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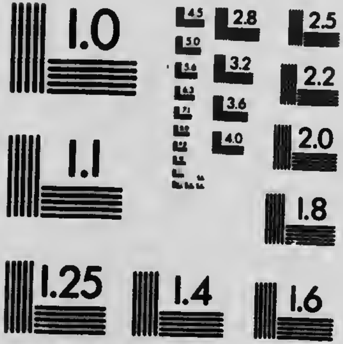

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THE HABITS AND LARVAL STATE OF *PLETHODON CINEREUS ERYTHRONOTUS*.

By W. H. Piersol, B.A., M.B.

THE HABITS AND LARVAL STATE OF *PLETHODON CINEREUS ERYTHRONOTUS.*

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Although *Plethodon cinereus* is considered by Cope ('89) "the most abundant salamander in the northern and central United States" its habits and development have received but little attention. Cope ('89) gives a brief outline and Wilder ('94) a scant mention, Montgomery ('01) adds a few points and describes the larvæ of one bunch of eggs. Reed ('08) discusses the coloration of adults. Kingsbury ('95) touches on the questions of the transference of sperm and the season of egg-laying but without coming to any definite conclusions. Sherwood ('95) gives a date on which eggs were found. As regards *Plethodon oregonensis* the behavior in captivity of a female found with her eggs is described by van Denburgh ('98), and Hubbard ('03) deals with some protective devices. There are several other papers in which Plethodon is mentioned but without reference to habits or development. The observations recorded below have been made partly in the field, partly in the laboratory, and on specimens from several localities, all however within a radius of fifteen miles from Toronto. Unless recorded as single occurrences, all observations have been verified in at least one subsequent season. Cope ('89) divides *P. cinereus* into three sub-species of which *P. cin. cinereus* and *P. cin. erythronotus* only are common. For the sake of ensuring uniformity the latter variety alone forms the subject of this paper. Many larvæ of *P. cin. cin.* have also been found and comparisons made with similar stages of *P. cin. eryth.* show that in the larva as in the adult the sole distinction between the two varieties is the coloration. The difference in geographical distribution which Cope mentions is not invariable, one bit of woodland may yield the two varieties in about equal numbers, another quite similar but a few miles away may contain *P. cin. eryth.* in abundance and but few *P. cin. cin.* No locality yielding either variety alone, or a majority of *P. cin. cin.* has been met with.

The typical coloration of the two sub-species is closely adhered to, the intermediates noted by Reed ('08) are very rare and even then approach closely the types; and only one specimen with much more than the normal amount of red was found. About 250 adults have been under examination, a number not so great as that used by Reed but sufficient to show that in this region there is less variation in colour than in the one where his studies were made.

Plethodon cinereus may be found in almost any wood in which the underbrush has not been entirely cleared away. They seek shelter under logs, fallen branches, flakes of bark separating from old stumps, or even masses of decaying leaves; the cracks of rotting logs and stumps are also favorite places. In the latter situation the variety *erythronotus* receives some protection from the red in its coloration, the shade of red is often that of the decaying wood and the dark edging is a fair reproduction of the dark and narrow cracks that run through the log. Occasional specimens may be found in the latter part of April; during the next three weeks they become abundant and by the middle of May can be found as plentifully as at any time in the year. Just where they pass the winter has not been determined though search has been made both early in the spring and late in the autumn; digging quite through stumps and logs embedded in the soil will not expose them, though it will probably result in finding the wood-frog, *Rana sylvatica*. A few trifling things have suggested that the animals follow down the cracks in the roots of old stumps to a considerable depth, but this has not been verified. Farther south Montgomery ('01) finds them in the same situations both winter and summer.

Plethodon is strictly nocturnal, so far at least as regards life above ground; however, a specimen that is suddenly uncovered is by no means dazzled by daylight; it may remain motionless for a minute or two or may at once crawl beneath the nearest shelter. Nor does it stop when under cover but keeping out of sight crawls rapidly to a considerable distance, so that if not captured as soon as exposed it runs a very good chance of escaping entirely. This sensitiveness to light has rendered disappointing the results from keeping specimens in a terrarium, an amount of light sufficient to reveal them at all either arrests all movement or sends them under shelter.

An examination of the stomach contents shows the food to consist of a variety of small insects; in one case the remains of a small spider were found.

In handling living specimens it will frequently happen that the end of the tail will apply itself closely to a finger in a semi-circular loop, and hold thus for a few seconds. This power may perhaps be regarded as the first step in the development of a prehensile tail such as is described for Autodax (Ritter & Miller, '99).

Two habits of Plethodon deserve notice as being of rare occurrence among Urodeles. When excited it occasionally aids its progress by leaping. In such cases as have been observed under conditions that admitted measuring the length of the leap it has been found about equal to the length of the animal's body. If the animal is running on a rather even surface it lands on its feet and continues the run having gained by its leap; but it will just as readily leap into difficulties. Held in the open hand it will frequently leap off, no matter what may be the height of the hand above the ground. In jumping the back is slightly arched and the front limbs with most of the trunk are raised in the air to about the height of one centimetre; then with a snap the tail is slapped against the surface over which the animal is moving and the body sharply straightens and shoots forward. The whole movement is so rapid that it cannot be distinguished with certainty whether the limbs aid in the leap. Two things suggest that they do; it is difficult to imagine a force to raise the anterior part of the body to the height it attains if it does not chiefly lie in a spring given by the anterior limbs. The posterior limbs are stouter and are in a good position to aid in the forward propulsion. The young as well as adults possess this power of leaping, indeed the only specimen observed to give a succession of leaps, three in fact, was one of 24 mm. The explanation of the greater development of the posterior limbs in the later larval stages, noted by Montgomery ('01), may lie in this habit. In this connection Cope ('89), says: "It frequently climbs to the summit of low vegetation, from which it springs by a sudden straightening or curvature of the body, as the case may be, in the manner of a caterpillar." The curvature and straightening in leaping are evident; the climbing of low vegetation to leap from it has not come under observation.

