Evolution of Sex in the Mollusca*

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IT IS the purpose of this paper to present some of the trends in the more general problem of evolution of sex in certain of the molluscan groups. The author is especially interested in the problems which arise by the interactions which occur when the male and female germ cells take origin and reach their maturity in the same gland, the hermaphrodite gland, or ovotestis, as it is sometimes called. While most of my work has been centered on the gastropods, especially the fresh-water snails where most unusual variations in structure and behavior have been observed, other groups offer many unusual conditions of sexuality. These variations take such trends as deviation in development, structural differences in arrangement of male and female germinal tissues, alternation of male phase with female phase in sexual cycles, the presence of the capacity for self-fertilization in some forms, the absence of this function in others, the production of abortive eggs, parthenogenesis and the occurrence of spermic dimorphism.

The existence of animals producing both male and female germ cells in a single gland has been known since the early Greeks. These hermaphrodite snails attracted the attention of Aristotle when he observed that members of the group, Testacea, which included the gastropod molluscs, reproduced like plants. In accordance with other Aristotelian explanations it is to be concluded that the young gastropods spring from the mud and slime of the ponds, lakes and rivers. This concept appears to have existed unchallenged until late in the sixteenth century when Androvandi[1] stated that snails reproduce by sexual methods (Baudelot, 1863). The renowned French naturalist, Cuvier (1846), working in the early nineteenth century failed to recognize the dual nature of the ovotestis and concluded that both *Planorbis* and *Lymnaea,* common pond snails, have separate sexes. Both of these forms are hermaphroditic, i.e., they are monoecious or unisexual.

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A study which has held the attention of many workers in biology is that of Carl von Siebold (1837) published a century ago in which the existence of spermic dimorphism was established. Basing his conclusions on observations on the history of the germ cells of *Paludina vivipara (Vivipara vivipara)* von Siebold showed that two very different kinds of sperm cells are produced in the gonad of this snail. This observer did not suggest the probable significance of these most unusual conditions, and after one hundred years their function is still a matter of uncertain speculation. This early work on the snail *Paludina,* has led to many classical studies in the fields of embryology and cytology of the gastropods.

The functional significance of these aberrant germ cells is a controversial subject of long standing. While some authors (Brock 1881; Lams 1909; Kuschakewitch 1911; and Gatenby 1917) consider them as abnormalities of development or products of degeneration. Others (R. Hertwig 1905; Reinke 1914; Hyman 1925; Furrow 1935) are impressed with their persistent character and complicated courses of development of some types and conclude that they must have some, at present unknown, physiological significance.[1]

Studies on the development of the fresh-water snails has offered much of interest to the student of morphology and experimental embryology. Growing out of this interest have come many concepts bearing on anatomy, taxonomic relations and physiology. In the field of anatomy the relation of the snail having unisexual characteristics or hermaphroditism, to those possessing bisexual or separate sexes continues to offer a fertile field for study.

It is clear from the results of investigations already at hand that in the hermaphrodite snails the male and female genital elements have a common origin, a condition of monoecism is set up which we may designate as **unisexual.** In such cases of unisexual monoecism a female or (male) animal develops at certain times spermatozoa in the ovary (or eggs in the testis). In consequence of this relationship of germinal elements one or the other sex becomes superfluous and more or less disappears. Special biological conditions accompany these phenomena. Under the classification of unisexual monoecism two generalized genital patterns exist in these hermaphrodite snails.

Using the structural relations of the male and female germinal elements as a basis of separation one may define one of these genital patterns as unsegregated. In this type the sex cells are not anatomically or histologically separated or restricted to a male zone or female zone in the ovotestis. The second pattern may be called segregated, because of the strict separation of the male germ cells from the female germ cells in the hermaphrodite gland.

The ovotestis of the unsegregated type is composed of a series of compartments or cysts which give the gonad the appearance of a compound acinus gland. The cysts containing both the male and female cells join a common outlet, the hermaphrodite duct which serves as both a sperma duct and an oviduct. This condition of sexuality exists in *Helix, Physa, Lymnaea, Planorbis,* and *Polygyra.*

While these forms are true hermaphrodites their reproductive cycles appear to be quite definitely divided functionally into a male phase during which the animal discharges spermatozoa, and later, into a female phase during which eggs are deposited. Referring to the structure of the ovotestis of these forms, while the male and female tissues are not anatomically segregated, the developmental processes of the male germ cells are separated from the female germ cells by a functional factor, a time interval. The duration of this time interval appears to vary considerably, and at times under certain experimental conditions, it may be shortened almost to the extent of complete elimination.

