COMMUNICATION

# Inheritance of Sparkling Scales (Ginrin) Trait in Ornamental Koi Carp

**Boris Gomelsky,\* Thomas A. Delomas, Kyle J. Schneider, Ammu Anil,[1] and Jeffrey L. Warner**

*Aquaculture Research Center, Kentucky State University, 103 Athletic Drive, Frankfort, Kentucky 40601, USA*

### Abstract

The purpose of this study was to investigate mechanisms of inheritance of the sparkling scales (ginrin) trait in ornamental koi, a variant of Common Carp *Cyprinus carpio*. The fish segregations of ginrin : nonginrin were recorded in three $F_1$ progenies obtained by crosses of ginrin × nonginrin and 16 $F_2$ progenies obtained by crosses of ginrin × ginrin and nonginrin × nonginrin. The segregations of ginrin : nonginrin in most $F_1$ progenies did not differ significantly from the 1:1 Mendelian ratio, while crossing nonginrin fish from $F_1$ progenies resulted in the appearance of only nonginrin fish in $F_2$. Based on these data, it was suggested that the ginrin trait in koi is controlled by a dominant mutation of one gene (*Gr/gr*): fish with genotypes *GrGr* and *Grgr* have ginrin phenotype, while fish with genotype *grgr* do not possess this trait. In most analyzed $F_2$ progenies obtained by crosses of ginrin × ginrin, the ginrin : nonginrin segregations were statistically different from the 3:1 and 2:1 theoretical ratios with permanent deficit of ginrin fish. It was suggested that the deviation of segregations from theoretical ratios resulted from increased mortality of ginrin fish as a result of possible negative pleiotropic effect of ginrin mutation on fish survival. The negative pleiotropic effect of ginrin mutation on fish growth was detected; nonginrin fish were substantially larger and heavier than ginrin fish from the same progenies raised in the same outdoor tanks.

The Japanese ornamental koi, a variant of Common Carp *Cyprinus carpio*, is one of the most popular decorative fish in many countries all over the world, including the USA. Koi were developed approximately two centuries ago in Japan and are known by large variability of colors and color patterns (Chapple 1999; Davies 1999; De Kock and Gomelsky, in press). The trait "sparkling scales" (or "ginrin" according to Japanese terminology) is characterized by the increased reflectivity of scales,

which makes ginrin koi very identifiable and attractive. This trait is not connected with a certain color; ginrin varieties of koi are known in many color types. It is impossible to detect ginrin trait at the larval stage; it becomes visible only after the formation of scales. Recently, Gur et al. (2014) found that enhanced reflectivity of scales in ginrin koi results from not only more intensive accumulation of guanine crystals than found in normal (nonginrin) koi but also from the specific orientation of the crystals and interdigitation between the different crystal stacks.

Currently, there is no available information on the inheritance the ginrin trait in koi. We analyzed segregation data in progenies obtained by crossings of ginrin fish to investigate a mode of inheritance of this trait. While several types of ginrin are distinguished in koi (Chapple 1999; De Kock and Gomelsky, in press), we investigated inheritance of the most common type of ginrin, termed "diagin" (or "diamond"). This type of ginrin is characterized by the presence of reflective streaks on scales.

## METHODS

The study was conducted at the Aquaculture Research Center, Kentucky State University, Frankfort, Kentucky. The general scheme of experiments included crossing fish with different phenotypes with regard to ginrin trait and analysis of ginrin : nonginrin segregations in two consecutive generations ($F_1$ and $F_2$). A total of 19 progenies were obtained and analyzed (Table 1). The $F_1$ progeny 1 was produced in 2003 by crossing a ginrin koi female with a nonginrin koi male. The $F_2$ progeny 4 was obtained in 2009 by crossing a ginrin female and a ginrin male from $F_1$ progeny 1. In 2010, $F_1$ progenies 2 and 3 were produced by crossing a ginrin koi female with a nonginrin koi male and a nonginrin Common Carp male (with wild-type dark color),

TABLE 1. Characteristics of parents and segregation of fish in progenies with regard to sparkling scales (ginrin) trait in koi. Ginrin : nonginrin segregations recorded at ages of 2 and 5.5 months followed by different lowercase letters are significantly different ($P < 0.01$), and significant differences of observed segregations from theoretical ratios ($P < 0.01$) are denoted with an asterisk.

