Ovariole Numbers in two Puerto Rican Oedionychina (Coleoptera)[1]

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ABSTRACT

Two Puerto Rican fleabeetles, *Alagoasa bicolor* (L.) and *Omophoita cyanipennis* F., have telotrophic ovarioles, in which one oocyte at a time suffers vitellogenesis. The process is simultaneous in all ovarioles. All mature eggs are laid in one ovipositional action, usually in one cluster. One female is capable of producing and laying, at intervals, several such clusters. The shortest interval between two ovipositions was found to be three days.

A. bicolor has 8 to 12 (mean, 9.85), and *O. cyanipennis* 12 to 19 (mean, 16.15) ovarioles per ovary. The difference is statistically significant and reflects genetic adaptation to different ecological niches. No significant difference was found between the ovariole numbers of the left and the right ovary of these species.

INTRODUCTION

Alagoasa (=*Oedionychus*) *bicolor* (L.) and *Omophoita cyanipennis* F., the two more common Puerto Rican Oedionychina fleabeetles, partially share habitat and food because both occur in coastal marshlands feeding on *Clerodendrum* (=*Volkameria*) *aculeata* (L.) (Verbenaceae). Both species also occur in the interior of the Island, where they feed on other foodplants. Thus the range of *A. bicolor* extends to drier grounds, to the calcareous haystack hills, where the beetle feeds on a sporadically abundant Verbenacean bush, *Aegiphila martiniquensis* Jacq. The habitat of *O. cyanipennis* extends from the well ventilated *Clerodendrum* to a more humid environment near the ground of the same marshes, where the low Verbenacean herb *Phyla* (=*Lippia*) *nodiflora* (L.) (probably with other *Phyla* spp.) is eaten, and to the edges of rivers and some lakes, where *Jussiaea* spp. (Onagraceae) are shared as foodplants with fleabeetles of the genus *Altica*.

Biological features that might be relevant to the different ecological requirements of these two Oedionychina have been studied in field and laboratory (17). It was observed, for instance, that *O. cyanipennis* lays more eggs at a time than *A. bicolor*. Because egg-laying habits are closely associated with ovarial and ovariolar structure (8), the observation warrants a study of these organs.

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Ovarial anatomy has been studied in only a few fleabeetles. *Epitrix* sp. has 6+6 ovarioles, each containing a chain of five oocytes in the process of vitellogenesis (18). Robertson (12) encountered 7+7 and 13+13 ovarioles in *Longitarsus* sp. and *Disonycha triangularis* Say, respectively. *Psylliodes brettinghami* Baly also has 13+13 ovarioles (16). Suzuki (15) found a high (mean, 53+53) and a very variable number of ovarioles in a polymorphous fleabeetle, *Pseudodera xanthospila* Baly. The number of mature ovarial eggs only slightly exceeds the ovariolar number in this species, each ovariole producing one egg, or seldom two, per oviposition. Thus it is to be expected that the female, exhausting its stock of ovarial eggs, lays nearly the same number of eggs as the total number of ovarioles, and then waits until a new set of eggs has been matured.

MATERIALS AND METHODS

Twenty females of each species were collected from Salinas in 1970-71. The ovaries were removed and the number of ovarioles counted in shallow glass cups provided with a layer of black wax onto which the organs were spread with insect pins. Ethanol 70% was used as the intermedium. Photographs of ovaries immersed in the intermedium were taken with an Exacta (Ihagee) camera mounted on a Bausch & Lomb stereozoom microscope.

For observation of oviposition, gravid females were isolated in Petri dishes whose bottom was covered by a slightly moistened filter paper. Cut *Clerodendrum aculeatum* leaves were offered as food. Leaf remnants and the filter paper were removed daily.

OBSERVATIONS

The ovaries of *A. bicolor* and *O. cyanipennis* are of the *Pseudodera* type, although with considerably fewer ovarioles (fig. 1). The principle one-mature-egg-per-ovariole is even stricter in these Oedionychina; two or more oocytes nearing maturity were never seen in any one ovariole. The ovarioles are telotrophic or possibly pseudotelotrophic (cf. 3). The distal tip of each ovariole, usually whitish-opaque, comprises a bullet-shaped germarium and, limited distally and proximally by a constriction, a small egg chamber containing an oocyte in its previtellogenic growth phase. Proximally to it is the oocyte in vitellogenesis or a mature egg. The ovarioles are in the same stage of development; i.e., they are synchronous. One or two empty ovarioles that have aborted the older oocyte, are sporadically encountered. Empty ovarioles due to incomplete oviposition are more seldomly met, which suggests that once the oviposition has begun, it continues until the end, without major interruptions. It seems that, undisturbed, the female of both species oviposits just one cluster of eggs in a small depression of earth. Captured specimens may lay smaller clusters and scattered eggs on any available surfaces.