The second noteworthy habit is also connected with escaping enemies. Plethodon will sometimes break off a portion of its tail. Two things suggested the existence of this habit before it was actually observed. In searching for Plethodons in decaying logs not infrequently as the covering is lifted the animal will be found crawling stealthily away from the bit of tail that is making itself very conspicuous by its violent movements. This will occur at times when so little force has been used in picking apart the log that it is difficult to conceive how the piece could have been broken or pinched off. Again about 10% of all specimens found show the end of the tail in the process of regeneration, raising the suspicion that it is a mutilation out of the ordinary. On one occasion when a young Plethodon had been repeatedly touched by a small rod it suddenly gave a jump breaking off at the same time the terminal third of its tail. Two adults while being held lightly by the tail cast off a portion of it, the separation occurring in the part grasped and leaving in the one case a stump 1 cm. and in the other 1.75 cm. long, measuring from anus to end of stump. In no case observed has the length of tail retained been less than .5 cm.; it was usually more. There does not seem to be any one place where separation greatly tends to occur. Incomplete separation has also been noted, the vertebrae and muscles separating but the skin failing to break; this causes a slight grooving of the tail as though an invisible thread were tied around, compressing it. Longitudinal sectioning was used to examine both proximal and distal pieces in those cases that occurred under observation, and the relation of parts in the wound was found to be as follows, (Figure 1.) Separation of the vertebral column occurs between vertebrae; this is the condition also in *P. oregonensis* (Hubbard, '03). In the muscle the myomeres are not broken but separation occurs in the myocomma opposite the middle of the last vertebra retained. The skin however does not break here but at the myocomma opposite the middle of the first vertebrae of the piece cast off. Two things are accomplished by this; first the wound that now terminates the animal's tail is protected by the extra length of skin which collapses laterally upon it and almost covers it in. Second, on the piece cast off considerable raw surface is left exposed, the irritation from which is doubtless largely responsible for the rapid contortions that occur. This piece must play an important part in the protective device for by its violent movements it would draw the attention and invite the first attack of an enemy.

A similar habit has been noted in *P. oregonensis* by Hubbard ('03) but there are distinct points of difference. Briefly in *P. oregonensis* on moderate stimulation the glands on the dorsum of the tail swell greatly and pour out an abundant secretion. Only the most powerful stimulation—the act of being swallowed by a snake, or being plunged into a fixing fluid without previously being anæsthetized—would rouse the animal to the point of sacrificing its tail. Separation always occurs at a constriction just behind the anus. No mention is made of the behaviour of the piece separated and, the subject of the paper being correlated protective devices, it is perhaps fair to assume that it presents no striking peculiarity. In *P. cin. eryth.* the tail shows neither constriction nor swelling nor does the great development of dorsal glands occur, the thickness of the dorsal skin being one-twelfth to one-eighth of the diameter of the tail, while it constitutes one-fourth of the swollen tail of *P. oregonensis*.

Owing to the extreme aversion to light already mentioned it has been impossible to ascertain in a terrarium the manner of fertilization of the eggs. That fertilization is internal, and that it precedes egg-laying by a considerable time may be inferred from the following. The female is provided with spermathecæ which are already filled with spermatozoa at a time when the eggs are yet in the ovaries and have not attained a greater diameter than two mm. Quite likely the spermathecæ are filled long before this because at this time no spermatozoa are to be found in the genital tract of the male. The testes are filled with spermatocytes which as Mongomery ('03) describes undergo their maturation during the summer; spermatozoa may be found after the middle of August. Further observations are necessary to determine whether transference occurs in autumn or in spring.

Although there is a total lack of secondary sexual characters it is usually possible to distinguish between the sexes owing to the thinness and translucency of the muscle and skin. Because of the dark colour of the testis and the light colour of the eggs the posterior part of the abdomen when viewed from beneath is dark or light according as the specimen is male or female. This distinction is most evident in the spring, the eggs being largest at that time but in most cases it can be made at any season. In addition, the cloacal glands of the male cause a whiteness and a swelling at the sides of the body just behind the posterior limbs.

There is considerable latitude for a Urodele in the time at which egg-laying occurs. The earliest date on which eggs have been found was June 16th—3 clusters, the eggs in early stages of segmentation; the latest is July 3rd—1 cluster, in the same condition. The difference is not due entirely to different seasons being early or late, nor to one bit of woodland being better sheltered and warmer than another, for clusters of eggs with the females on guard and other females with the season's eggs yet in the ovaries have been found in the same log on the same day. The date, Oct. 25th, given by Sherwood ('95) for the finding of eggs of Plethodon is not accompanied by any description of them; and its exceptional lateness leaves the meaning of his observation doubtful.

The eggs of the one individual seem to be deposited all at the one time. No female was found guarding a cluster of eggs having also any in the oviduct or even in the ovary that were nearly full size. It is however not at all uncommon to find an egg in one ovary about half-size; this should be associated with the small egg of some bunches described below and considered as one that should have been laid this season but which, having failed to develop its proper amount of yolk, is retained in the ovary.

As a situation for the eggs marked preference is shown for logs almost entirely embedded in the humus, logs that have decayed to a point where the substance is friable with large cracks running lengthwise. In one of these cracks the eggs are hung from the roof like a little bunch of grapes (Figures 2 and 3). Rarely a similar cavity within a decaying stump is selected. All the localities in which Plethodon has been found contain conifers and almost without exception it is in coniferous wood that the eggs have been found; though the adults may be found plentifully in wood of all kinds. Usually the eggs are placed from three to five inches beneath the surface of the log, at which depth its substance is constantly moist, and it can well be imagined that the air is saturated with water vapour. They are always accompanied by the female and if in exposing them she has not been alarmed she will be found holding the dorsal surface of her head and neck against the under side of the bunch. That it is the female that remains on guard was determined by the dissection of over twenty specimens. In only one case was a male found by eggs and then in company with a female; the eggs were several days advanced in development and the presence of the male was perhaps merely an accident. Cope ('89) and Mongomery ('01) speak of finding the animals and their eggs under stones but if the above mentioned shelters are available they are always preferred. Wilder ('94) notes that the adults are seldom to be found under stones. Sherwood ('95) gives the habitat as beneath logs and stones, while the eggs are to be found in damp moss and beneath the bark of decaying stumps.