Some evidence has been obtained to show the probable significance of this fluctuation in the extent of this time interval which occurs between the male phase and the female phase. If individuals of *Planorbis* are reared in mass cultures reproduction occurs regularly by cross fertilization. If however, individuals are segregated at the time of hatching and permitted to live in strict isolation the snails in such cultures will upon reaching sexual maturity reproduce by using the method of self-fertilization. In the latter case the time factor (or interval) which separated the normal functional phases has become reduced to such an extent as to allow the eggs to reach maturity about the same time that the sperm cells complete their course of development. In another pond snail, *Lymnaea,* similar conditions exist. Colton (1921) preventing cross breeding by isolation for forty-seven generations found that only temporary alteration in the sexual cycle occurs. The nature and cause of these changes in sexual cycles in Planorbis and Lymnaea are not definitely known.

In a marine gastropod, *Crepidula plana,* an unusual condition of sexuality exists. *Crepidula* is hermaphroditic, but completely protandric, i.e., the male and female phases are completely separated in time. The male phase develops first. This phase is then normally followed by a period of transition in which the animal exhibits characteristics of both sexes, a condition of hermaphroditism. Toward the close of the life-span the animal becomes completely transformed into a female. Under experimental conditions if the male is removed from the vicinity of the larger individual the male genital organs degenerate, and after a brief period of sexual activity the animal becomes female. The nature of the stimulus exerted by the larger individual has not been ascertained.

The fresh-water prosobranchiate gastropod, *Valvata tricarinata* (fig. 1), illustrates the second or segregated type of sex differentiation. Here a sex condition exists in which the animal is definitely a Protandric Hermaphrodite. The snail is first male in function and after a brief transformation period or sex reversal the animal takes on the function of a female.

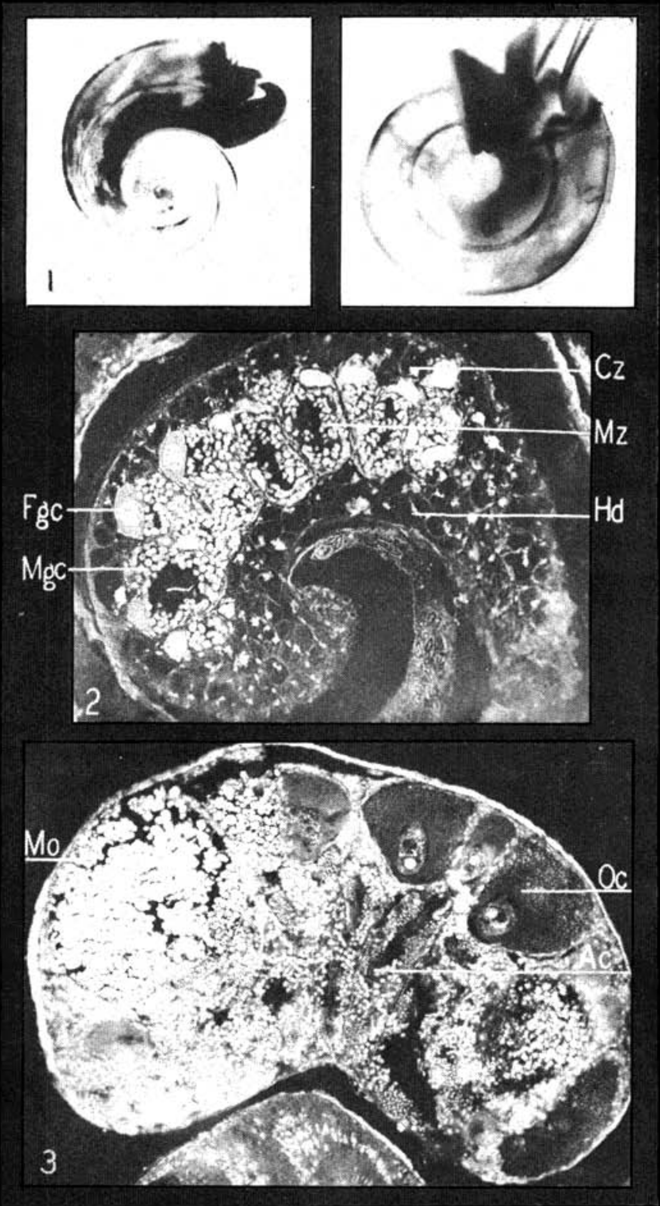

Fig. 1.—A young Valvata at the beginning of the first sexual cycle. Age 135 days. (X 17).

