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GENETICAL EXCHANGES BETWEEN ONE *BIOMPHALARIA GLABRATA* (GASTROPODA: PLANORBIDAE) AND A VARYING NUMBER OF PARTNERS

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When one pigmented Biomphalaria glabrata *is mated with 1 to 20 albino snails, the percentage of albino parent producing pigmented offspring decreases while the percentage of parent laying albino offspring increases. If the number of snails/group increases, the mean duration of the use of allosperm decreases.*

Key words: Planorbidae – pigmentation – albino – selfing – crossing

Mature *Biomphalaria glabrata (B.g.)* are simultaneous hermaphrodite. If reared in isolation, snails reproduce by selfing (Brumpt, 1941). If virgin snails are paired, they copulate and crossing replaces selfing; when the exogenous sperm is exhausted, selfing is resumed (Paraense, 1955).

A snail mated with a varying number of partners may copulate as a male or as a female. When it acts as a male, it is possible to determine how many partners, acting as a female, are cross-fertilized.

This paper intends to compare the proportion of cross-fertilized partners, that is to say the significance of the genetical exchanges, and also the length of the use of the allosperm, in variously sized groups of snails.

MATERIAL AND METHODS

The genetical control of pigmentation in *B.g.* has been studied by Newton (1954) but mainly by Richards from 1967 (see review in Richards, 1985). Albinism may be used as a genetic marker: Newton (1955), Paraense (1955).

The snails used in these experiments were mature Brazilian *B.g.* (diameter of the shell from 12.0 to 13.0mm) raised in isolation from hatching. Snails of two genotypes were used:

– pigmented snails: homozygous CC.
– albino snails: homozygous cc.

In each experiment, one pigmented snail was mated with 1, 2, 3, 4, 5, 6, 8, 10, 15 or 20 albino snails. The duration of the mating was proportional to the number of albino and was: 1, 2, 3, . . . or 20 days. The volume of water was proportional to the number of snails (65 ml per one albino snail).

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After mating, the albino snails were bred in isolation and the offspring daily controlled until exhaustion of the allosperm received from the pigmented partner.

The pigmentation of the offspring was early detected on embryos through examining the presence or lack of pigmentation of the eyes. The pigmentation of the offspring (= F1) from albino snails allowed to determine that albino parents reproduced by crossing. For each duration of mating, the experiment consisted of 5 series of 5 different pigmented snails. The temperature was constant: 25°C and the photoperiod was 12L/12D.

On the whole, 50 pigmented snails and 370 albino snails were used, 10,063 clutches laid by albino snails were monitored.

RESULTS

After mating, the daily examination of the offspring of albino *B.g.* allows to determine the proportion of albino snails that have produced pigmented F1, albino F1, have laid no clutch or have died (Table).

If all the groups are pooled, the percentages for the 3 types of snails are:

– albino producing pigmented offspring: (207/370) 55.9%
– albino producing albino offspring: (134/370) 36.2%
– sterile or dead albino: (29/370) 7.8%.

According to the size of the groups of snails mated, the proportions of the 3 types of albino snails can be tested ,by the chi-square test. Though being high, the value of chi^2 (26.97 for 18 degrees of freedom) does not reach the level of probability $p = 0.05$ and the differences are to be regarded as not significant.

The percentage of snails producing albino or pigmented F1 can be related to the number of mated albino (Fig. 1).

TABLE

Analysis of the offspring of albino *Biomphalaria glabrata* mated with one pigmented snail

Number of albino mated with one pigmented snail	1	2	3	4	5	6	8	10	15	20
Duration of mating (days)	1	2	3	4	5	6	8	10	15	20
Number of albino producing pigmented F1	4	8	10	16	14	21	23	29	38	44
Number of albino producing albino F1	1	2	5	3	10	9	14	16	33	41
Number of albino laying no clutch or dead	0	0	0	1	1	0	3	5	4	15
Sum	5	10	15	20	25	30	40	50	75	100