Among Urodeles that do not lay their eggs in water contact between the body of the female and the eggs seems to occur in all cases; Amphiuma (Hay '88) and Autodax (Ritter and Miller '99, and Ritter '03) coil round them, Desmognathus (Wilder '99) inserts herself among the eggs wearing them like a necklace or belt. *Plethodon oregonensis* (van Denbrugh '98) is described as holding the bunch in a loop of her tail and moving them from place to place. But as this was after removal from their natural surroundings it is quite possible that the eggs had been torn from their original support and that part of the mother's uneasiness arose from their unattached condition. The Cæcilians (Gadow '01) also when not viviparous coil round their eggs.

The number of eggs in a cluster varies from three to twelve. The number of ovarian eggs in advanced condition, in specimens taken just before the egg-laying season is also within these limits and the length of the incubation precludes a second brood in the one year. Consequently the preservation of the species must depend upon the larval stages being so perfectly adjusted to surrounding conditions that the mortality is very small, rather than—as is the case with most Urodeles—upon the production of large numbers of young. The slender and almost cylindrical form of body (the proportion of length to greatest breadth being fourteen to one) in an animal so small, along with the necessity for producing eggs containing a large amount of yolk are doubtless factors determining the small number of eggs; another will be mentioned later.

The necessity for the large amount of yolk in the egg arises from the purely terrestrial development of the larva. Aquatic larvæ have at command the minute and abundant fresh-water plankton as food supply and are thus at an early age rendered independent of the nourishment provided in the yolk. The insect life that constitutes the early food of the terrestrial Plethodon is of larger size than much of the plankton and much less abundant. Consequently the animal on leaving the egg must be able to wait for food through comparatively long intervals and also to capture food of larger size than an aquatic larva need do. Both of these things demand an advanced development that can only occur when a considerable quantity of yolk is provided.

Each egg is surrounded by a series of mucous spheres as is customary in Urodeles. In their natural condition the number of these is rather difficult to determine but after soaking a few minutes in water they swell somewhat and the following is plainly seen:—an innermost sphere very close to the surface of the egg; a second enclosing this but separated from it by a greater interval than that between the innermost sphere and the egg; occasionally this sphere is represented by two, one of them fitted very closely around the other. The outermost sphere—usually the third—fuses with the outermost spheres of neighboring eggs at all points of contact. On its surface are threads and bands of a milky white mucus which seems tougher than the rest, which is transparent; these are especially numerous between eggs and at the upper part of the bunch where several uniting form the stalk by which the cluster is suspended. This mode of attachment is probably derived from one originally like that of Desmognathus (Wilder '99) in which each egg of the cluster is independent of all the rest and has its own cord joining it to the common stalk. The tension of the envelopes, especially the innermost, is needed to preserve the spherical shape of the egg. These envelopes are very tough; a weak hypochlorite solution will soften them so that they can be removed but when their support is gone the egg, even in water, flattens until the vertical diameter is little more than half the transverse. In the younger stages it is therefore necessary to fix and harden the egg first and remove the membranes later, they should be removed as soon as possible for if left around the egg the latter will in time disintegrate. The method devised by Morgan ('91) has proved the most satisfactory.

As development proceeds the amount of fluid between the egg and the innermost sphere increases markedly, thus relieving the growing embryo from pressure.

The eggs vary from 3.5 to 4.5 mm. in diameter. In many of those bunches which contain several eggs there is one egg considerably smaller than the others; with this exception there is great uniformity in the size of the eggs of the one cluster. The considerable variation noted above exists between the eggs of different clusters.

The colour of the egg is a very pale yellow, a tint due to the yolk for no pigment is present. The upper part of the egg being the more free from yolk is almost white. Variation exists in the tint of the eggs of different clusters, the range being between very pale cream and light orange-yellow.

The usual rotation of amphibian embryos in their earlier stages occurs also in Plethodon but is modified by the large amount of yolk present. In the usual type of amphibian embryo, such as Amblystoma or Rana, the amount of yolk is not so great as to render it impossible for the embryo to turn over when the course along which the ciliary movement urges it so demands. Until the Plethodon embryo has reached a.length of 6 mm. it lies along a meridian of the yolk mass and a true forward movement would require the yolk at times to be uppermost. Whether because the ciliary movement lacks force to drive it into this position or for some other reason less obvious the rotation that occurs is around the vertical axis. There is no uniformity of movement even in eggs of the same bunch; an occasional one will be motionless and the others about evenly divided between motion to right and motion to left. A little later when the embryo twists itself into the horizontal plane the appearance in rotation is that of the ordinary amphibian embryo but the same lack of uniformity of direction obtains, some few embryos will not be moving at all, of the rest the head will be preceding in some cases bu' the tail in quite as many others. This latter direction was not expect nd caused an examination of Amblystoma eggs to be made subsequently to determine if anything comparable was to be found there. Eycleshymer ('95) notes an early irregularity of direction but this is not the impression derived from a brief examination of larvæ in later stages; nor is it to be expected from the account of the ciliation of Rana and Triton larvæ given by Assheton ('96). The stage of developement of Amblystoma equivalent to the one of Plethodon in which the backward movement is so marked is that in which the gills are beginning to appear and the larva is curved laterally in a semicircle to accommodate itself to its spherical envelope. At this stage nearly all embryos examined will be found moving slowly forward very nearly in the horizontal plane of the body; some few will be motionless and about 1% will be moving backward. It is not difficult to mark these latter by thrusting small splinters of wood through the jelly until their points almost touch the sphere surrounding the larva; a few hours later these individuals will be found moving forward and another set moving backward. Reversal of direction has also been noted in some Plethodon larvæ. Evidently the condition in Plethodon is nothing peculiar to the genus but an exaggeration of one found elsewhere among Urodeles. How widely spread it may be and whether it means a reversing of the usual movements of the cilia are points left for future determination.

