

4. External characters of mature frogs belonging to two *les* populations, three *rid* populations, *esc* G and various kinds of intra- and interspecific hybrids were examined. The dorsal ground color, dark spots on the back and dorsomedian stripe were observed, and the body length, tibia length, first-toe length, and length and height of the inner metatarsal tubercles were measured.

5. Hemoglobin, serum albumin and 18 kinds of enzymes extracted from the skeletal muscles and livers of the foregoing six kinds of frogs were analyzed by the method of starch-gel electrophoresis. Electrophoretic patterns of a total of 26 loci of these proteins and enzymes were examined. In *les* L and *les* I, all of them

consisted of homozygous alleles, except ME–B in *les* L and MPI and α–GDH in *les* I. The electrophoretic patterns of these two populations are called the $L^L \cdot L^L$-type and $L^I \cdot L^I$-type, respectively. These two populations differ from each other in phenotypes of ADH–B, AAT–B and ME–B.

In *rid* F, *rid* T and *rid* S, 19, 21 and 20 of the above 26 loci consisted of homozygous alleles, respectively. The electrophoretic patterns of these three populations are called the $R^F \cdot R^F$-type, $R^T \cdot R^T$-type and $R^S \cdot R^S$-type, respectively. They slightly differed from one another in eight loci, Ab, LDH–B, PGM, MPI, ME–B, ALD, Pep–A and AAT–B, and completely differed from those of the two *les* populations in ten loci, Hb, Ab, LDH–B, 6–PGD, MPI, ME–B, ALD, Pep–A, ADH–B and SOD–A.

In the electrophoretic patterns of *esc* G, 14 of the 26 loci showed hybrid patterns consisting of two alleles derived from *rid* and *les*, while the others consisted of homozygous alleles. These electrophoretic patterns are called the $R^G \cdot L^G$-type.

6. In the intraspecific hybrids between *les* L and *les* I, between *rid* T and *rid* F, between *rid* T and *rid* S, and between *rid* S and *rid* F, the electrophoretic patterns were of the $L^L \cdot L^I$-, $R^T \cdot R^F$-, $R^T \cdot R^S$- and $R^S \cdot R^F$-type, respectively. In the interspecific hybrids between *les* L and *rid* F, between *les* L and *rid* T, between *les* L and *rid* S, between *les* I and *rid* F, between *les* I and *rid* T, and between *les* I and *rid* S, the electrophoretic patterns were of the $L^L \cdot R^F$-, $L^L \cdot R^T$-, $L^L \cdot R^S$-, $L^I \cdot R^F$-, $L^I \cdot R^T$- and $L^I \cdot R^S$-type, respectively.

In LL-type hybrids between *les* L♀ and *esc* G♂, No. 1, and between *les* I♀ and *esc* G♂, No. 1, the electrophoretic patterns were of the $L^L \cdot L^G$-type and $L^I \cdot L^G$-type. In LR-type hybrids from the same combinations, the electrophoretic patterns were of the $L^L \cdot R^G$-type and $L^I \cdot R^G$-type. In RR-type hybrids between *rid* T♀ and *esc* G♂, No. 1, and between *rid* S♀ and *esc* G♂, No. 1, the electrophoretic patterns were of the $R^T \cdot R^G$-type and $R^S \cdot R^G$-type. In the RR-type hybrids obtained from a mating, *rid* T♀, No. 2 × *esc* G♂, No. 2, the electrophoretic patterns were of the $R^T \cdot R^G$-type.

7. The testes of intraspecific hybrids of *les* or *rid* were normal and very similar to those of the controls in size and inner structure, except those of intraspecific hybrids between a female *rid* S and a male *rid* T. The testes of interspecific hybrids between female *les* L and male *rid* F or T, between female *les* I and male *rid* F, T or S, between female *rid* T and male *les* L or I, and between a female *rid* S and male *les* L or I were usually very abnormal and contained no normal spermatozoa, although there were a few exceptional cases, in which a few normal spermatozoa were found.

Of the interspecific hybrids between female *les* L or I and a male *esc* G♂, No. 1, those of the LL-type had normal testes containing compact bundles of normal spermatozoa, while those of the LR-type had almost or partially normal testes. Of the interspecific hybrids between female *rid* T or S and a male *esc* G♂, No. 1, those of the RR-type had mostly normal testes containing compact bundles of normal spermatozoa, while those of the RL-type had almost normal testes containing some normal spermatozoa or abnormal testes containing a few normal or

abnormal spermatozoa.

8. Male intraspecific hybrids of *les* or *rid* were slightly inferior to the control populations in reproductive capacity. Male interspecific hybrids between *les* and *rid* were usually sterile, although those obtained from matings, *les* I♀ × *rid* S♂ and *rid* S♀ × *les* L♂, were sometimes fertile to some extent and most of normally cleaved eggs became metamorphosed frogs. LL- or LR-type males of the interspecific hybrids between female *les* and male *esc* G♂, No. 1 were fairly fertile. RR- or RL-type males of the interspecific hybrids between a female *rid* T and male *esc* G♂, No. 1 were somewhat fertile and produced some metamorphosed frogs, while those between a female *rid* S and male *esc* G♂, No. 1 were mostly sterile.

