

THE SPERMATOPHORES OF DIEMYCTYLUS.

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SINCE several months will probably elapse before I shall have fully ready for publication my study of the habits and development of the newt (*Diemyctylus viridescens*, Raf.), I here describe in advance some of the more remarkable features in the process of fertilization. Although the process in its main outlines has been recently observed by Zeller,¹ it seems pardonable briefly to supplement his description, both because I observed the process independently while still in ignorance of Zeller's observations, and because, working as I was with the advantage of abundant material, I was able to discover several interesting facts that appear to have escaped Zeller completely.

The fertilization of the Urodela has been until lately very imperfectly understood, and this lack of positive knowledge is the more surprising now that it has been demonstrated by the fine observations of Gasco and Zeller that a few days of ordinarily careful observation at the suitable time of year are all that is required in order to obtain a comprehensive knowledge of the process. F. Gasco has been the pioneer in this field. He was the first to describe the method of fertilization in the European triton (*Triton alpestris*), and a year later he followed this with a minute and spirited account of the amours of the Axolotl, worthy of the highest praise.² As pointed out by Zeller, however, Gasco's discoveries have not as yet received due recognition, and in the recent text-books of zoölogy the old view of direct cloacal contact is still adhered to. Nearly a hundred years before Gasco, in 1785, Spallanzani had proved that, at least in the case of several European aquatic salamanders, the fertilization of the eggs is internal, and that there

¹ E. Zeller, Ueber die Befruchtung bei den Urodelen. *Zeitschr. f. wiss. Zool.*, Bd. XLIX., 1890, p. 583.

² F. Gasco, Gli amori del tritone alpestre, Geneva, 1880; Les amours des Axolotls, *Zool. Anz.*, IV., 1881, pp. 313, 328.

is no direct cloacal contact between the sexes. Spallanzani was in ignorance, however, of the way in which the spermatozoa entered the cloaca of the female, and believed that the spermatozoa discharged by the male were diffused in the water and thence found their way to the genital opening of the female.

Up to about ten years ago there had been few important advances on the facts established by Spallanzani, and there had been serious retrogression in one respect; namely, that of assuming—in the face of Spallanzani's distinct proof to the contrary—a direct cloacal contact. This retrograde step was hastened by v. Siebold's significant discovery of an accumulation of spermatozoa in the cloaca of the female salamander (*Salamandra maculosa*) in a sort of, "*Receptaculum seminis*." V. Siebold¹ was led to believe that this "receptacle" could be filled with spermatozoa only by means of a true copulation, and this has been until very recently the generally received opinion.

As regards the American newt, the more obvious phenomena of the breeding season have been long known and commented upon. As spring approaches, a crest appears on the tail of the male, already broader than that of the female, the cloacal regions in both sexes appear somewhat enlarged, and both male and female shine in rather livelier colors. All these external features have been greatly exaggerated by some writers; the general appearance of newts captured in April is not strikingly different from that of those captured in October. In one respect, however, the male has added materially to his attractions. All the way up and down the inside of the hind legs, as well as on the adjoining parts of the body, are developed round, black, wart-like elevations. These warts are hard and rough, and undoubtedly aid the male in clasping the female more firmly. They grow yellow and soft and lose their distinctive character soon after the breeding season is past. These black prominences were, I believe, first carefully described by Braun,² although they had been noticed by different observers long before his time. The hind limbs of the male are throughout the year much larger and stouter than the corresponding limbs of the

¹ C. T. v. Siebold, Ueber das Receptaculum seminis der weiblichen Urodelen. *Zeitschr. f. wiss. Zool.*, IX., 1858, p. 463.

² M. Braun, Ueber äussere Hilfsorgane bei der Begattung von Triton viridescens. *Zool. Anz.*, I., 1878, p. 124.

female, and thus afford a ready means of distinguishing between the sexes. They are also much larger than the fore limbs of both sexes.

It has been suspected by most writers on the subject that the fertilization of *Diemyctylus* is internal, and this has been recently demonstrated to be the case by Gage.¹ The demonstration of internal fertilization is by no means difficult; one has only to isolate any female freshly captured, say between April 15 and June 15, to be convinced that internal fertilization is the normal procedure in this species. Almost every female so isolated will for at least several days after her capture continue to lay fertilized eggs. In one instance an isolated female under my observation laid fertilized eggs for nineteen days after her separation from a male. I shall describe the egg-laying of this species more in detail in my coming paper.²

I have found, furthermore, spermatozoa in the cloaca of the female in nearly all the specimens examined between the first of May and the first of July. These spermatozoa are not inside the mouth of the oviduct, as might be expected, but are closely packed in the ducts of two groups of gland-like structures situated in the cloacal wall just below the entrance of the oviducts. These ducts are undoubtedly identical with the "Samentaschen" described long ago by v. Siebold (*loc. cit.*) in the European salamanders and tritons. Blanchard,³ who has recently investigated the structure of the pelvic and cloacal glands of the Urodela, makes on this point the following statement: "La glande que v. Siebold a décrite dans la cloaque de *Salamandra*

¹ *American Naturalist*, April, 1891, p. 380.

