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GENERAL GENETICS

Inheritance of Parental Genomes by a Hybrid Form *Rana "esculenta"* (Amphibia, Ranidae)

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Abstract—In this study, quantitative analysis of paternal genome inheritance by a hybrid form *Rana "esculenta"* (= *Rana esculenta* L., 1758 × *Rana ridibunda* Pall., 1881) (Amphibia, Ranidae) was examined. The hybrid form examined was characterized by a polymodal mode of inheritance (genome of any of the parental species can be inherited). The absence of correlation between the proportion of normal gametes and either sex or ploidity of the producer was demonstrated. The gametes produced could be both haploid and diploid (hybrid or homozygous). The mechanism of alloploid reproduction is discussed.

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INTRODUCTION

The present study was focused on characteristics of the mode of inheritance specific to hybrid frog *Rana "esculenta"* (Amphibia, Ranidae), which was made based on quantitative analysis of the genotypes of gametes produced by hybrid animals. Hybrid frog *Rana "esculenta"* is one of the well-known forms of hybrid origin. This frog is characterized by unusual mode of reproduction. The first studies analyzing this phenomenon, showed that *Rana "esculenta"* individuals produced the gametes containing only the lake frog genome (LR ⟶ R) [1, 2]. Analogous mode of reproduction (called as hemiclonal) was earlier described in interspecific fish hybrids of the genus *Poeciliopsis* [3]. Thus, hybrid frog *Rana "esculenta"* can be reproduced through backcrossing to that parental species, whose genome is not inherited. However, more detailed analysis of the mode of inheritance specific to hybrid *Rana "esculenta"* frogs showed that it had some specific features. First, in some parts of the species range, hybrid form inherits exclusively of another parental species, the pool frog (LR ⟶ L) [4]. Second, in some populations the hybrids produce more than one class of gametes of different genotype and/or ploidity [5]. Finally, in many natural populations contain allotriploids, which are not reproductively isolated from parental species [6]. At the same time, alloploids of the genus *Poeciliopsis* are characterized by gynogenetic reproduction [7]. For these reasons, the mode of reproduction typical of hybrodogenetic frog *Rana "esculenta"* cannot be considered as hemiclonal in traditional interpretation of this term.

In this study, quantitative analysis of the inheritance of parental genomes by hybrid frog *Rana "esculenta"* was performed.

MATERIALS AND METHODS

Data source. The data on gamete genotypes (shown in Table 1) were taken from the literature and obtained in the present study (for the methods, see below).

Determination of gamete genotypes was performed by means of electrophoretic analysis of germ cell suspension (for males) or individuals eggs (for females). Frogs were caught in 1992 through 2005. Standard methods of sample preparation and electrophoresis were used [4, 8].

Sample preparation. Live animals were transported to the laboratory, where they were anesthetized with ethylic ether of 3-aminobenzoic acid and killed. Gonads were removed. To examine mature egg mass from the ovaries by means of electrophoresis, individual eggs were isolated under a binocular micrpscope with the help of preparation needles. Then, the eggs were separated from the tissue fluid by placing on a piece of filter paper for 10 to 20 s. After that, each egg was placed into 1–2-ml tube. The tubes were added with two to three drops of 10% sucrose solution stained by addition of bromphenol blue. The tubes were closed and frozen for 12 h. After thawing, each egg was squashed in the tube, and the tubes were shacked several times for more complete mixing of the egg content with the sucrose solution. To analyze male germ cells, testes were washed in distilled water, dried on filter paper, and squashed between two slide plates.

Table 1. Numbers of hybrid frogs *Rana "esculenta"* with different modes of parental genome inheritance

Sex	Soma	Gamete genotypes								n	N	Method	Literature source
		R	L	RR	LL	LR	L + R	L ≫ R	Oth.				
1. Western Europe													
1.1. Germany													
♀♀	LR	3	0	0	0	1	0	0	1	5	9	1, 2, 6	[5, 6, 9, 16, 17]
	LLR	0	2	0	1	0	0	0	0	3			
	LRR	1	0	0	0	0	0	0	0	1			
♂♂	LR	2	16	0	0	0	6	2	0	26			
	LLR	0	12	0	2	0	1	10	0	25			
	LRR	17	0	0	0	0	0	0	0	17			
1.2. Denmark													
♀♀	LR	1	0	0	0	5	0	0	1	7	3	3	[15]
	LLR	0	0	0	0	0	0	0	1	1			
♂♂	LR	0	0	0	0	0	0	0	1	1			
	LLR	1	4	0	0	0	0	0	0	5			
	LRR	1	0	0	0	0	0	0	0	1			
1.3. Poland													
♀♀	LR	9	0	0	0	5	2	0	9	25	6	1, 5	[9, 16–19]
	LRR	9	0	0	0	0	0	0	1	10			
♂♂	LR	12	1	0	0	0	1	0	1	15			
	LLR	0	1	0	0	0	0	0	0	1			
	LRR	10	0	0	0	1	0	0	1	12			
1.4. Switzerland													
♀♀	LR	7	0	0	0	0	0	0	0	7	3	2, 5	[2, 19, 20]
♂♂	LR	2	0	0	0	0	0	0	0	2			
1.5. Yugoslavia													
♀♀	LR	32	0	0	0	0	0	0	0	32	2	5	[21]
♂♂	LR	2	0	0	0	0	0	0	0	2			
1.6. Austria													
♀♀	LR	47	0	0	0	0	2	0	0	49	1	1, 2, 4	[19, 22–24]
1.7. Hungary													
♂♂	LLR	0	0	0	55	0	0	0	0	55	1	2, 4	[24]
2. Eastern Europe													
2.1. Ukraine													
2.1.1. Danube River basin													
2.1.1.1. Transcarpatia													
♀♀	LR	35	0	0	0	0	0	0	0	35	6	5	Personal data
2.1.1.2. Mouth of the Danube River													
♀♀	LR	0	8	0	0	0	0	0	0	8	3	5	"
♂♂	LR	0	21	0	0	0	0	0	0	21			
2.1.2. Dnieper River basin													
♀♀	LR	15	0	0	0	1	0	0	0	16	4	2, 5	"
♂♂	LR	32	0	0	0	3	3	0	0	38			
2.1.3. Don River basin													
♂♂	LR	1	5	0	0	1	3	0	0	10	1	5	"
	LRR	1	0	0	0	0	0	0	0	1			