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**Does the genetic constitution of the EGG influence
the fission frequency of the offspring in planarians?**

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Biologia. — *Does the genetic constitution of the EGG influence the fission frequency of the offspring in planarians?* Nota (*) di MARIO BENAZZI (**), GIUSEPPINA BENAZZI LENTATI (**) e PAOLO DERI (***), presentata (***) dal Socio M. BENAZZI.

ABSTRACT. — Research carried out on the freshwater planarian *Dugesia benazzii* by crossing biotypes differing for their power of fissioning, has shown that the offspring differ in the ratio between fissiparous and sexual specimens, according to the genetic constitution of the mother. The AA. discuss this result, also considering data obtained in preceding investigations.

KEY WORDS: Planarians; Fissioning; Influence of the mother.

RIASSUNTO. — *Possibile effetto materno sulla frequenza della scissiparità nei nati di planarie.* Ricerche compiute sulla planaria d'acqua dolce *Dugesia benazzii* incrociando biotipi con diversa attitudine alla scissiparità, hanno dimostrato che il rapporto tra i discendenti scissipari e sessuati differisce a seconda della costituzione genetica della madre. Gli Autori discutono questo risultato in considerazione anche dei dati ottenuti in precedenti ricerche.

INTRODUCTION

This new research has been carried out on the populations from Paradojo and from Roccapina (Corsica) of *Dugesia benazzii* Lepori, a planarian (Tricladida, Paludicola) widely distributed in Sardinia, Corsica and Capraia and consisting of various biotypes (cf. Benazzi and Benazzi Lentati, 1976).

The population from Paradojo belongs to the diploid amphimictic biotype; the specimens used for the present research never fissioned.

The population from Roccapina belongs fundamentally to the triplo-hexaploid biotype, in which the somatic line is triploid, the oocytes are hexaploid and pseudogamous, while the spermatocytes are diploid. However, this population is characterized by the simultaneous presence, in each individual, of hexaploid pseudogamous oocytes and triploid amphimictic oocytes. The latter, through a peculiar maturation process, produce haploid eggs which, after

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fertilization, may give diploid offspring. Firstly, all individuals from Roccapina were sexual but, after a long period of laboratory culture, many specimens lost their sexuality and started to reproduce by fission (Giannini and Puccinelli, 1969; Benazzi and Giannini, 1970; Benazzi Lentati and Deri, 1980 *a, b*; Benazzi Lentati and Benazzi, 1981).

The birth of diploid offspring from fertilized triploid oocytes, made it possible to cross triploid individuals from Roccapina with individuals from Paradojo and the results have provided insight into certain genetical questions, particularly concerning the control of fissioning.

MATERIAL AND METHODS

In 1981, eleven fertilized individuals of Roccapina (Rp) were cultured separately in order to obtain the cocoons (ovigerous capsules) laid by each single specimen. In the following year, each specimen was crossbred with a specimen of Paradojo (Prj) and the cocoons laid by the partners of the mates were collected. The progeny was examined karyologically and with reference to the ratio between fissiparous and sexual specimens.

The karyological study was accomplished on both oocytes and regenerative blastemas, following the technique used in our previous research.

RESULTS

The juveniles were studied at the age of 7-8 months, when sexuality normally takes place.

a) Progeny from Rp :

Only four of the eleven specimens cultured produced cocoons, giving the following offspring:

specimen n. 2: 1 fissiparous, 5 sexual

specimen n. 7: 8 fissiparous, 11 sexual

specimen n. 8: 2 fissiparous, 5 sexual

specimen n. 11: 6 fissiparous, 11 sexual.

In total, 17 fissiparous and 32 sexual offspring; the ratio fissiparous: sexual is 0.53:1.

b) Progeny from the cross $Rp \times Prj$ - mother unknown :

9 fissiparous, 31 sexual; the ratio is 0.29:1.

c) Progeny from the cross $Rp \text{♀} \times Prj$:

8 fissiparous, 18 sexual; the ratio is 0.45 : 1.

d) *Progeny from the cross Prj ♀ × Rp :*

5 fissiparous, 38 sexual; the ratio is 0.13 : 1.

Firstly these results, summarised in Table I, confirm the chromosomal transmission of the fission-controlling factors, established by Benazzi in 1974. In fact, fissiparous specimens occurred in the progeny of the cross $\text{Prj } \text{♀} \times \text{Rp } \text{♂}$, in which the fission factors were certainly brought by the sperm, since the Prj individuals never fissioned. Secondly, the ratio between fissiparous and sexual specimens in the offspring of Rp individuals outnumbers that observed in the progeny of the cross $\text{Rp} \times \text{Prj}$. Thirdly, in this cross the ratio differs according to the mother: 0.45 : 1 in the offspring from $\text{Rp } \text{♀}$ and 0.13 : 1 in the offspring from $\text{Prj } \text{♀}$.