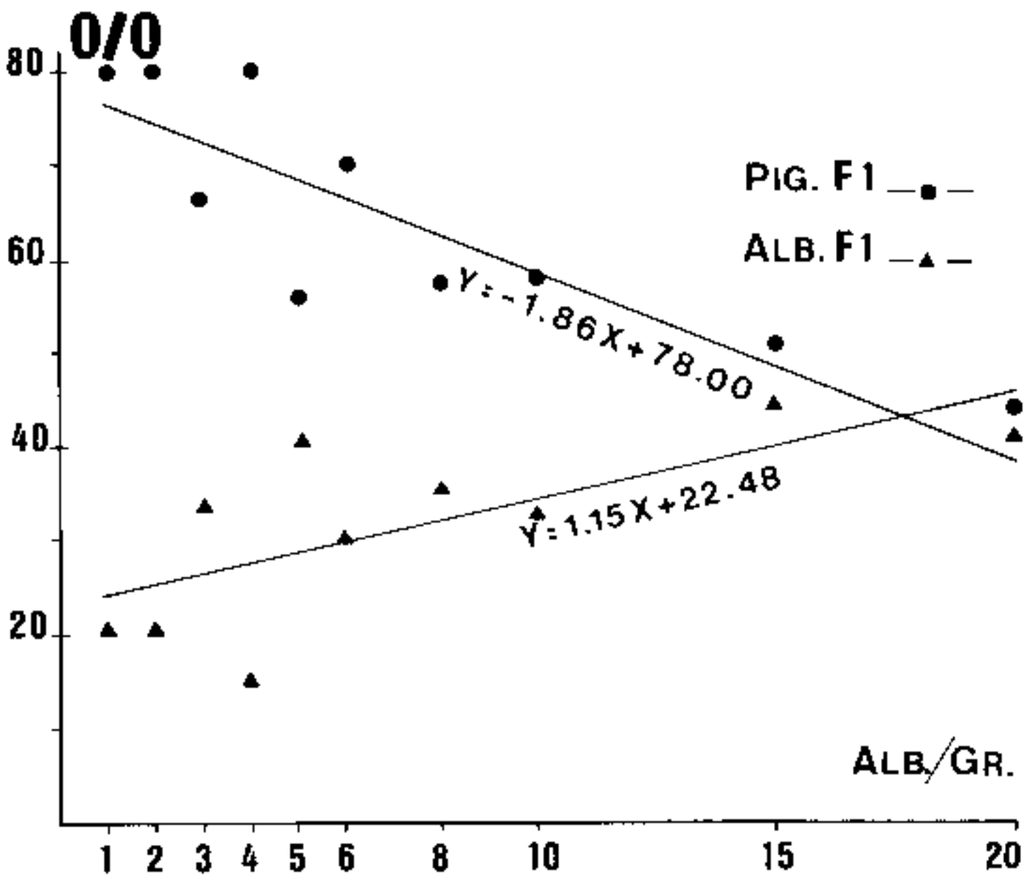

Fig. 1: Percentage of albino (= self-fertilized) and pigmented (= cross-fertilized) offspring related to the number of albino parents. ALB./GR: number of albino snails per group.

There is a statistically significant linear correlation between the percentage of snails producing pigmented or albino offspring and the number of albino parents per group:
– pigmented F1: $r = -0.86 < 0.01$
– albino F1: $r = +0.71 < 0.05$
(for 8 degrees of freedom).

When the number of mated albino snails increases from 1 to 20, the percentage of snails producing pigmented F1 decreases linearly (observed values: 80 to 44%, theoretical values: 76.2 to 37.0%). On the contrary, when the size of the groups increases, the percentage of snails producing albino F1 increases linearly (observed values: 20 to 41%, theoretical values: 23.6 to 45.5%).

If the rates of parents producing albino or pigmented offspring are related to the numbers of fertile parents, the statistical results are slightly different but we observe likewise a highly significant linear correlation:
– pigmented F1: $r = -0.81 < 0.01$
– albino F1: $r = +0.81 < 0.01$.