| Progeny number | Phenotype of parents | | Origin of parents (F1 progeny number) | | Number of fish analyzed ($n$) | Segregation | | Ginrin: nonginrin ratio | Theoretical ratio (s) | $P$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | Female | Male | Female | Male | | Ginrin | Nonginrin | | | |
| | | | | | **First generation (F1)** | | | | | |
| 1 | Ginrin | Nonginrin | | | 49 | 27 | 22 | 1.23:1 | 1:1 | <0.70 |
| 2 | Ginrin | Nonginrin | | | 596 | 266 | 330 | 0.81:1 | 1:1 | <0.01* |
| 3 | Ginrin | Nonginrin | | | 411 | 188 | 223 | 0.84:1 | 1:1 | <0.10 |
| | | | | | **Second generation (F2)** | | | | | |
| 4 | Ginrin | Ginrin | 1 | 1 | 156 | 92 | 64 | 1.44:1 | 2:1 / 3:1 | <0.05/<0.0001*[a] |
| 5 | Ginrin | Ginrin | 2 | 2 | 529 | 228 | 301 | 0.76:1 | 2:1 / 3:1 | <0.0001*[a] |
| 6 | Ginrin | Ginrin | 2 | 2 | 534 | 267 | 267 | 1:1 | 2:1 / 3:1 | <0.0001*[a] |
| 7 | Ginrin | Ginrin | 2 | 2 | 273 | 106 | 167 | 0.63:1 | 2:1 / 3:1 | <0.0001*[a] |
| 8 | Ginrin | Ginrin | 3 | 3 | 357 | 187 | 170 | 1.10:1 | 2:1 / 3:1 | <0.0001*[a] |
| 9 | Ginrin | Ginrin | 3 | 3 | 360 | 175 | 185 | 0.95:1 | 2:1 / 3:1 | <0.0001*[a] |
| 10 | Ginrin | Ginrin | 2 | 3 | 594 | 333 | 261 | 1.28:1 | 2:1 / 3:1 | <0.0001*[a] |
| 11 | Ginrin | Ginrin | 3 | 2 | 610 | 340 | 270 | 1.26:1 | 2:1 / 3:1 | <0.0001*[a] |
| 12 | Nonginrin | Nonginrin | 2 | 2 | 340 | 0 | 340 | 0:1 | 0:1 | |
| 13 | Nonginrin | Nonginrin | 3 | 3 | 427 | 0 | 427 | 0:1 | 0:1 | |
| 14 | Ginrin | Ginrin | 2 | 2 | 184 | 23 | 161 | 0.14:1 | 2:1 / 3:1 | <0.0001*[a] |
| 15 | Ginrin | Ginrin | 2 | 2 | 243 | 131[b] | 112[b] | 1.17:1 z | 2:1 / 3:1 | <0.0001*[a] |
| | | | | | 661 | 266[c] | 395[c] | 0.67:1 y | 2:1 / 3:1 | <0.0001*[a] |
| 16 | Ginrin | Ginrin | 2 | 2 | 293 | 103[b] | 190[b] | 0.54:1 z | 2:1 / 3:1 | <0.0001*[a] |
| | | | | | 666 | 192[c] | 474[c] | 0.41:1 z | 2:1 / 3:1 | <0.0001*[a] |
| 17 | Ginrin | Ginrin | 3 | 3 | 648 | 472[b] | 176[b] | 2.68:1 z | 2:1 / 3:1 | <0.001*/ <0.15 |
| | | | | | 1,007 | 744[c] | 263[c] | 2.83:1 z | 2:1 / 3:1 | <0.0001*/<0.50 |
| 18 | Ginrin | Ginrin | 3 | 3 | 575 | 354[b] | 221[b] | 1.60:1 z | 2:1 / 3:1 | <0.01*/<0.0001* |
| | | | | | 1,470 | 870[c] | 600[c] | 1.45:1 z | 2:1 / 3:1 | <0.0001*[a] |
| 19 | Ginrin | Ginrin | 3 | 3 | 422 | 211[b] | 201[b] | 1.05:1 z | 2:1 / 3:1 | <0.0001*[a] |
| | | | | | 621 | 289[c] | 332[c] | 0.87:1 z | 2:1 / 3:1 | <0.0001*[a] |

[a]For both theoretical ratios 2:1 and 3:1.
[b]Recorded for fish at 2 months of age.
[c]Recorded for fish at 5.5 months of age.

