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SELF-FERTILIZATION IN THE FRESHWATER SNAILS *HELISOMA DURYI* AND *HELISOMA TRIVOLVIS*

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Fifty specimens of five strains (10 per strain) of Helisoma duryi *from Lima (Peru), St. Croix (Virgin Islands), Formosa (Brazil), Cartago (Costa Rica) and St. Vincent (Lesser Antilles), reared in isolation for about 150 days, laid 103 eggs. The numbers of eggs laid by the 10 specimens of each strain were respectively (viable eggs in parenthesis): 44 (26), 1 (1), 5 (0), 15 (7) and 38 (0). Egg production widely varied between the individuals of each strain, there being in all strains, except St. Vincent, a number of specimens (3 to 9) which did not lay any eggs. After the observation period the isolated specimens, including those that laid no eggs, readily engaged in cross-breeding when mated and brought forth large numbers of eggs.*

Self-fertilized F_1s are fully interfertile, producing normal cross-fertilized offspring.

Ten specimens of Helisoma trivolvis *(strain from Zempoala, Mexico), also reared in isolation for about 120 days, laid 646 eggs, of which 74 were inviable.*

Our data, added to those from a few previous studies cited in the text, show that self-fertilization is not so efficient an alternative mode of reproduction in H. duryi *as in many other planorbids (it is a little more efficient in* H. trivolvis *than in* H. duryi*). Thus,* H. duryi *benefits much less from functional hermaphroditism which, besides other advantages, enables a single virgin individual to found a new population.*

Key words: planorbid snails – *Helisoma duryi* – *Helisoma trivolvis* – self-fertilization

Self-fertilization has been observed in many families of pulmonate gastropods. Particularly among the Planorbidae, the following species proved capable of selfing (references being made only to the first publication for each species): *Anisus vortex* (Chadwick, 1903), *Planorbis planorbis (= marginatus)* (Holzfuss, 1914), *Planorbarius corneus* (Holzfuss, 1914), *P. metidjensis* (Brumpt, 1928), *Gyraulus parvus* and *Promenetus exacutus* (Colton, 1918), *Bulinus truncatus (= contortus)* (Brumpt, 1928), *B. forskali* (Larambergue, 1939), *Indoplanorbis exustus* (Brumpt, 1936), *Biomphalaria alexandrina (= boissyi)* (Larambergue, 1939), *B. glabrata* (Brumpt, 1941), *B. tenagophila (= nigricans)* (Paraense & Deslandes, 1955a), *B. straminea (= centimetralis)* (Paraense & Deslandes, 1955b), *B. peregrina (= inflexus)* (Paraense & Deslandes, 1956), *B. schrammi (= janeirensis)* (Paraense, 1956), *B. occidentalis* (Paraense, 1981), and *B. kuhniana* (Paraense, 1988).

Besides the mentioned species, self-fertilization has also been observed in this laboratory in the planorbids *Biomphalaria amazonica, B. intermedia, B. oligoza, Drepanotrema anatinum, D. cimex, D. depressissimum, D. heloicum, D. kermatoides, D. lucidum, D. pileatum, Acrorbis petricola, Antillorbis nordestensis* and *Plesiophysa ornata.*

On November 12, 1956, the senior author collected from a drainage ditch at Puente Piedra, on the Pan-American highway, north of Lima (Peru), a sample of *Helisoma,* including several albinos, which had been previously identified as *H. peruvianum* (Broderip, 1832) by Dr. W. Weyrauch (Arrarte, 1953: 8). On December 5 of the same year the senior author collected from an artificial pond in the Botanical Garden of Havana, Cuba, another *Helisoma,* also including albinos, identified as *H. caribaeum* (Orbigny, 1841) by Dr. C. G. Aguayo (see Aguayo & Jaume, 1947). As they were anatomically indistinguishable, showing the characteristics of *H. duryi* (Wetherby, 1879), we successfully tried, in April 1957, to cross specimens from both samples, using individuals reared in isolation since hatching which were lying fertile, although few, selfed eggs. Self-fertilization being a common occurrence amongst Planorbidae, no special importance was attached to such cases.