In the two samples of 20 females each, *A. bicolor* has 8 to 12 ovarioles per ovary, while *O. cyanipennis* has 12 to 19 (table 1). Means are 9.85 + 0.04 and 16.15 + 0.08, respectively. The difference is statistically significant ($t = -18.74^{xx}$). The sample of *A. bicolor* shows less deviation than that of *O. cyanipennis* with variation coefficients of 8.14% and 12.19%, respectively. There is no significant difference between the ovariole numbers of the left and the right ovary. The means are 9.90 and 9.80 in *A. bicolor,* and 16.16 and 16.38, respectively, in *O. cyanipennis.*

Oviposition histories are still too scant for comparison of the fecundity of these species. Table 2 shows results of twelve ovipositions by eight females. All females were collected from nature and kept and fed in captivity until they died. Obviously the number of eggs they may have laid before captivity remains unknown.

FIG. 1.—Right ovary of *Alagoasa bicolor* (left) and *Omophoita cyanipennis* (right). The former has 11 ovarioles, the latter, 17. – 11 ×.

In all but two cases, only one egg cluster was laid, the number of eggs per cluster usually fitting well in the range of total ovariole numbers in each species. *O. cyanipennis* #2 might be a specimen captured during its oviposition in nature.

For *A. bicolor,* the shortest interval between two clusters was 3 days (#1), the longest 28 days (#3). Thus the whole process of vitellogenesis can be completed in 3 days. For *O. cyanipennis,* the only interval observed was of 4 days (#1).

Data on two Puerto Rican Oedionychina show that 1) eggs mature simultaneously in all ovarioles of a female, one egg per ovariole; 2) mature eggs are laid practically in one ovipositional action; and 3) *O. cyanipennis* lays 1.7 times more eggs per oviposition than *A. bicolor*. It still remains to be shown whether the total number of eggs laid by the former species also exceeds that of *A. bicolor.*

DISCUSSION

In the compound gonads of Coleoptera, the ovarioles are homologous with testis components called by a variety of names, including testis follicles (it would be better to speak of testis vs. ovary and testicle vs. ovariole; unfortunately, testis and testicle have already been widely used as synonyms). These "gonadions" have a common ontogenic history from pole cells through repeated association with somatic cells to the adult units of gamete production (14). The process is under complicated genetic control.

TABLE 1.—*Number of ovarioles per ovary in* Alagoasa bicolor *and* Omophoita cyanipennis *(20 females in both samples)*

Species	Variation	Ovariole number											
		8	9	10	11	12	13	14	15	16	17	18	19
	Right ovaries		5	13	1	1							
Alagoasa bicolor	Ovarioles		45	130	11	12							
	Left ovaries	2	4	10	4								
	Ovarioles	16	36	100	44								
	All ovaries	2	9	23	5	1							
	Ovarioles	16	81	230	55	12							
Omophoita cyanipennis	Right ovaries					1	3	1	1	3	6	4	1
	Ovarioles					12	39	14	15	48	102	72	19
	Left ovaries						2	4		4	2	7	1
	Ovarioles						26	56		64	34	126	19
	All ovaries					1	5	5	1	7	8	11	2
	Ovarioles					12	65	70	15	112	136	198	38

TABLE 2.—*Number of eggs laid by five* A. bicolor *and by three* O. cyanipennis *females in captivity*

Female Number	1970					1971				
	8.XII	11.XII	20.XII	24.XII	31.XII	5.I	7.I	8.I	27.IV	11.V
Alagoasa										
1	19	19			18					
2							18			
3		19						15[1]		
4							12 ± 6[2]			
5						20[1]				
Omophoita										
1			32	32						
2										13 + 1[2]
3									35	

[1] Eggs scattered.

[2] Female died during oviposition; ovarial eggs (later number) encountered by autopsy.