The rate of rotation varies greatly, extremes of one minute and three and one half minutes having been noted under similar conditions.

The service of the rotation to the embryo probably is that it prevents adhesion between the egg and the envelopes. Smith ('06) found this occurring in eggs of Cryptobranchus lying in dishes in the laboratory; interference with development resulted. He makes no mention of rotation in the eggs but suggests that gentle rocking due to the current of the stream in which the eggs are laid prevents adhesion under natural conditions. Apparently in eggs laid in waters that have no current—as Amblystoma or Rana—or in other equally quiet situation—as Plethodon—the rotation suffices to prevent adhesions until the embryo beginning muscular movements is past all danger of their occurrence. Besides rotation other movements in embryos of 6 to 7 mm. are performed at intervals and consist of elevating the head from the yolk and waving it from side to side. As development proceeds these movements pass into occasional wrigglings of the tightly coiled larva whereby the whole position within the envelope often becomes altered.

Development and growth are very rapid for a few days, an embryo of 5 mm. will increase in length to 9 mm. in six days; but at this point the processes become much slower and to increase from 9 mm. to 11 mm. requires fourteen days. This change in the rate of growth is shown very plainly in sections by a sudden diminution in the number of mitotic figures which from being very numerous in the smaller embryos become rare after the length of 9 mm. is passed. In its later stages development is retarded in the central eggs of a cluster where the embryos are smaller and show but little reduction of the gills while the outer ones are larger and have the gills almost entirely absorbed (compare Figures 13 and 14). Measurements of a typical case gave central embryos 17.5 mm. with gills 1.75 mm. long and outer embryos 20 mm. with gills reduced to

.25 mm. A similar condition is found in Amblystoma, Rana and other amphibia where the eggs are laid in clusters; the cause being the difficulty with which respiration is carried on in the central eggs.

Escape from the mucous envelope occurs when the larva has reached the length of 20 to 25 mm.; this is about the first week of September. The outer larvæ of a cluster escape first but remain with the mother beneath their less developed brethren. Respiration is now more perfect in these; in a few days their gills have dissappeared and they also escape. However the interval does not suffice to bring them so far on in development as were the outer ones when they escaped; they have absorbed less yolk and are shorter. They also seem unfit to come in competition with their more favored brethren of the outside of the bunch of eggs, their movements being comparatively feeble and ineffective; many of them probably die. Thus is supplied another factor tending toward the production of small numbers of large eggs; for those young will be best fitted for life that come from broods where all the nourishment available as yolk is divided among but few eggs, so few that none are crowded into the centre of the cluster.

The family does not scatter at once, an unusual thing among Urodeles that have attained their adult form, but accompanied by the mother, perhaps led by her, the brood leaves the interior of the log to live beneath stones, fragments of wood or bark, lying on the surface of the ground, or even among layers of mouldering leaves. If not disturbed when uncovered the young will be found in contact with the body of the mother, probably to obtain moisture; for the localities in which they now are contain little moisture at this season of the year. The families do not hold together for long. In the latter part of September a few solitary young will be found and early in October all the broods seem to have broken up. The rate of growth in Plethodon must vary enormously in different individuals, for at this season it is easy to collect a series beginning with young accompanying the mother and ending with full grown specimens, the increase in size being so gradual that it is impossible to draw with certainty a line between this year's and last year's broods. Apparently the ability to withstand the winter is independent of size for early in May an occasional specimen will be found that is little larger than the young at the time they escape from the egg—that is less than 30 mm. in length.

The following description of the external appearance during development is based upon the examination of over 170 embryos that had been fixed in Zenker's fluid and preserved in 80% alcohol, the members of each bunch being kept together and separate from other bunches. In the series twenty different stages of development are represented, though only the most important of them will be described. As the eggs vary somewhat in size so do the individuals of the same stage of development; the descriptions given are those of average specimens, extremes in any direction (very few in number) being disregarded.

The embryo may be considered as well defined upon the yolk when the medullary folds are complete and approximated through a little more than the posterior half of their extent. (Figure 4). Together they give this part of the embryo a width of .75 mm. except at the posterior end where they separate slightly before becoming continuous giving here a width of 1 mm. In their anterior part the folds are widely separated giving to that part of the head an extreme breadth of 1.5 mm. In front of this part an almost transverse piece connects them while behind it, they converge, meeting at a point a little anterior to the middle of the body. In living specimens placed in a strong light a delicate scalloping of the inner margins of the folds in the cranial region indicates clearly the neuromeres, but no method yet used has succeeded in preserving them through fixation. In a corresponding stage in the eggs of some Amphibia the areas of brain substance that will form the optic vesicles are indicated by depressions, sometimes pigmented (Eycleshymer '93), but in Plethodon no trace of these can be found. The length of the figure defined by the medullary folds is three millimetres.

Larva 5 mm. Figure 5.

The form of the body is still determined by the yolk and the central nervous system. The medullary folds are in apposition throughout. The head is raised off the yolk as far back as the midbrain; eyes and ears are indicated externally. Behind the head the mesoblast makes a border on each side of the spinal cord extending but a short distance laterally over the yolk. The anterior three-fifths of it is divided into ten somites opposite the third and fourth of which it is thickened forming the beginning of the anterior limb. The posterior two-fifths of the mesoblast is not yet divided into somites. The medullary folds flatten and a little in front of the well marked blastopore disappear.

Larva 5.5 mm. Figure 6.

The pharyngeal region is now distinct and shows four gill arches; sections, however, show that the gill slits are not yet perforate. Posteriorly a crescent shaped furrow, the horns pointing forward, defines the termination of the body and marks its tendency to rise off the yolk.