In 1959, DeWitt & Sloan observed 4 specimens of *H. duryi* from Levy County, Florida, USA, kept in isolation for 380 days (2 speci-

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mens) and 434 days (1 specimen), which did not lay any eggs; and for 790 days (1 specimen), which laid 4 abortive eggs on the 647th day. Madsen et al. (1983) reported no egg-laying by 10 specimens of a Florida strain and an unstated number (seemingly 60) of a Bamburi (Kenya) strain, isolated for 9 weeks and 2-3 months, respectively; they concluded that "*H. duryi* appear unable to reproduce by self fertilization" (Madsen et al., 1983: 189).

In this paper the results of an investigation made in this laboratory on the subject are presented.

MATERIAL AND METHODS

Five strains of *H. duryi* (LI, SC, FO, CO and SV) and one of *H. trivolvis* (Say, 1817) (LQ) were used. They originated from samples collected (except CO) by the senior author, as follows:

- LI, from drainage ditch at Villa, Lima, Peru, April 8, 1965;
- SC, from pond at Cathrines Rest, south of Christiansted, Saint Croix (Virgin Islands), May 5, 1967;
- FO, from pond connected with Canabrava river, Formosa municipality, Goiás state, Brazil, August 15, 1972;
- CO, from Coris river, Cartago province, Costa Rica, August 12, 1976 (collector Gerardo Rojas);
- SV, from ornamental pond in the Botanical Gardens, Kingstown, Saint Vincent Island, May 18, 1985;
- LQ, from Laguna de Quila, Zempoala, Morelos state, Mexico, July 9, 1986.

Ten specimens of each strain, with 2 mm in shell diameter, were isolated in small aquaria containing 300 ml of dechlorinated tap water and, at the bottom, a bit of a mixture of screened reddish soil and ground oyster shells (10:5) as a source of mineral nutrients and of grit to aid the gizzard in its food-grinding function. One-third of the water content of each aquarium was renewed once a week. Up to 5 mm in diameter the snails fed on air-dried lettuce leaves, and thereafter on fresh lettuce. The room temperature varied from 21 to 27 °C during the observation period. Egg capsules, when produced, were deposited on the underside of floating Styrofoam tablets (sometimes on the aquarium wall), from which they were removed to small petri dishes with aquarium water for examination under the stereomicroscope. The snails of each strain were numbered in the order of egg-laying. Eggs were considered inviable when they failed to divide or stopped development at any stage before hatching. Viable eggs, therefore, were those that developed to hatching. All the isolated *H. duryi* except three were observed for 150 days (Table I), and 10 but three *H. trivolvis* were observed for 120 days (Table II).

To test the possibility of low egg-production being a peculiarity of the *H. duryi* specimens under observation, and not a consequence of isolation, at least a pair of snails of each strain was formed after the observation period.

RESULTS

As shown in Table I, the 50 isolated specimens of *H. duryi* produced 66 egg capsules summing up 103 eggs, of which 34 were viable and 69 inviable (hatching rate 33%). The proportion of viable to inviable eggs in the five strains was as follows: LI, 26:18; CO, 7:8; SC, 1:0; FO, 0:5; SV, 0:38.

Not infrequently jellylike masses were deposited by snails of any strain, either egg-layers or not. Many such masses contained all components of an egg capsule, including or not albumen vesicles, but without egg cells.

To test the interfertility of selfed individuals, the two viable F_1s from LI 7 were raised together, laying the first eggs on the 52nd day after hatching, when 5.5 and 7 mm in shell diameter. They were kept together for six additional days, when they laid 9 egg capsules with 105 eggs (103 viable, 2 inviable). From the 8th to the 12th days (postmating period) the larger specimen laid 15 egg capsules with 249 eggs (241 viable, 8 inviable), and the smaller one only 4 with 30 eggs (all viable). The first 20 hatched F_1s from each snail were kept in aquarium (capacity 40 liters) and gave origin to a flourishing colony which was discontinued 6 months later.

All the *H. duryi* that were mated after the period of observation in isolation readily copulated and produced large numbers of eggs. The following is an example of the results, which will be detailed in another paper on cross-fertilization:

TABLE I

Egg-laying as observed in 5 strains of *Helisoma duryi:* LI (Lima, Peru), SC (Saint Croix, Virgin Islands), FO (Formosa, Brazil), CO (Coris, Costa Rica), and SV (St. Vincent, Lesser Antilles). Each specimen isolated with 2 mm in shell diameter and observed (unless otherwise stated) for 150 days.