This would seem to indicate that the genetic constitution of the egg affects the offspring, and such a conjecture seems to be substantiated by similar results obtained by Benazzi (cf. Benazzi and Benazzi Lentati, 1983) when crossing specimens of Prj (constantly sexual) with specimens from Castello Pino (CP), another Corsican population of *Dugesia benazzii*, which presents both sexual and fissiparous specimens.

The results were as follows:

a) *Progeny from CP:*

In total, 27 fissiparous, 46 sexual; the ratio fissiparous: sexual is 0.58 : 1.

b) *Progeny from Prj:*

In total, 18 fissiparous, 58 sexual; the ratio fissiparous: sexual is 0.30 : 1.

Likewise, these results seem to indicate the influence of the genetical constitution of the egg in the manifestation of the fission-controlling factors. Certainly, although this assumption may seem to be insufficiently documented, it is nevertheless supported by factual data.

A final question concerns the chromosome set of the planarians examined here (Table I). Roccapina produced 49 individuals, 4 of which were triploid and sexual and certainly originated from hexaploid pseudogamous oocytes. The other 45 offspring were diploid, 28 sexual and 17 fissiparous, and originated from triploid amphimictic oocytes, as explained above. Roccapina ♀ fertilized by Paradojo gave 6 triploid and 20 diploid offspring, 12 sexual and 8 fissiparous. All the descendants from Paradojo fertilized by Roccapina, both sexual and fissiparous, were obviously diploid.

We should like to emphasize that the chromosome set of the fissiparous specimens remains constantly diploid, as already shown by Deri (1984).

As already stated, all results reported here concern the first period of our studies. In the following years (1984-'86), a great number of individuals gradually died. However, various specimens born from Roccapina and from hybrids $\text{Rp} \times \text{Prj}$ survived. These specimens were either sexual or fissiparous. Some of the sexual specimens survived long enough to lay cocoons, while others fissioned. Conversely, some fissiparous individuals became sexual and some

TABLE I.

Populations	N° of offspring	Sexual			Fissiparous		
		N° of individuals	chromosome set		N° of individuals	chromosome set	
			3 n	2 n		3 n	2 n
Roccapina	49	32	4	28	17	—	17
Roccapina × Paradojo ♀ unknown	40	31	—	31	9	—	9
Roccapina ♀ × Paradojo	26	18	6	12	8	—	8
Paradojo ♀ × Roccapina	43	38	—	38	5	—	5

of the latter laid cocoons. Therefore, an alternation between the two reproductive modalities in a single individual or strain, where the chromosome set is constant, may occur.

These facts show the complexity of the relationship between fissioning and sexuality ⁽¹⁾.

CONCLUDING REMARKS

Our present research brings a new contribution to the knowledge of genetic control of fissioning in planarians. The existence of "fission controlling genes" located in the chromosomes was demonstrated by Benazzi (1974). Certain data now suggest the possibility of a maternal control, namely the influence of the egg. It is difficult to assess the degree of this influence and its genetical bases, considering that fissioning also appears in offspring from non-fissiparous strain, even though a low percentage of them are involved. This fact suggests that fissioning is a multifactorial character, a statement that is also supported by other data derived from our cross-breeding research (Benazzi Lentati, 1982).

(1) Obviously, we refer here to the genetic control alone, since the rhythm of fissioning is largely influenced by external factors, particularly temperature (for a summary in this connection, cf. Benazzi and Gremigni, 1982).

The possibility should also be borne in mind of inducing sexuality in fissiparous planarians by feeding them on tissues from sexual planarians (cf. Grasso and Benazzi, 1973). Probably, the sexualizing substances administered as food exert their action by interfering with the genetic factors which in the agamic planarians are responsible both for the inhibition of the development of the genital apparatus and for the activation of fissioning phenomena.

In this context, two hypotheses may be advanced. The first is that some offspring of non-fissiparous strain receive from the father a sufficiently high number of factors to cause fissioning in the absence of the maternal effect. The second hypothesis is that even sexual strains possess fission factors, but only to a limited extent, for which reason fission never appears no matter how these factors are combined in the mating among these individuals; however, sexual individuals in which, occasionally, a greater number of factors are present, may produce fissiparous offspring, after fertilization with sperm of the fissiparous race. Such a hypothesis had been already proposed by Benazzi Lentati (cf. Benazzi Lentati, 1970) in relation to other characters of planarians, such as asynapsis and polyploidy. The validity of this hypothesis was documented by subsequent investigations (Benazzi Lentati, 1982).

By way of a final annotation, we should like to underline the possibility of reversion between sexuality and fissioning in a single individual or strain. Such an occurrence shows that the fission-controlling genes, for unknown reasons, may be repressed or derepressed and this is in agreement with the theory put forward by Benazzi (1974) that the fissiparous specimens which reach sexuality retain their fission-controlling genes.

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