Fig. 2.—Photomicrograph of a longitudinal section of the ovotestis of a young individual. The segregation of the male and female zones is shown.

Unlike Crepidula the development of the female phase is in a manner contingent upon the influence of older individuals. The young Valvatas develop normally whether they are reared in mass cultures or in strict isolation. In Valvata, as in Planorbis, the male and female germ cells differentiate early in development of the animals and follow independent courses. In Valvata, however, the male tissues are completely separated, anatomically, from the female elements (fig. 2), representing a condition of gonad structure which does not exist in the other forms already mentioned.

This separation of germinal elements is accomplished early in embryonic development by the segregation of the germ cells into the female zone which occupies the cortex of the gonad, and by a similar segregation of the male germ cells into the acini which compose the medullary or central region of the ovotestis. This arrangement of embryonic male and female tissues which has been reported recently in two classes of mollusca, certain snails, and the eastern oyster, is also found in certain vertebrates, particularly some amphibians. The latter forms include an indifferent or hermaphrodite stage in their gonadal differentiation.

This phenomena of segregation of reproductive tissues in snails is of further interest because of the relation of the structural condition to the functional behavior of these male and female tissues. In some forms, the protandric hermaphrodites, this relationship determines the order of sexuality, i.e., the animal is first male because of the position of the male germ cells with respect to the hermaphrodite duct. Following the discharge of the spermatozoa, a brief transition period follows during which complete reversal occurs, and the snail assumes female characteristics. The female germ cells (fig. 3) migrate from the cortical region through the medullary zone to reach the hermaphrodite duct. Since both sex cells utilize the hermaphrodite duct the question of self-fertilization arises.

The functional stability of the separation of these two tissues in Valvata has been tested repeatedly by attempts at self-fertilization. Over sixty animals have been reared in strict isolation by segregating the young as they emerge from the egg-capsules. These segregated snails did not reproduce. This fact is construed as further evidence

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Fig. 3.—A photomicrograph of a cross-section of the ovotestis at the beginning of the male phase.

LEGEND

Cz—cortical zone (female)
Mz—medullary zone (male)
Hd—hermaphrodite duct
Fgc—female germ cells
Mgc—male germ cells
Mo—mature egg cell
Oc—young ovocyte
Ac—acinus containing mature spermatozoa and developing spermatocytes

supporting the idea of stability of separation of the germinal elements in this form, a condition which is in harmony with the independence of the transition phase (time factor). The alternation of the sexual phases (fig. 4) continues throughout the life span of *Valvata tricarinata*. While these male and female elements are separated, their activity in the hermaphrodite gland is productive of other complications which alter the course of development of some of the germ cells, both male and female.

These deviations take the forms of abnormal development in the maturation of the male germ cells, a course which ends in the production of atypical spermatozoa. These cells vary in development, cytological structure, and behavior from the typical or normal male germ cells. In studies on two European species of fresh-water snails, *Valvata piscinalis,* and *Valvata cristata,* another complication to the problem has been added. *Valvata piscinalis,* the Bavarian species, has a perfectly normal spermatogenesis and consequently does not produce abnormal spermatozoa. The Italian form, *Valvata cristata,* on the other hand, shows a strong tendency toward abnormality and produces regularly both normal and atypical spermatozoa. The American species, *Valvata tricarinata,* shows even stronger tendencies toward increasing abnormality by producing four types, one normal type and three atypical sperm forms. On the basis of origin the atypical cells may be classified as variations of one general type, thus maintaining strict spermic dimorphism. A fourth species, *Valvata japonica,* has been examined and the existence of atypical spermatogenesis noted, but information necessary to complete the classification of this form is at present lacking.

These fresh-water snails present an interesting series with respect to the degree of development of this increasing abnormality and may be placed in order on the basis of the degree of deviation from the normal condition. *Valvata piscinalis* would be placed first, *Valvata cristata,* second, and *Valvata tricarinata* third. The position of the Japanese species in this series is at present undetermined.

These complications in the germ cell cycle of these animals have been made even more significant by the recent discovery of the existence of a case (Artom 1933) of abortive ovogenesis or atypical development of the female germ cells in *Valvata piscinalis.* Here cells which appear in the male germinal epithelium assume the characteristics of the female germ cells. Continued growth and differentiation of these cells results in the production of egg-like cells which may be designated as pseudo-ova. There is further interest in this phase of the problem because of the apparent, at least in this case, parallel evolution of this abnormal tendency in both the male and female lines of germ plasm in this group.