² The possibilities of mal-observation may be estimated perhaps by a quotation from a recent paper ("Notes on the Life-History of the Common Newt," Colonel Nicolas Pike, *American Naturalist*, XX., 1886, p. 17): "The males dart about, gyrating round their chosen mates, heading them off in their endeavors to escape, and when they have at last won the victory they seize the females round the lumbar region and remain thus often for hours. The milt and ova pass simultaneously, and the operation takes some time, but it is generally accomplished under cover of darkness. The older females often deposit 150 to 300 eggs at a time, which they attach to twigs in the water or long grass. The eggs are very small at first, but rapidly swell." The eggs, so described, were undoubtedly the eggs of some species of *Amblystoma*. That the "milt and ova" do not pass "simultaneously" is abundantly evident from the observations recorded in my paper.

³ R. Blanchard, Sur les glands cloacale et pelvienne et sur la papille cloacale des Batraciens urodèles. *Zool. Anz.*, IV., 1881, pp. 9, 34.

maculosa femelle, et qu'il a désignée sous le nom de *Receptaculum seminis*, a une situation anatomique et une structure identiques à celles de la glande pelvienne du mâle. . . . Je ne crois pas exacte l'opinion de v. Siebold relativement au rôle physiologique de cette glande chez la femelle, car je n'ai vu dans aucun cas de spermatozoides engagés dans les tubes de cette glande." V. Siebold's careful descriptions and figures would seem, notwithstanding, to leave no doubt as to the presence of spermatozoa in all the species of female Urodela examined by him, and it is certain that in *Diemyctylus*, spermatozoa ensconced in these ducts may be detected without difficulty.

The question as to how the spermatozoa find their way to these snug resting-places is one of considerable interest. Why should they enter these small ducts and there lie dormant, in preference to passing *en masse* up the oviducts, or to entering the alimentary canal, or even to issuing from the mouth of the cloaca? It appears to me probable that the explanation lies in what Pfeffer has called "positive chemotaxis." Pfeffer found, as is well known, that certain chemical substances, as malic acid, attract spermatozoa (positive chemotaxis), and that others, as chloroform, repel them (negative chemotaxis). For example, the mucilage in the central canal of the archegonia of *Pteris* contains a trace of malic acid, and Pfeffer has shown that this amount is sufficient to attract spermatozoa to the mouth of the canal. A similar explanation has been given by some bacteriologists to account for the gathering of leucocytes at inflammatory foci. It is supposed that the leucocytes have been drawn thither in virtue of their chemotactic properties which were brought into play by the metabolic bacterial poisons, or, as now seems more likely, by the freed albuminoid constituents of the bacterial cell.

It seems highly probable that the pelvic gland of the female newt may secrete a substance—proteid or otherwise—with a positively chemotactic effect and thus draw the spermatozoa into its ducts. At all events, such a supposition may serve for a provisional hypothesis. I shall reserve a further consideration of the structure and significance of this gland until my later paper.

The most favorable time to watch the process of copulation is between the first of April and the middle of May. After

about May 15th there is a perceptible slackening in the "Liebesspiel," and spermatophores are rarely discharged after the first of June. The male, heretofore amorous to an extraordinary degree, has by the latter date become comparatively quiescent and unsusceptible.

If at any time during the month of April several pairs of newts are freshly captured from the ponds, and the sexes kept apart over night, the phenomena of copulation may be observed on bringing the animals together in pairs on the following morning. In many cases an interesting courtship precedes the actual clasping of the female. As soon as the male becomes aware of the presence of the female in his neighborhood, he becomes somewhat agitated, and usually begins to move stealthily towards the female with an air of exaggerated caution. It not infrequently happens that the latter, on perceiving his approach, darts away in a state of great excitement, and has to be patiently approached again and again by her unwearied suitor. When the male is finally allowed to come into the immediate neighborhood of the then passive female, he usually enters upon a series of contortions resembling those witnessed at the time of the discharge of the spermatophores. After a few seconds of this suggestive "Vorspiel" the male vaults quickly upon the back of the female and clasps her tightly around the body with his strong hind legs. When the animals have been for some time in captivity, or a number of individuals of both sexes are together in one aquarium, this deliberate courtship is not observed, and the male clasps the female without any ceremonious preliminary. It often happens that he first catches the female by the hinder part of the body, but if he retains his hold for longer than a few minutes, he invariably moves forward until he has the female securely clasped under her throat, either directly before or directly behind her fore legs. Once in this position no attempt of the female can dislodge him, and he may cling there for hours. On a number of occasions I have seen females appear much the worse for this rough usage, and on one occasion an apparently robust female lay as if dead for several hours after the male had left her, although she eventually revived.