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respectively. Reared in earthen ponds to age 3, $F_1$ progenies 2 and 3 reached sexual maturity in 2013 and were used in crosses for the production of nine $F_2$ progenies 5–13. Progenies 5–7 were obtained by crossing ginrin fish from $F_1$ progeny 2, while progenies 8 and 9 were obtained by crossing ginrin fish from $F_1$ progeny 3. Progenies 10 and 11 were produced by crossing ginrin parents from different $F_1$ progenies. Progeny 10 was obtained by crossing a ginrin female from progeny 2 with a ginrin male from progeny 3, while the reciprocal cross was used for the production of progeny 11. Also, in 2013 progenies 12 and 13 were produced by crossing between nonginrin fish from $F_1$ progenies 2 and 3, respectively. In 2014, six additional $F_2$ progenies (numbers 14–19) were produced by crossings between ginrin fish from $F_1$ progeny 2 (progenies 14–16) and between ginrin fish from $F_1$ progeny 3 (progenies 17–19) as described in Table 1.

All progenies were obtained by artificial spawning in a hatchery. Artificial spawning techniques were as described by Gomelsky et al. (2011). In order to induce final oocyte maturation in females and spermiation in males, fish parents were injected with carp pituitary extract (Argent Chemical Laboratories, Redmond, Washington) at 3 mg/kg of body weight. Eggs were artificially fertilized in plastic bowls and were treated with an 8:1 (volumetric) water : cow milk mixture to remove adhesiveness. For each cross, eggs taken from one female were fertilized with sperm taken from one male. Embryos were incubated in McDonald jars; hatched larvae were collected in mesh hapas, which were placed in water flow-through raceways. In 2003, 500 swim-up larvae from progeny 1 were stocked for rearing in a 0.04-ha earthen pond and reared for 6 months when segregation ginrin : nonginrin was recorded in all raised fish. Swim-up larvae from the other 18 progenies (numbers 2–19) were stocked for rearing in separate 20-m$^3$ outdoor tanks at 2,000–4,000 larvae (quantities volumetrically estimated) per tank. Tanks were supplied with water from a 0.2-ha reservoir. The fish were fed an artificial diet but also consumed zooplankton and benthic organisms that developed in tanks or flowed in with the reservoir water. After 5–5.5 months of rearing, tanks were drained and all juveniles were collected. Segregations ginrin : nonginrin in progenies 2–13 were determined based on analysis of randomly taken samples of reared juveniles. Segregations ginrin : nonginrin in progenies 15–19, obtained in 2014, were determined twice, at fish at ages of 2 and 5.5 months. The random samples of 2-month-old fish were taken from the tanks, and after recording of data fish were returned to the same tanks for further rearing. All the 5.5-month-old fish raised in tanks were examined for ginrin segregations in progenies 15–19; random samples (from 32 to 69 fish per sample) of ginrin and nonginrin 5.5-month-old fish from these progenies were also measured and weighed. Segregation of progeny 14, obtained in 2014, was determined only for the 2-month-old fish (all raised fish were analyzed) since fish were not returned to tank for further rearing.

Segregations of fish in progenies with regard to presence or absence of ginrin trait were compared using a chi-square test (Zar 1999). Differences in mean total lengths and weights between groups of fish were evaluated by a Student's $t$-test (Zar 1999). Differences were considered significant at $P < 0.01$.

## RESULTS

In this long-term study only two clearly distinguishable fish phenotypes were observed: ginrin and nonginrin. Such alternative variability is typical for qualitative traits controlled by a low number of genes and inherited according to Mendel's principles. The working hypothesis was that ginrin trait is controlled by a mutation of one gene and therefore observed ginrin : nonginrin segregations were compared with Mendelian ratios typical for a monohybrid cross (when one gene is involved), i.e., 1:0, 1:1, 3:1 and 2:1. The results showed that fish segregations in $F_1$ were close to the 1:1 Mendelian ratio, which resulted from crossing heterozygous individuals with homozygotes for recessive allele. In order to determine which allele (controlling either ginrin or nonginrin phenotype) is dominant and which is recessive, the $F_2$ progenies were obtained by crossing of $F_1$ fish of the same phenotype (i.e., ginrin × ginrin and nonginrin × nonginrin). Parental genotypes in both crosses can be determined based on which ratio appears in each cross. Cross of two homozygotes for the recessive allele will give only fish with the parental phenotype, while cross of two heterozygotes will result in the 3:1 theoretical ratio in the progeny if all genotypes are viable or in the 2:1 theoretical ratio if homozygotes for the dominant allele are inviable.