Strain/ Snail No.	1st egg capsule (day after isolation)	Shell diameter (mm)	Egg-laying period (days)	Egg capsules laid	No. eggs	Viable	Inviable	Eggs per capsule	Remarks
LI 1	54	9	15	8	11	9	2	1-2	
LI 2	54	10	22	11	16	12	4	1-4	
LI 3	56	9	7	2	2	2	–	1	
LI 4	68	12	1	1	1	–	1	1	Died 79th day
LI 5	72	11	1	1	2	–	2	2	
LI 6	82	12	12	2	4	1	3	1+3	
LI 7	107	15	10	3	8	2	6	1-4	
LI 8-10	–	13-15	–	–	–	–	–	–	
Subtotal				28	44	26	18		
SC 1	63	10	1	1	1	1	–	1	
SC 2-10	–	12-14	–	–	–	–	–	–	
Subtotal				1	1	1	–		
FO 1	76	11	1	1	1	–	1	1	
FO 2	86	14	1	1	1	–	1	1	
FO 3	148	14	28	2	3	–	3	1+2	Observed 180 days
FO 4-10	–	13-18	–	–	–	–	–	–	
Subtotal				4	5	–	5		
CO 1	55	12	1	1	2	1	1	2	
CO 2	63	12	1	1	1	–	1	1	
CO 3	81	13	16	2	2	1	1	1	
CO 4	87	13	1	1	3	2	1	3	
CO 5	94	14	34	3	6	3	3	1-3	
CO 6	134	14	1	1	1	–	1	1	
CO 7-10	–	13-15	–	–	–	–	–	–	
Subtotal				9	15	7	8		
SV 1	52	13	1	1	2	–	2	2	
SV 2	56	11	1	1	1	–	1	1	
SV 3	56	14	11	4	10	–	10	2-3	Died 94th day
SV 4	56	13	30	5	7	–	7	1-2	
SV 5	56	14	8	2	2	–	2	1	
SV 6	59	14	25	2	3	–	3	1+2	
SV 7	64	11	1	1	1	–	1	1	
SV 8	72	12	1	1	1	–	1	1	
SV 9	78	13	30	4	6	–	6	1-2	
SV 10	84	13	25	3	5	–	5	1-2	
Subtotal				24	38	–	38		
TOTAL				66	103	34	69		

LI 5 x LI 9 – Joined together at 16:20 hr of Nov. 24, 1986. Copulation began at 16:50 and still continued at 19:00, when observation was interrupted. The next morning at 8:00 they were found in copulation, which ended at 9:10. About 14:00 (nearly 21 hr after beginning of first copulation) LI 5 laid 40 eggs (35 viable, 5 inviable); about 17:40 LI 9 laid 34 eggs (all viable). They were then placed in separate aquaria. For the next 30 days LI 5 laid 75 egg capsules with 1,620 eggs (1,573 viable, 47 inviable), and LI 9 laid 61 egg capsules with 1,265 eggs (1,193 viable, 72 inviable).

All the isolated specimens of *H. trivolvis* laid selfed eggs (Table II). Their productivity varied widely, from 2 to 400 eggs, during an average observation period of 110 days, with a proportion of viable to inviable eggs of 572: 74 (hatching rate 88%).

TABLE II

Egg-laying as observed in 10 specimens of *Helisoma trivolvis* from Laguna de Quila, Mexico, isolated with 2 mm in shell diameter and observed (unless otherwise stated) for 120 days.

Snail No.	1st egg capsule (day after isolation)	Shell diameter (mm)	Egg-laying period (days)	Egg capsules laid	No. eggs	Viable	Inviable	Eggs per capsule	Remarks
1	48	10	18	14	73	67	6	1-12	Observed 66 days
2	59	11	25	13	27	20	7	1-4	Observed 90 days
3	62	11	1	1	2	1	1	2	
4	68	12	34	4	4	3	1	1	
5	69	11	52	41	400	392	8	1-16	
6	69	10	13	6	21	16	5	1-8	Died 83rd day
7	75	10	39	19	35	27	8	1-5	
8	84	13	18	6	8	5	3	1-2	
9	87	13	40	15	37	28	9	1-6	
10	91	12	28	9	39	13	26	2-7	
Total				128	646	572	74		

DISCUSSION

The above observations show that *H. duryi* is capable of selfing, but such capacity is very low in comparison with other planorbid species so far investigated and widely varies among different populations. It is probable that most inviable eggs, which did not undergo the first cleavage, were in reality mere egg cells, not true zygotes. As compared with the other strains, LI was more prolific and produced a proportionally larger number of viable eggs, followed by CO. SC produced a single viable egg, and the remaining two (CA and SV) laid only inviables.