While this problem takes the form of almost uncompromising controversy some particularly definite trends should be pointed out.

(1) From both physiological and morphological evidence some investigations show that atypical spermatozoa are rudimentary eggs.

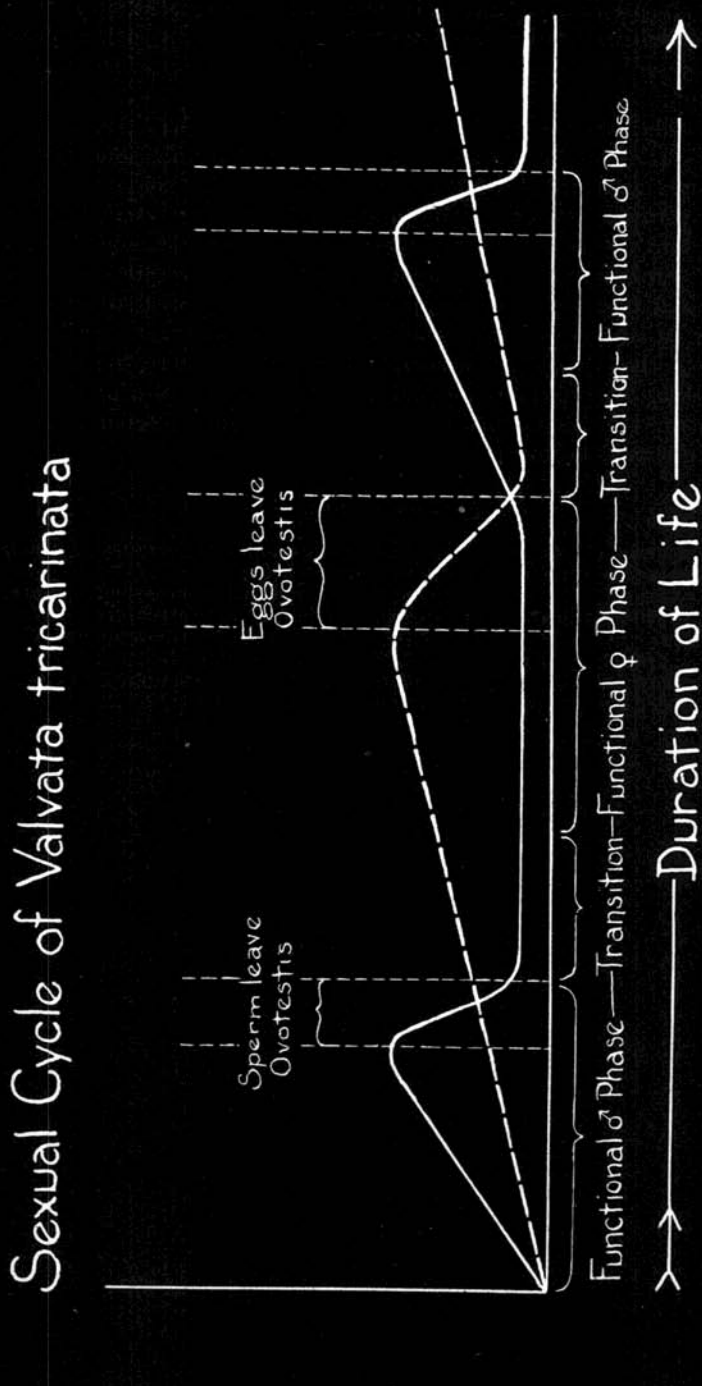

Fig. 4.—A diagram to illustrate the phase history of the hermaphrodite gland during the male and female stages of the sexual cycle of *Valvata tricarinata*.

(2) A possibility of the atypical spermatozoa possessing the capacity for fertilization has been suggested. In this light such conditions would represent a stage intermediate between parthenogenesis and true fertilization.

(3) The more recent investigations suggest that these atypical germ cells are entirely without function, and that this abnormal condition arises as a result of the interaction between these two widely differing germinal tissues. The studies on *Valvata tricarinata* show that the fate of these abnormal germ cells is complete degeneration.

(4) Finally, it is clear that in certain hermaphrodite snails where the male and female elements appear functionally separated, the sexual cycle may be altered by forced changes in sexual behavior. And, it has been shown that in certain hermaphrodite snails, where the male and female tissues are separated not only in function, but also in structural arrangement, the functional cycle is in no manner altered by forced changes in sexual behavior.

BIBLIOGRAPHY

[1] For reviews of the literature and bibliography the reader is referred to the following recent publications on this problem:

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