The number of ovarioles per female is a population biological parameter of importance, because it is connected with fecundity. Kambysellis and Heed (6) define fecundity potential (F_p) of a species as $F_p = pgr$, *where*

p = number of ovarioles per female, g = number of mature eggs per ovariole, and r = rate of egg maturation. F_p is normally modified by environmental factors, resulting in a realized fecundity (F_r). In this equation, the environment presumably affects r most and p least, the latter depending on the early ontogenic (pre-eclosion) number and organization of pole cells. The genetics seems to play a major role thereby. Thus transplantation of a mono-ovariolar ovary anlage of *Drosophila crassifemur* to species having over 40 ovarioles does not induce extra ovarioles in the transplantate (6). Inbreeding and selection experiments with *Drosophila melanogaster* (9) suggest that perhaps 60% of the variation in ovariole number is genetic in origin. A still stricter genetical control is suspected in the beetle *Tribolium castaneum* (5.86 + 0.59 ovarioles per ovary, coefficient of variation 10%) (1).

Nutrition of the larvae is the strongest environmental factor capable of modifying genetically determined ovariole numbers. Starved larvae produce small adults with a reduced number of ovarioles. High correlation between body size and ovariole number found by Suzuki (15) in a fleabeetle, *Pseudodera xanthospila,* might be of such origin. In a genetically caused variation, body size and ovariole number are not correlated in *Drosophila* (6, 9, 10). Body size increased by polyploidy does not coincide with increased ovariole numbers in the *Calligrapha* beetles (13). Differences of ovarial numbers between the left and the right ovary seem to be due to a chance in *Drosophila* as well as in *Pseudodera* and the two Oedionychina.

Number of eggs laid does not always correspond with the number of ovarioles. Several eggs mature simultaneously in each ovariole of many beetles (8, 15). Ovarioles function asynchronously in some Drosophilids (6) and scarabs (8), to the extreme that only one egg per female matures at a time, although 12 ovarioles are present (8). Reduction of ovariole number may be physiologically compensated for by an increased production of eggs through the remaining ovarioles (9). Nevertheless, the species-specific, genetically determined ovariole number is in some degree of positive correlation with the total egg production. Parasitic biology, for instance, requires large initial progenies; accordingly, *Meloë* has over 200 ovarioles per female (12). Protected juvenile stages, on the other hand, allow reduced progenies. The scarabs practicing extensive parental care (nidification) have only one ovariole per female (4, 5, 8, 12), total egg production being just a few eggs per female. This condition may have developed through asynchrony of ovarial function as in the provisioning scarabs Ochodaeinae and Geotrupinae (8). The subsocial Passalidae have four ovarioles per female, as do also the Curculionidae and Scolytidae that have relatively well protected preadult stages (7, 8, 12). But Hawaiian Drosophilids occupying the nutritionally hazardous "flower niche" have also reduced ovariole numbers (6), which shows that increasing of the egg output is not the only way to cope with such problematical environments. In this case, increased parental care (ovovivipary) is involved, together with the female's capacity of retaining mature eggs in her ovary until promising oviposition conditions are met.

These examples suggest that Dollo's principle (*cf.*2) of irreversible reduction of meristic characteristics during evolution does not apply well here. There still seem to be in insects gene reserves for a free selection of ovariole numbers adaptable to changing biological requirements of the species. Thus drastically different ovariole numbers may occur in closely related species (*cf. Harpalus, Silpha, Ctenicera, Ampedus, Coccinella,* in Robertson's list: 12). Within a species, geographic differences may exist (11).

As to the presently studied Oedionychina, biological differences explaining the species-specific ovariole numbers may eventually turn out. At present, it seems probable that the higher motility of *O. cyanipennis* (17) and its association with the floodable *Phyla* vegetation, where massive death of preadults is possible, are population-suppressive hazards whose effects must be compensated for by an increased egg production.

RESUMEN

Dos alticinos puertorriqueños, *Alagoasa bicolor* y *Omophoita cyanipennis,* tienen ovariolos telotróficos, donde sólo un oocito a la vez pasa la vitelogénesis. Todos los huevos maduros se ponen en una oviposición, generalmente en uno o pocos grupos. Una hembra repite la oviposición a intervalos. El intervalo más corto observado entre dos oviposiciones de una hembra fue de 3 días.

Las especies difieren en el número de los ovariolos. *A. bicolor* tiene de 8 a 12 (promedio, 9.85) y *O. cyanipennis* de 12 a 19 (promedio, 16.15) ovariolos por ovario. La diferencia es estadísticamente significativa y refleja adaptación genética a nichos ecológicos distintos. No se encontró diferencia significativa entre el número de ovariolos de los ovarios izquierdo y derecho.

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