Though thus hidden from view by he beginning of the tail, sections show the blastopore opening into the bottom of this furrow. At this time the increase of fluid around the egg begins. The whole body is assuming a cylindrical form and standing out from the yolk which is slightly flattened near it, and markedly flattened in the region against which lies that part of the body from the anterior limbs forward.

Larva 6 mm. Figure 7.

During the growth from 5.5 mm. a twisting of the anterior part of the body through 90 degrees has occurred so that one side of the head is now turned toward the yolk; of eleven specimens this was the right side in nine, the left side in two. That portion of the body attached to the yolk, *i.e.*, all posterior to the pharyngeal region, shares in the twisting and becomes curved laterally upon the yolk in such a fashion that the anterior three-fourths of the dorsal surface is brought into the one plane. Opposite and external to the last three somites now distinguishable is, on each side of the body, a low mound of thickened tissue—the beginnings of the posterior limbs. The terminal millimetre of the tail is quite cylindrical and free from the yolk. The first traces of pigmentation now appear on the dorsal surface of the anterior part of the body.

Larva 9 mm. Figure 8.

The anterior part of the body has more than doubled in thickness and has grown so far off the yolk that the anterior limbs are now free from contact with it. This gradual freeing of the body from its attachment to the yolk is brought about by growth of the central part of the body crowding off the extremities, accompanied by but little pinching off of the connection between body and yolk; for the length of body attached to the yolk has remained, and will for some time yet remain, constant at 3.5 to 4 mm. As the body is thus projected forward those parts of it that were spread out laterally on the yolk move ventrally and unite in the middle line. This is well shown in the anterior limbs which from projecting dorsally as at first are compelled by this movement at last to point outwardly. They are now .35 mm. long. Similar growth backward has brought the posterior limbs to the verge of the attachment of body and yolk posteriorly. These limbs are yet represented by rounded thickenings only. All traces of the gill arches have disappeared from the surface while the external gills have appeared as three points .25 mm. in length. The costal grooves are visible and pigment in a broad band extends over the dorsal surface of the neck and anterior half of the trunk.

Larva 9.5 mm. Figure 9.

The eye is now pigmented. The mouth is well defined and the gular fold projects a little over the base of the gills; these now appear as three points on a common base. The anterior limbs have a length of .5 mm. the posterior of .25 mm.; the latter are now attached on the line between yolk and body, consequently the anus lies in the free part of the body posterior to the yolk.

The accumulation of fluid between the egg and the innermost envelope has increased the diameter of the egg and envelopes together from 4.5 or 5.5 to 6.5 or 7 mm. This is not due to a thickening of the walls of the spheres but to such a distension of the inner one that yolk and larva together occupy only the lower two-thirds of the cavity. No further enlargement of the cavity occurs, consequently the larva becomes more and more closely coiled as its length increases, for the diminution of yolk that soon becomes noticeable does not compensate for the increased bulk of the larva.

The rotation ascribed to cilia on the ectoderm has been noticed in some larvæ of this stage of development, but in none later.

Although the blood is not yet red a hand lens will reveal the following plan in the circulation over the yolk mass, the vessels appearing as colourless lines against the white background of the yolk; the direction of flow can be followed as the corpuscles are easily visible. Small arteries metamerically arranged run laterally over the yolk; they branch and anastomose in such fashion that a network two or three meshes in width is formed between the margin of the body above and the vein in which they terminate ventrally. (Figure 9). Usually there are two such veins at first, a right and a left; at a variable time in later development one disappears, as is usual in Urodeles. Sometimes the anterior part of the network on one or both sides collects into a separate vein, making for a time three or four separate trunks that unite just posterior to the heart. Sections show these vessels all lying, as might be expected, in the splanchnic mesoblast which has ere this completely surrounded the yolk.

Larva 10.5 mm.

At about this length sections show for the first time perforation of the gill pouches, two only—the first and second—ever become perforate. The anterior limbs show the first indications of digits in that their extremities are flattened and show a terminal notch and a shallow groove leading to it on each side. The posterior limb is not appreciably flattened.

Larva 11 mm.

Each division of the anterior limb above noted is showing two tubercles, the four digits being thus indicated. The posterior limb has exchanged its rounded contour for an angular one but no notches or grooves appear on it.

Larva 12 mm. Figures 10 and 11.

The digits of the posterior limbs appear as five tubercles, the second and the third of which are the most prominent.

Larva 16 mm. Figure 12.

The posterior limbs are growing the more rapidly; they are now as long as the anterior ones—2.5 mm.—and much stouter. Both pairs are provided with well developed toes. The gills have developed greatly each being two to three mm. long and consisting of a central stem with six or eight side branches. Considerable variation in the length of the gills is found in larvæ from different broods in what is otherwise the same stage of development, the shorter gills having also the shorter side branches. Some diminution of the yolk mass is for the first time noticeable, its vertical depth having lessened, though the attachment to the body is still along 3.5 mm. of the ventral surface. Sections show that in larvae from 9 mm. onwards the body walls are actually complete, but the more ventral part of the mesoblast is so much thinner than the dorsal and the line along which the two parts meet is so sharp as to produce in the entire larva the appearance of having body walls developed only over the upper part of the yolk mass. At this stage rather more than the dorsal half of the yolk is covered by this thickened part of the body wall. The pigmentation typical of the adult is complete.

Larva 17.5 mm.

The posterior limb has outgrown the anterior, the lengths being 3 mm. and 2.75 mm. respectively. The length of the gills is reduced to 1.75 mm. or less. The yolk mass has so diminished as to be almost covered in by the thicker parts of the body wall, only a portion 2.5 mm. long and .5 mm. broad projecting slightly in the mid-ventral line.

Larva 20 mm. to 25 mm. Figure 13.
(just on the point of escaping from the mucous envelopes.)

The anterior and posterior limbs are 3 mm. and 3.5 mm. long respectively. The yolk mass is almost entirely covered in. The gills are reduced to a few small points not over .25 mm. long. Sections of several larvæ of this general stage but differing slightly in development show that both the gill slits become closed before escape from the envelopes occurs, the second one being the first to close.