Data on fish segregation in progenies with regard to the presence or absence of ginrin trait are presented in Table 1. In $F_1$ progenies 1 and 3 segregations ginrin : nonginrin did not differ significantly from the 1:1 Mendelian theoretical ratio. In progeny 2, segregation was close to the 1:1 ratio (0.81:1) with deficit of ginrin fish, but this difference was statistically significant ($P$-value = 0.009). In progeny 3, which was obtained by cross ginrin female with nonginrin Common Carp male with wild-type dark color, all fish (both with and without ginrin trait) had the paternal dark color. As an illustration, photographs of ginrin and nonginrin koi and ginrin fish with dark wild-type color from $F_1$ progenies are shown in Figure 1.

Segregations ginrin : nonginrin in $F_2$ progenies obtained by crossing ginrin fish were very variable (Table 1). In progeny 4 the ratio was 1.44:1, which did not differ significantly from the 2:1 theoretical ratio but significantly differed from the 3:1 theoretical ratio. In progeny 17 segregations recorded at both 2-month-old and 5.5-month-old fish fit the 3:1 theoretical ratio but differed significantly from the 2:1 theoretical ratio. In 12 other $F_2$ progenies obtained by crossing ginrin fish (numbers 5–11, 14–16, 18, and 19) observed segregations were significantly different from both theoretical ratios (2:1 and 3:1) because of deficit of ginrin fish; ginrin : nonginrin ratios in these progenies varied from 0.14:1 in progeny 14 to 1.60:1 for 2-month-old fish in progeny 18. In progeny 15, segregation ginrin : nonginrin recorded for 5.5-month-old fish differed significantly from 2-month-old fish, having a smaller proportion of ginrin fish. In the other four progenies (numbers 16–19), segregations recorded
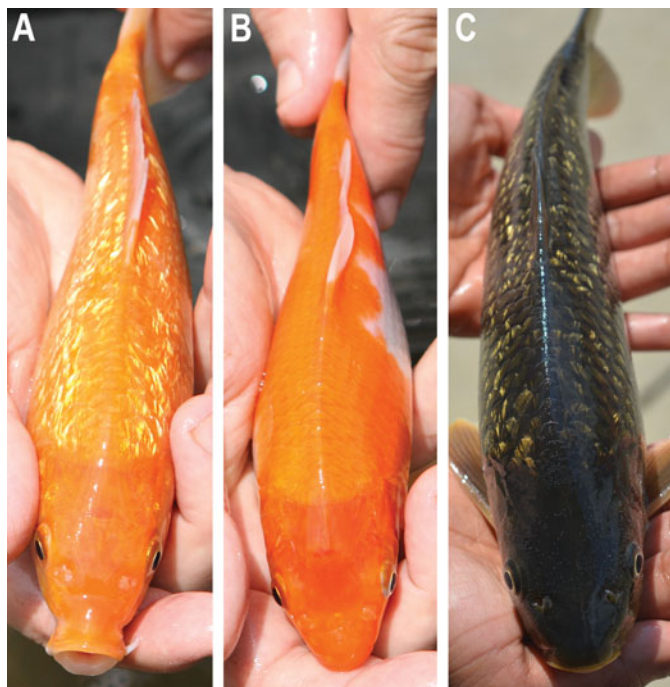
FIGURE 1. **(A)** Ginrin koi from progeny 2 (age = 17 months); sparkling streaks on scales are clearly visible. **(B)** Normal (nonginrin) koi from progeny 2 (age = 17 months). **(C)** Ginrin fish with common carp wild-type dark color from progeny 3 (age = 36 months); sometimes these fish are called "shiny carp." Note small breeding tubercles on fish head and back which are typical for males of this species during spawning season.

for fish of different ages did not differ significantly, although in three progenies (16, 18, and 19) some decrease in proportions of ginrin fish was observed (Table 1). Two $F_2$ progenies (12 and 13), which were obtained by crossing nonginrin fish, consisted of nonginrin fish only (Table 1).

Nonginrin fish had significantly larger mean total lengths and mean weights than ginrin fish from progenies 15–19, which were reared in the same outdoor tanks (Table 2). Mean lengths of nonginrin fish were about 19% (progenies 17–19) to 42% (progeny 15) larger than mean lengths of ginrin fish. Differences in mean weights between nonginrin and ginrin fish were even more profound, nonginrin fish being 1.6 times (progeny 19) to 2.7 times (progeny 15) heavier than ginrin fish.