When the male is thus mounted, a period of comparative quiet ensues, lasting from thirty minutes to several hours in individual

cases. During this period the animals remain on the floor of the aquarium in almost exactly the same spot, and the male is not, as incorrectly stated by most observers, "jerking the female unmercifully around during the whole time." On the contrary, both animals are well-nigh motionless, with the exception of the often-described fanning movement of the tail of the male. This half-stroking, half-fanning motion is kept up with more or less rhythmical regularity, first on one side and then on the other, and probably serves to excite both animals, although heretofore it has been not unnaturally regarded by many observers as for the purpose of diffusing the spermatozoa throughout the water. The female responds by slowly raising her tail until it forms an angle of 45° , or even a right angle, with her body, and occasionally repeats in her turn the slow fanning movement.

From this condition the male passes gradually into a more violent stage, which has been wrongly stated by some writers to extend over the whole of the foregoing period. This more violent stage usually lasts for only about ten minutes, and during this time the unhappy female is dragged, jerked, and pulled over the whole floor of the aquarium, the entire body of the male meanwhile quivering with intense excitement. The cloaca of the male at the same time begins to swell and to show a few whitish papillæ projecting from the sides. At the climax of his agitation the male, after a few rapid bendings of his body from side to side, leaves the female, and with his tail slightly raised, his cloaca widely distended with numerous white protruding papillæ, throws his whole body into a series of rapid and strenuous undulations, and waits for the female to follow him. If she does this and presses her head lightly against his tail and cloacal region, the male soon deposits a spermatophore and then creeps on to a distance of a few centimeters, where, if the female still continues to follow him, he soon deposits another. I have often seen one male discharge as many as three spermatophores in this way, but have never seen one individual discharge at one time more than this number.

The spermatophore consists, broadly speaking, of three parts: a thick, irregular gelatinous mass about six millimeters in diameter which adheres to the bottom of the aquarium; a tough elastic spine projecting upwards from this base; and, borne on

this spine, an approximately spherical mass of spermatozoa about one and one-half millimeters in diameter, this mass being a sort of concretion of small balls of spermatozoa. The whole structure is very simple as compared with the elaborate bell-shaped spermatophore of *Triton alpestris* described and figured by Zeller (*loc. cit.*).

After the male has deposited his first spermatophore in the manner above recorded, he moves ahead a few centimeters with the female closely following him. In this forward movement of the female she quite naturally brushes over the spermatophore, and, if all goes well, the mass of spermatozoa adheres to the cloacal lips, and thence passes, in part at least, into the cloacal chamber. More frequently the spermatozoa adhere to the rough skin in the neighborhood of the cloaca, and do not come into close relations with the opening itself. A considerable number of the spermatophores, moreover, are not touched at all by the female, but are passed by on one side or the other. I should think that in my aquaria about one spermatophore in five fulfilled its mission, but it is possible that in the ponds the number of failures is not so large.

As to the way in which the spermatozoa actually enter the cloaca of the female there has been some difference of opinion. Gasco has described the female Axolotl as holding the spermatophore firmly with her hind legs and pressing the mass of spermatozoa into her cloaca, but Zeller has been unable to confirm this observation. Zeller at first thought that the European triton took up the spermatozoa actively by means of the widely opened lips of her cloaca, but he has very lately¹ abandoned this view, and now holds that the spermatozoa, by virtue of their own activity, pass up between the *tightly closed* cloacal lips. Zeller attempts no explanation of the fact that the spermatozoa choose to pass into the female cloaca rather than into the surrounding water. Indeed, it is difficult to understand just why this movement in precisely the right direction should occur, unless we suppose a positively chemotactic influence to attract the spermatozoa into the cloaca. It is not improbable that the pelvic gland of the female may be stimu-

¹ Ernst Zeller, Berichtigung betreffend die Samenaufnahme der weiblichen Tritonen. *Zeitschr. f. wiss. Zool.*, LI., 1891, p. 737.

lated to secretion during the "Liebesspiel," but I do not care to enter at present into a full consideration of that question.

In *Diemyctylus* the pointed spine above described sometimes plays an important part in the entrance of the spermatozoa. I have in several cases, in females watched from below, seen the tip of the spine covered with spermatozoa actually pass directly between the closed cloacal lips. The elastic spine, easily bent down by the passage of the female over it, and as easily springing up when the entrance to the cloaca is reached, functioning thus as a sort of penis, would seem admirably adapted for effecting the entrance of the spermatozoa, but I do not think that the spermatozoa obtain an entrance only in this way. The springing up of the spine is apparently of rather infrequent occurrence, and I am constrained to think that this is not the sole and invariable mode of entrance. It much more frequently happens that the cloacal lips and the surrounding skin are thickly smeared with spermatozoa, and I am inclined to believe that, as in the European form, the spermatozoa then find their way to the "Samentaschen" by virtue of their own activity.

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