In their development the digits of the posterior limb but partly bear out the expectations of Cope ('89). He would regard Hemidactylium with its posterior foot possessing only the first four digits as having for permanent form that which is larval in Plethodon. Dealing with *P. cinereus* he finds the adult has the outer digit longer than the inner, but in younger specimens it is shorter and in his youngest (18 mm. only but having already lost its gills) it is but a minute tubercle, "and in a little earlier stage cannot but be wanting though this I have not seen." On this point fifty-one larvæ were examined covering twelve stages, beginning with larvæ of 11 mm. long and ending with the smallest found living alone, its length being 23 mm. In larvæ of 12 mm. the whole five digits appear at once and the fifth is no less prominent than the first. There follows a brief period—*viz.* until the larva attains a length of 16 mm.—in which the rate of growth of the fifth digit as compared with that of the first, varies; of twenty-nine specimens within these limits the first exceeded the fifth in sixteen, the fifth exceeded the first in three, and in ten they were equal. (Seven broods are represented in this, in four of them only were all the larvæ alike on this point). This period alone is in accord with the argument of Cope. In all larvæ over 16 mm. (thirteen in number representing four stages) the external toe was longer than the internal.

EFFECTS OF TERRESTRIAL DEVELOPMENT.

The influence of a purely terrestrial development is seen ch... y in the following points.

The large amount of yolk in the egg in proportion to the size of the animal, a point already dealt with.

The yolk mass retains its globular form until late in development (larvæ of 13 to 15 mm.), when the absorption of its substance causes it to become fusiform. In aquatic larvæ the mass early elongates to produce a slender body capable of rapid darting movements, a necessity not laid upon the yolk in the inactive larva of Plethodon.

The development of limbs occurs early. Traces of the anterior limbs are distinct in larvæ of 5 mm. and of the posterior limbs in those of 6 mm. In Amblystoma these traces appear in larvæ of 7.5 mm. and 13 mm. respectively. From the large size of the posterior limbs in his larvæ Montgomery ('01) was led to suggest the possibility of their development before the anterior limbs, contrary to the usual condition in Urodeles. This proves not to be the case, though they do appear earlier than usual and grow more rapidly.

The development of gills is retarded. No trace of them as separate points is found until the larva reaches a length of 8 or 9 mm.; in Amblystoma the same occurs at a length of 6 mm. Looking at limbs and gills together the contrasts are marked; when Plethodon first shows external gills its posterior limbs have been for some time distinct; when Amblystoma first shows posterior limbs its gills are 1.25 to 1.5 mm. long and plentifully branched.

It is of general occurrence that the gills of such amphibian larvæ as have no free aquatic life are proportionately longer than those of larvæ that do. The condition in Salamandra atra as described by Chauvin ('77), shorter and stouter gills being assumed when aquatic life was forced on the larva, is typical. This obtains also in Plethodon, the filaments as well as the main trunks of the gills being much longer but much less numerous than in aquatic larvæ of the same size, *e.g.* those of Amblystoma. Such marked reduction in the number of filaments does not occur among all Urodele larvæ of non-aquatic development. In aquatic larvæ the gills are largely directed backward to afford as little resistance as possible to passage through the water; in Plethodon they spread out as widely as possible, the direction being a matter of indifference. The point of importance is that they apply themselves to as much of the mucous envelope as possible and so place themselves where they can best obtain a supply of oxygen.

Plethodon has neither the balancers nor the adhesive discs common among other amphibian larvæ.

The body of a Plethodon larva is from the first that of a terrestrial animal, cylindrical and without trace of median fins. Like the larva of Autodax (Ritter and Miller '99) it has lost the swimming instinct; when placed in water it sinks to the bottom and falls on one side; often indeed it twists its body and [illegible]hes violently but such movements never result in any progression or even in temporarily regaining balance. They seem to be only the wriggling that occurs periodically within the egg envelopes; it can always be induced by any stimulation of the larva.

The complete darkness in which the development of Plethodon takes place is partly responsible for peculiarities in colouring. Pigment is entirely lacking in the egg nor does it appear in the larva until a length of about 6 mm. is reached. When pigmentation does begin it rapidly assumes the pattern and colours of the adult; this is evidently related to the fact that when the larva issues from the egg envelopes it at once assumes the habits and habitat of the adult. The lack of a free larval life differing from that of the adult renders unnecessary the distinctive larval colouration so common among Amphibia. At the same time the surrounding darkness renders it safe for the larva to receive the colouration of the adult. The reason why the larva of Autodax (Ritter and Miller '09; Ritter '03) should under somewhat similar circumstances show a darker colour than the adult may lie partly at least in the fact that its development occurs in dimly lighted cavities and not in absolute darkness as does that of Plethodon.

Amblystoma (or Spelerpes), Desmognathus, Plethodon, and Autodax form an interesting series the members of which, taking larval and adult life together, show an increasing adaptation to terrestrial life. The first is terrestrial only in adult life and returns to the water to lay its eggs. Desmognathus (Wilder '99) begins its development on land like Plethodon but near the water; it leaves the egg while yet a larva completing its development in the water and accordingly stands as an intermediate between Amblystoma and Plethodon. The habitat of the adult Desmognathus, never far from a stream, also shows a less degree of adaptation to terrestrial life than that attained by Plethodon whose habitat bears no relation to bodies of water. On the other hand Autodax is less dependent on moisture in its surroundings even than Plethodon. I have had adult Plethodons die in confinement from conditions of no greater dryness than those described as supported by Autodax (Ritter and Miller '99). Moreover the prehensile tail, the greater ability in leaping and more intelligent use of the power would also indicate more perfect adaptation to terrestrial conditions than has been attained by Plethodon. As larva, Autodax has entirely lost the fringed condition of the gills; Plethodon still retains these fringes but in such varying degrees in different individuals as to indicate their decadence as organs. The degree of parental care of eggs and larvæ increases regularly in the series Amblystoma, Desmognathus, Plethodon and Autodax.