9. In female intraspecific hybrids of *les*, ovulation occurred almost normally, and eggs were normal in developmental capacity. Ovulation occurred in 19 of 28 female interspecific hybrids between three female *les* L and two male *rid* F. While 12 of them laid only normal-size eggs, the other seven laid a mixture of normal-size and large eggs. These two kinds of eggs were almost normal in developmental capacity. Ovulation occurred in three of 15 female interspecific hybrids between two female *les* L and a male *rid* T. All these female hybrids laid a mixture of normal-size and large eggs. The two kinds of eggs were slightly inferior to those of the foregoing female interspecific hybrids in developmental capacity. Ovulation occurred in eight of 21 female hybrids between three female *les* L or I and male *esc* G♂, No. 1. The eggs were uniform in size and somewhat inferior in developmental capacity.

10. Control male *les* L or I produced nearly an equal number of males and females by mating with females of the same population. Males of reciprocal intraspecific hybrids between *les* L and *les* I produced nearly an equal number of females and males, or extremely numerous females together with a few males by mating with females of the same population as the female parents. Males of reciprocal hybrids among *rid* T, F and S produced nearly an equal number of females and males or extremely numerous females together with a few males by mating with female *les* L.

LL-type male interspecific hybrids between female *les* L or I and male *esc* G, No. 1 produced nearly an equal number of LL- or RL-type females and males by mating with female *les* L or I, or a female *rid* T, while LR-type male hybrids from the same combinations produced extremely numerous females together with a few males of the LR- or RR-type by mating with female *les* L or I, or a female *rid* T.

A male interspecific hybrid between a female *rid* S and a male *les* L or male *esc* G, No. 1 also produced extremely numerous females and a few males of the LR-type by mating with female *les* L.

11. From each of two kinds of eggs in size obtained from interspecific hybrids between female *les* L and male *rid* F or T, nearly an equal number of females and males was produced by fertilization with sperm of *les* L.

From female reciprocal intraspecific hybrids between *les* L and *les* I, nearly

an equal number of females and males was produced by mating with male *les* L. From female interspecific hybrids between female *les* L or I and a male *esc* G, nearly an equal number of females and males of the RL-type was produced by mating with male *les* L.

12. LL-type male hybrids between female *les* L or I and male *esc* G, No. 1 produced LL-type offspring which were of the $L^L \cdot L^{L-G}$- or $L^I \cdot L^{I-G}$-type in phenotype by backcrossing with female *les* L or I. While the LR-type male hybrids obtained from the same combinations produced LR-type offspring which were of the $L^L \cdot R^G$- or $L^I \cdot R^G$-type in electrophoretic patterns by mating with female *les* L or I, they produced RR-type offspring which were of the $R^T \cdot R^G$-type by mating with a female *rid* T. An LR-type male hybrid between a female *les* I and a male *rid* S produced LR-type offspring which were of the $L^I \cdot R^S$-type in phenotype by backcrossing with female *les* I. RR-type male hybrids between a female *rid* T and a male *esc* G, No. 1 produced LR-type offspring which were of the $L^L \cdot R^{T-G}$-type in phenotype by mating with female *les* L, while RL-type male hybrids obtained from the same combination produced LL-type offspring which were of the $L^L \cdot L^G$-type in phenotype by mating with the foregoing female *les* L. RR-type male hybrid between a female *rid* S and a male *esc* G, No. 1 produced LR-type offspring which were of the $L^L \cdot R^{S-G}$ type in phenotype by mating with female *les* L.

When normal-size eggs of female hybrids between female *les* L and male *rid* F or T were fertilized with sperm of male *les*, they became frogs which were various from about LL-type to about LR-type in appearance and of the L^L–$R^F \cdot L^L$- or L^L–$R^T \cdot L^L$-type in phenotype, in contrast to large eggs which became LLR-type triploids, being of the $L^L \cdot L^L \cdot R^F$- or $L^L \cdot L^L \cdot R^T$-type. LR-type female hybrids between female *les* L or I and a male *esc* G, No. 1 produced RL-type offspring which were of the $R^G \cdot L^L$-type in phenotype by mating with male *les* L.

13. It is evident that the single male *esc* G, No. 1 underwent hybridogenesis and produced two kinds of spermatozoa, one containing a *les*-genome and the other containing a *rid*-genome, by eliminating one of the two genomes.

The two male hybrids between a female *les* I and a male *rid* S and between a female *rid* S and a male *les* L produced spermatozoa containing a *rid*-genome by eliminating a *les*-genome. Hybridogenesis did not occur in the female hybrids between female *les* L and male *rid* F or T.

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