## DISCUSSION

Segregations of ginrin : nonginrin in two $F_1$ progenies did not differ significantly from the 1:1 Mendelian ratio, while segregation in the third $F_1$ progeny was close to this theoretical ratio. Also, crossing nonginrin fish from $F_1$ progenies resulted in the appearance of nonginrin fish only in two $F_2$ progenies. Based on these data and the above-discussed Mendelian principles, the investigated type of ginrin in koi is suggested to be controlled by a dominant mutation of one gene (*Gr/gr*). Fish with genotypes *GrGr* and *Grgr* have the ginrin phenotype, while fish with geno-

type *grgr* do not possess this trait. In this case, the $F_1$ progenies, which demonstrated the 1:1 theoretical segregations, resulted from crossing heterozygous ginrin fish (*Grgr*) with nonginrin fish homozygous for recessive allele (*grgr*). Crossing nonginrin fish *grgr* from $F_1$ progenies resulted in nonginrin fish with the same parental genotype (*grgr*) in $F_2$ progenies.

The suggested mode of inheritance presumes appearance in $F_2$ progenies, obtained by crossing heterozygous ginrin fish with genotype *Grgr*, either the 3:1 theoretical ratio (ginrin : nonginrin; if all resulting genotypes are viable) or the 2:1 theoretical ratio (if homozygous fish for the dominant allele, *GrGr*, are not viable). However, only in two $F_2$ progenies did the observed segregations fit either theoretical ratio; in progeny 4 segregation did not differ from the 2:1 ratio, and in progeny 17, segregations recorded both at 2-month-old and 5.5-month-old fish did not differ from the 3:1 ratio. In the other 12 $F_2$ progenies, obtained by crosses ginrin × ginrin, the ginrin : nonginrin segregations were statistically different from both theoretical ratios (3:1 and 2:1), varying from 0.14:1 to 1.60:1 with a permanent deficit of ginrin fish. Based on these data we suggest that the deviation observed in these progenies' segregations from theoretical ratios resulted from increased mortality of ginrin fish (both *GrGr* and *Grgr*) compared with nonginrin fish (*grgr*).

In 2014, the data on mean total lengths and weights of 5.5-month-old ginrin and nonginrin fish were recorded in five $F_2$ progenies. In all analyzed progenies nonginrin fish were significantly larger and heavier than ginrin fish raised in the same tanks. The observed difference was very substantial; the mean weights of nonginrin fish were from 1.6 to 2.7 times larger than the mean weights of ginrin fish from the same tanks. These data show that ginrin mutation has negative pleiotropic effect on fish growth. It is reasonable to suggest that this mutation also has a negative pleiotropic effect on fish survival resulting in shift of observed segregations of ginrin : nonginrin in progenies from theoretical ratios.

Also, in $F_2$ progenies obtained in 2014, segregations of ginrin : nonginrin at different fish ages (2 and 5.5 months) were recorded. Earlier, Gomelsky et al. (1996, 1998) in studies on inheritance of black patches in koi have detected that recording segregations with regard to melanin pigmentation is more accurate at larval stage than at the juveniles stage (after pond rearing), which was attributed to different viability of pigmented and unpigmented fish. In contrast to melanin pigmentation, it is impossible to detect the ginrin trait at larval stage. In order to identify the earliest age at which segregations of ginrin: nonginrin can be determined, we observed fish periodically after the larvae were stocked in the outdoor tanks. The first signs of ginrin trait became visible approximately 6 weeks after stocking and ginrin : nonginrin segregations were recorded for 2-month-old juveniles. In progeny 15 the ginrin : nonginrin ratio for 5.5-month-old fish had shifted significantly lower for ginrin fish than was recorded when the fish were 2 months old. The observed shift in ratios in this progeny was caused by increased mortality of ginrin fish in the period between the two recordings.