The production of pigmented F1 by albino snails is due to cross-fertilization using allosperm. The duration of the use of allosperm varies according to the number of albino snails per group (Fig. 2).

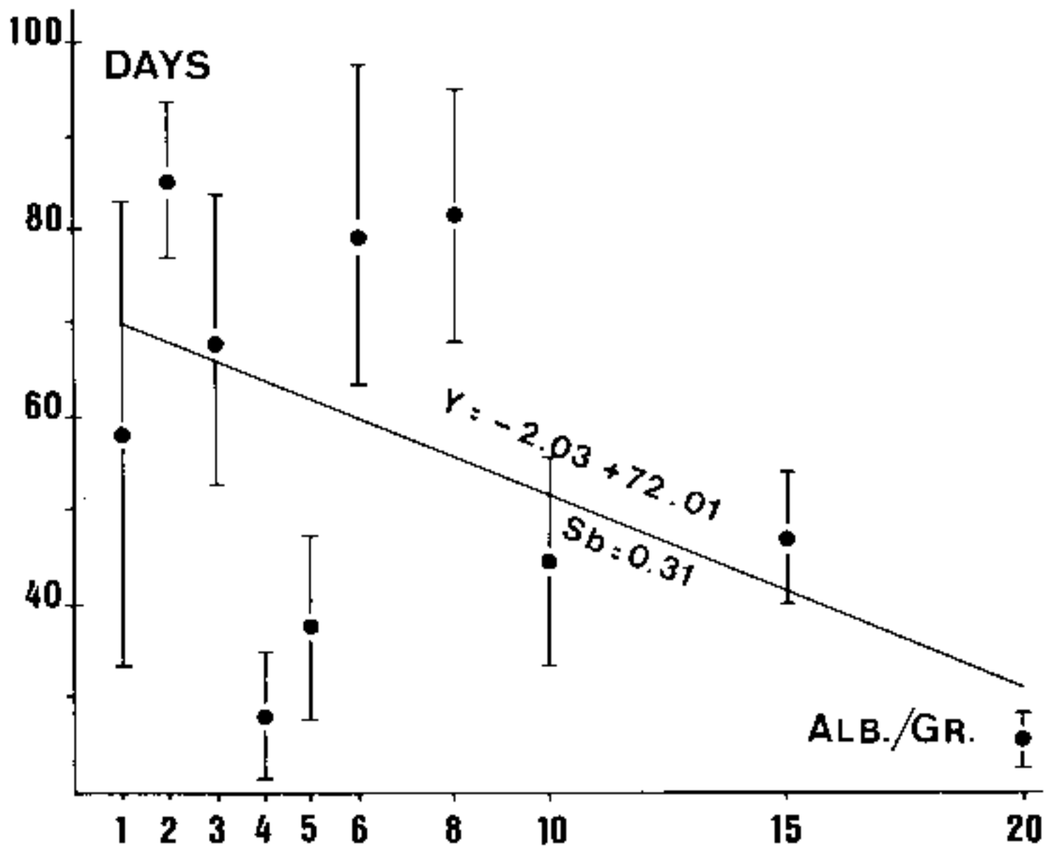

Fig. 2: Length of the use of the exogenous sperm by crossed albino *B.g.* related to the number of mated snails, expressed in days. The fiducial-limits of each mean are given for the level of probability $p = 0.05$. Sb: standard deviation of the slope of the regression line. ALB./GR: number of albino snails per group.

The duration of the use of the exogenous sperm presents an extended variability. The extreme values are 3 and 127 days. If all the values (n = 207) obtained in different groups are pooled, the mean value is m = 50.1 ± 2.1 days.

For each of the varying groups, the mean value of the duration of the use of allosperm is statistically linearly correlated to the number of albino snails per group:
$r = 0.41 < 0.01$ (degrees of freedom: 205)
$(-0.54 < r < -0.24$ for $p = 0.01)$.

When the number of snails per group increases, the length of the use of allosperm decreases.