Our data also show that self-fertilization is not so efficient an alternative mode of reproduction in *H. duryi* as in many other planorbids, e. g. *Biomphalaria glabrata* (see Brumpt, 1941; Paraense, 1955, 1956). As a matter of fact, only to mention the family Planorbidae, a gradation from self-sterility to full self-fertilization in isolated individuals has been observed not only in different species but also in populations of one and the same species. As another example of absolute self-sterility, with no egg-laying at all, *Planorbis carinatus* may be cited (Larambergue, 1939: 79-80, 2nd series of experiments) besides the strains of *H. duryi* studied by Madsen et al. (1983). Self-sterility with deposition of inviable eggs was observed in the Levy County strain of *Helisoma trivolvis* studied by DeWitt & Sloan (1959) and in our FO and SV strains of *H. duryi* (Table I). Production of viable selfed eggs, although in minority as compared with inviable ones, was observed in *Planorbarius corneus* by Allen (1935) and in our LI, SC and CO strains of *H. duryi* (Table I). Finally, a clear predominance of viable over inviable eggs was shown by our strain of *H. trivolvis* (Table II).

Cross-fertilization is by far the usual mode of reproduction in the above-mentioned species. In *B. glabrata*, *B. tenagophila* and *B. straminea* careful observations have shown that exclusive cross-fertilization, up to exhaustion of inseminated sperm, follows copulation between conspecific mates (Paraense, 1955, 1956; Paraense & Deslandes, 1956). The same was observed in *H. duryi* by DeWitt & Sloan (1959) and Madsen et al. (1983). As regards *Bulinus truncatus*, however, Larambergue (1939) showed that in a strain from Cairo cross-fertilization predominated but always coincided to some extent with selfing.

Another conclusion to be drawn from the above-mentioned observations is that *H. duryi* benefits much less (and *H. trivolvis* a little more than *H. duryi*) from functional hermaphroditism which, besides other advantages, enables a single virgin individual to found a new population.

RESUMO

Autofecundação nos moluscos planorbídeos *Helisoma duryi* **e** *Helisoma trivolvis* – Cinquenta espécimes de cinco cepas (10 de cada cepa) de *Helisoma duryi* de Lima (Peru), St. Croix (Ilhas Virgens), Formosa (Brasil), Cartago (Costa Rica) e St. Vincent (Pequenas Antilhas), criados isoladamente durante cerca de 150 dias, depositaram 103 ovos. Os números de ovos postos pelos 10 espécimes de cada cepa foram respectivamente (ovos viáveis entre parênteses): 44 (26), 1(1), 5 (0), 15 (7) e 38 (0). A produção de ovos variou amplamente entre os indivíduos de cada cepa, havendo em todas elas, exceto na de St. Vincent, certo número de espécimes (3 a 9) que não puseram nenhum ovo. Depois do período de observação os espécimes isolados, inclusive os que não puseram ovos, prontamente passaram a copular quando acasalados e produziram grande número de ovos.

Os F_1s gerados por autofecundação foram perfeitamente interférteis, produzindo descendência normal por fecundação cruzada.

Dez espécimes de *Helisoma trivolvis* (cepa de Zempoala, México), também criados isoladamente durante cerca de 120 dias, depositaram 646 ovos, dos quais 74 foram inviáveis.

Nossos dados, somados aos de poucos estudos anteriores citados no texto, mostram que no *H. duryi* a autofecundação não é um modo alternativo de reprodução tão eficiente quanto em muitos outros planorbídeos (no *H. trivolvis* é um pouco mais eficiente que no *H. duryi*). *H. duryi*, portanto, beneficia-se muito menos do hermafroditismo funcional que, além de outras vantagens, capacita um único indivíduo virgem a fundar uma nova população.

Palavras-chave: moluscos planorbídeos – *Helisoma duryi* – *Helisoma trivolvis* – autofecundação

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