TABLE 2.   Mean total lengths and weights of 5-month-old ginrin and nonginrin koi reared in the same outdoor tanks. Means of the same variable in a row followed by different lowercase letters are significantly different ($P < 0.01$).

| | Mean $\pm$ SD total length (cm) | | Mean $\pm$ SD weight (g) | |
| Progeny number | Ginrin | Nonginrin | Ginrin | Nonginrin |
| --- | --- | --- | --- | --- |
| 15 | 7.7 $\pm$ 1.3 z | 10.9 $\pm$ 1.6 y | 6.9 $\pm$ 4.1 z | 18.3 $\pm$ 8.4 y |
| 16 | 8.9 $\pm$ 1.5 z | 11.9 $\pm$ 2.1 y | 10.5 $\pm$ 4.7 z | 24.8 $\pm$ 12.2 y |
| 17 | 8.1 $\pm$ 2.2 z | 9.6 $\pm$ 2.9 y | 9.2 $\pm$ 7.8 z | 15.7 $\pm$ 12.6 y |
| 18 | 6.9 $\pm$ 1.4 z | 8.2 $\pm$ 2.4 y | 5.5 $\pm$ 3.3 z | 9.8 $\pm$ 8.3 y |
| 19 | 8.0 $\pm$ 1.9 z | 9.5 $\pm$ 2.1 y | 8.6 $\pm$ 6.0 z | 13.5 $\pm$ 8.6 y |

In four other analyzed progenies there was no statistically significant difference in ratios ginrin : nonginrin recorded at different fish ages, although in three progenies (16, 18 and 19) some decrease in proportion of ginrin fish was observed. In progenies 15, 16, 18, and 19 segregations recorded for 2-month-old fish were already significantly different from the 2:1 and 3:1 theoretical ratios due to shortage of ginrin fish. Based on these results it may be that the supposed increased mortality of ginrin fish, which caused a shift in segregations from theoretical ratios, occurred mostly during the first 2 months life, possibly before this trait becomes clearly visible in all fish with genotypes *GrGr* and *Grgr*.

As indicated above, ginrin : nonginrin segregations in two $F_1$ progenies (1 and 3) did not differ significantly from the 1:1 theoretical ratio. In $F_1$ progeny 3 observed segregation differed from this theoretical ratio significantly, but the *P*-value (0.009) was close to the critical value of 0.01. These data indicate to relatively good viability of ginrin fish with suggested genotype *Grgr* in $F_1$ progenies. However, in most $F_2$ progenies segregations of ginrin : nonginrin were considerably shifted not only from the 3:1 ratio but also from the 2:1 ratio because of a deficit of ginrin fish; this suggests decreased survival of *Grgr* fish. How can the difference in survival of heterozygotes *Grgr* in $F_1$ and $F_2$ progenies be explained? As described above, most of the $F_2$ progenies (4–9 and 12–19) were obtained by crossing fish from the same $F_1$ progenies; this means that these $F_2$ progenies were produced by crossing full sibs. Two $F_2$ progenies (numbers 10 and 11) were obtained by crossing ginrin fish from two different $F_1$ progenies (numbers 2 and 3). These $F_2$ progenies were produced by crossing half-sibs because the $F_1$ progenies 2 and 3 were obtained by crossing one ginrin female with two nonginrin males. Both full-sib and half-sib crosses, as crosses of close relatives, can result in inbreeding depression, which in fish and other aquaculture animals frequently decreases viability (Kincaid 1976; Evans et al. 2004). In $F_2$ progenies of ginrin $\times$ ginrin parents, the decreased viability caused by inbreeding depression may have influenced smaller ginrin fish more intensely than larger nonginrin fish, resulting in a deficit of ginrin fish in segregations. It may also be that any unfavorable factors that decrease fish survival impact ginrin fish more strongly than nonginrin fish and result in larger shift of

ginrin : nonginrin segregations from theoretical ratios. To some extent the $F_2$ progeny 14 data confirm this possibility; in this progeny we observed the lowest fish survival (<200 fish were harvested) and the smallest proportion of ginrin fish (ginrin : nonginrin was 0.14:1). However, segregations of ginrin : nonginrin in progeny 17 (for ages 2 and 5.5 months) did not differ significantly from theoretical ratio of 3:1. This suggests that under favorable conditions ginrin fish with genotype *GrGr* can survive.

As mentioned above, until now there was not any information on inheritance of the ginrin trait in koi. Our findings indicate that this trait is under control of a dominant mutation of one gene (*Gr/gr*). Negative impact of ginrin trait on fish growth and possibly on fish survival was observed, which complicates investigation of this trait inheritance. Further studies should be aimed at investigating segregations in progenies produced from fish of different origin and raised in different conditions. Also, it would be interesting to find out whether different types of ginrin in koi are controlled by different alleles of the same gene or by mutations of different genes. In that regard, crossings between koi with different types of ginrin could be informative.

## ACKNOWLEDGMENTS

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