EXPERIMENTS.

To determine what part the mother may play in the incubation various plans of development under artificial conditions were tried. If removed from their natural surroundings and suspended in air the eggs show signs of rapid loss of moisture and the larvæ soon die. To obtain an atmosphere as moist as that in which they naturally hang, clusters of different ages were suspended over water, each cluster in a wide-mouthed bottle the cork of which had two shallow grooves cut down the sides to admit small quantities of air. The bottles were kept in a cellar where the temperature was practically the same as that of the natural situation of the eggs. In all the clusters development proceeded without interruption, in some cases for as much as twenty-five days when an impending absence from the laboratory rendered it necessary that the experiments be terminated and the larvæ were fixed. About eight per cent. of the larvæ always die under this artificial incubation, in some bunches no deaths at all occurring, in others several. This is quite striking, for no unfertilized eggs or dead larvæ were ever found under natural conditions. Three things may account for this; injury in conveying to the laboratory, the growth of mould during incubation, and lack of the normal increase of fluid between the egg and the inner envelope. Mould on the eggs although never encountered under natural conditions sooner or later makes its appearance on all eggs reared as above described. It does not however always have an early fatal effect, for all the larvæ in a bunch have been found alive after having been quite obscured for two days by a growth of mould. The increase of fluid between egg and envelope can hardly be said to occur under these artificial conditions and presumably some pressure is exerted upon the larva. These things suggest that the female may in some way prevent the growth of mould on the eggs and also supply them with moisture and an endeavour was made to test this in the following way. In a wide-mouthed jar pieces of the log in which the eggs were found were arranged to form a little chamber in which the female was placed and the piece suspending the eggs then added as a roof; more fragments were placed upon this and the surface covered with a little humus and moss, a few drops of water were occasionally sprinkled on the surface. Jars so prepared were kept under the same conditions as the bottles previously mentioned for three weeks, by which time mould would certainly have appeared on eggs kept in bottles, but none was found, and the amount of fluid surrounding the larva was as great as natural. In a subsequent set of experiments it was found that even thoroughly wetting the cluster two or three times a day, in addition to keeping it over water as before, would not suffice to bring about the normal accumulation of fluid. This was only obtained by allowing the lower end of the cluster to remain in contact with the surface of the water in the bottle for about twelve hours out of each twenty-four.

No final statement should be based on such scanty experimental evidence but such weight as it has is entirely in support of the supposition that the mother in this case—and presumably in similar cases reported among Urodeles—does along the lines mentioned actively promote the welfare of her brood.

In those last mentioned and in other experiments in which the clusters of eggs were entirely immersed in running water it was noticeable that the mucous envelopes would imbibe readily a small quantity of water and swell slightly in consequence, but the limit to this process was usually reached within the first half hour, nor did any second period of imbibition occur. No softening of the envelopes was to be noted even after constant immersion for three weeks. These qualities of the mucus mark it as different from that of most amphibian spawn which continues to absorb water and to soften until the larvæ escape. They probably are to be considered adaptations to prevent rains of even most unusual duration from softening the mucus and turning loose the larvæ prematurely.

The bottle method before described was used to test the possible effect of light upon development. Several bunches were exposed to daylight, which however never became direct sunlight, while others of the same stage of development were kept in entire darkness as controls, the temperature being in each case, within limits of variation of three or four degrees, the same. At the end of twenty-five days no difference in the degree of development of the two lots was to be detected. The lack of pigment in the egg might be put forward but the whole explanation cannot rest on this for early in the life of the larva pigment appears in the skin and rapidly increases in amount; and in the experiment this pigment was present for the last twenty days. In the experiments of various investigators to determine the effect of light upon growth Amphibian larvæ in aquaria have frequently been used; in which case the oxygen and part of the food have been derived from the water. Since both these things would be more abundant in the better lighted aquaria, factors must be allowed for, whose exact influence is unknown. In the present case the food and oxygen factors are the same for both sets of larvæ and the uncertainty of result due to several factors varying simultaneously is lacking.

POINTS ARISING OUT OF THE LUNGLESS CONDITION.

In Amphibia generally the function of the skin as an organ of respiration accessory to the lungs has long been recognized. Later Maurer ('98) drew attention to the advantageous position for purposes of respiration held by the capillaries of the bucco-pharynx, many of them being situated in the epithelium itself. To these localities therefore the attention of investigators was naturally directed in seeking the means which would compensate for the lack of lungs. The conclusions reached were not uniform, some investigators accepting both skin and bucco-pharynx with more or less of the œsophagus as sharing with something like equal importance in the respiration, others concluding that the skin is no more efficient in respiration in lungless salamanders than in those with lungs. Some examinations of Plethodon along these lines was in progress but ceased when the paper of Seelye ('06) on the Circulatory System of Desmognathus came to hand for the points already dealt with showed that the conditions in Plethodon would be but a repetition of those in Desmognathus: and would lead to the same conclusion, namely that as an organ of respiration the skin is much more important in lungless than in lunged salamanders. The same paper also gives a sufficient review of the question and its literature so all that will be attempted here is to bring forward three additional pieces of evidence in support of the above conclusion.