DISCUSSION

On isolated *B.g.*, self-fertilization occurs easily in the laboratory.

If selfing is the only mode of reproduction, there is a loss of genetical variability, the population tending to homozygosity. On the contrary, crossing prevents this loss and the population keeps its variability.

In Planorbidae, it is commonly admitted that, in groups of snails, crossing prevails: Paraense (1956), Richards (1973), Mulvey & Vrijenhoek (1981), Madsen et al. (1983), Monteiro et al. (1984), Rudolph & Bailey (1985), Rollinson (1986).

In *B.g.*, the present results show that albino snails mated with one pigmented snail may produce pigmented offspring. This cross-fertilization may have two origins. The classical explanation is copulation between a pigmented snail acting as a male and an albino snail acting as a female. Recently, Monteiro et al. (1984) have described sperm sharing in three species of *Biomphalaria:* the cross-fertilized intermediate snail is able to transfer the exogenous sperm received from a donor to a recipient. This may play a partial role in our experiments, although, in other experiments, we have never succeeded in transferring sperm from an intermediate snail to a recipient.

Paraense (1959) in *B.g.* and Rudolph & Bailey (1985) in *Bulinus* show that selfing may not be suppressed if a virgin snail acting as a female is mated with a previously cross-fertilized partner. This probably explains why, in the present experiments, though the length of the mating increases proportionally to the size of the groups, the percentage of cross-fertilized snails decreases. Besides, if the sharing of sperm occurs, the pigmented snail may copulate as a female with an albino partner, then transfers the allosperm to a third recipient albino snail. In such a case, copulation as a male of the pigmented snail would not be detected.

The mean value of the use of allosperm (about 50 days) is consistent with the results of Paraense (1955) but the extreme values (3 and 127 days) are more extended than those given by Paraense (1955) (25 and 68 days). It must be noted that these values may be encountered in all the groups considered. The highest value for the duration of the use of allosperm is very similar to that in *Bulinus* (= 123 days) (Rudolph & Bailey, 1985) and slightly inferior to that in *Helisoma* (5 months) (Madsen et al., 1983).

Larambergue (1939) and Rudolph & Bailey (1985), in *Bulinus* noted an extended duration of allosperm use after multiple copulations. In *B.g.* this may explain why the usage of foreign sperm decreases when the number of partners increases. When two snails are paired, several copulations probably occur, the quantity of allosperm transferred is important and the use of allosperm is long. On the contrary, when one pigmented snail is mated with several albino, the successive copulations occur preferentially with new partners; the quantity of allosperm transferred to each partner and the duration of its usage decreases.

The genetical exchanges between a snail and a varying number of partners decrease when this number increases. Neverthless, the percentage of crossing remains important (lower value: 44%). It is possible that after longer matings the percentage would be higher. Paraense (1955), segregating albino snails collected in the field, observes that they all produce pigmented offspring resulting from cross-fertilization. According to different authors and the present results, it appears that, in *B.g.*, crossing is the dominant mode of reproduction, even though it is a potentially self-fertilizing species.

In these experiments, only the cross-fertilizations due to the pigmented snail acting as a male are detected. Copulations between albino snails are probably numerous. If they occur at the same rate as for the pigmented snail, the genetical exchanges between snails of similar sizes are sufficiently numerous to fasten heterozygosity.

RESUMO

Trocas genéticas entre uma *Biomphalária glabrata* (Gastropoda: Planorbidae) e um número variado de parceiros —Quando uma *Biomphalaria glabrata* pigmentada é posta em presença de um a vinte parceiros albinos, a percentagem de indivíduos parentais que produzem, por fecundação cruzada, uma descendência pigmentada, decresce. Ao contrário, a proporção de indivíduos parentais cuja descendência é de albinos aumenta.

Quando o número de caramujos albinos por grupo aumenta, a duração média da utilização dos espermatozóides estranhos recebidos do parceiro pigmentado decresce.

Palavras-chave: Planorbidae – pigmentação – albino – fecundação cruzada

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