First, as noted in the paper itself the value of the cutaneous capillary network for respiration will depend upon the permeability of the membrane through which diffusion must take place. The fact that this membrane is the epidermis and not the entire skin renders exact experimentation impossible. Nevertheless the experiments performed by Seelye indicate that the entire skin of lungless forms is much more permeable than that of those with lungs and it would be strange to urge that the difference in the cutis accounts for this for it is the lungless forms that have the thicker cutis. This point of structure is, according to Seelye, the only one of general distinction between the skins of the two types in question; a conclusion that it is hard to understand unless it is due to the presence of two European forms with lungs among those examined. A more trustworthy comparison would be one between forms that live in the same environment and in the case of Plethodon this is possible, for small specimens of *Amblystoma punctatum* and of *Diemyctylus viridescens* in its terrestrial stage of life are occasionally found along with *Plethodon cinereus*. The skins of specimens so found and of adult Plethodons of about the same length were examined all being submitted to the same procedure, *viz.* the entire animal was fixed in Zenker's fluid with the usual after treatment, then from similar regions of head, trunk, and tail, pieces from dorsal, ventral, and lateral aspects were sectioned perpendicularly to the surface. The only considerable and constant difference in the epidermis is one of thickness. To estimate this correctly several measurements in micra were made from each piece of skin and these were averaged. Finally the figures thus obtained for each of the areas investigated were averaged to obtain a figure that would fairly represent the average thickness of the epidermis over the whole body. These averages were 22.4 micra for Plethodon, 46 micra for Amblystoma, and 44 micra for Diemyctylus. Consequently as regards this factor unless we assume a most improbable thing, namely that the epidermis of Plethodon is of a material less permeable than that of Amblystoma and Diemyctylus, we must conclude that of the three the skin of the lungless form Plethodon is fitted to be by far the best respiratory organ.

Second. The bucco-pharyngeal respiration is indeed established very soon after escape from the egg yet even in the adult it may be suspended for a considerable time without serious inconvenience. When confined in a glass vessel the animal will occasionally rest the ventral surface of head, neck, and more or less of the trunk against the glass; the adhesion between the glass and the moist and sticky skin is sufficient to prevent the respiratory movements. I have frequently seen this continue for two or three hours and have found the position of the body apparently unchanged after even much longer intervals, but in these cases observation not being continuous it is possible that the animal may have moved for a time and then resumed its exact original position, but such a thing is unlikely.

Third. There is a period of a few days in the life of a Plethodon during which such respiration as occurs at all must take place through the skin. This is the period just prior to the escape from the egg envelopes. The gills attain their maximum of development—a length of 3 mm.—in larvæ of about 15 mm.; after this they decrease in size and for some time before the escape of the larva are reduced to small points not over .25 mm. in length. No movements of the ventral pharyngeal wall are to be observed at this time so it cannot be that there exists a mode of respiration similar to the aquatic pharyngeal respiration noted in *Diemyctylus*, both *viridescens* (Gage '01) and *torosus* (Ritter '97), the fluid within the egg envelope playing fc hodon the part of the surrounding water for Diemyctylus. Conse whatever oxygen is used by the larva must be absorbed thro the skin. The amount of oxygen required by the larva may well be less than that required by the free-living animal yet it is by no means an inconsiderable fraction of it. The muscular activity in the beating of the heart and the wriggling of the larva within the envelopes that occurs not infrequently is probably little less than that of the free-living animal, which though capable of active movement rarely indulges in it, forming in this respect a marked contrast to Diemyctylus. If the larva can carry on its respiration through its skin alone, hampered as it is by the surrounding fluid and envelopes, it is difficult to escape the conclusion that in the free-living stage as well the skin must be an important factor in respiration.

The development of gills in the first place is governed by the same necessity as exists in other Amphibia; sections show that the beginning of their degeneration coincides with the skin becoming sufficiently developed for the circulation in it to become somewhat extensive; and that their diminution keeps pace with the elaboration of the cutaneous circulation, just as in most Amphibia it accompanies the increasing activity of internal gills or lungs.

EARLY DEVELOPMENT AND DEVELOPMENT OF INTERNAL ORGANS.

Studies in these fields have revealed several points of interest which it is proposed to consider in a future paper.

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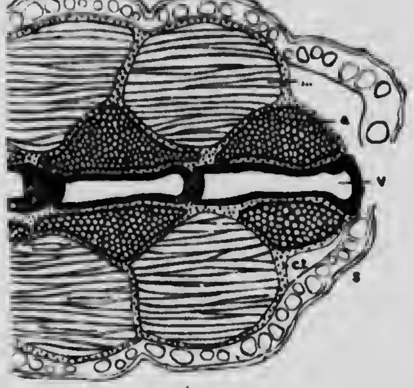
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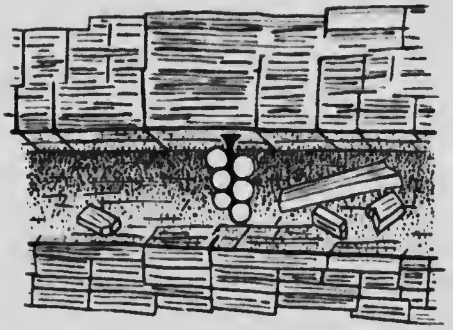
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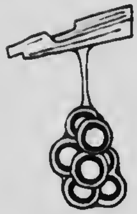
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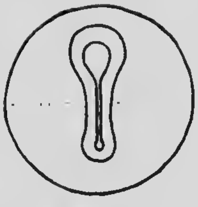
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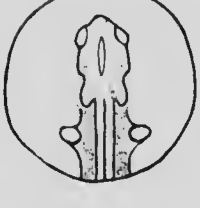
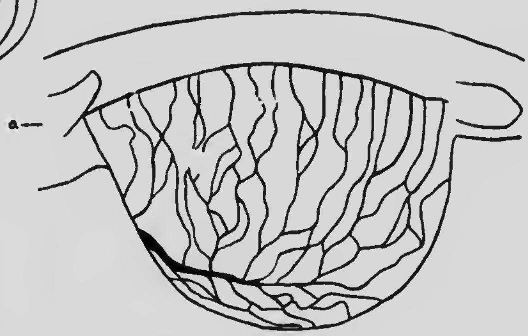


Fig. 5


Fig. 6


Fig. 7


Fig. 8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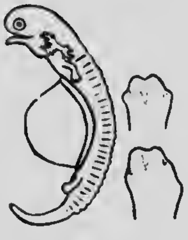
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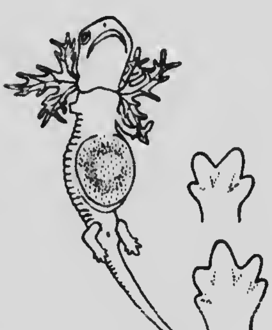
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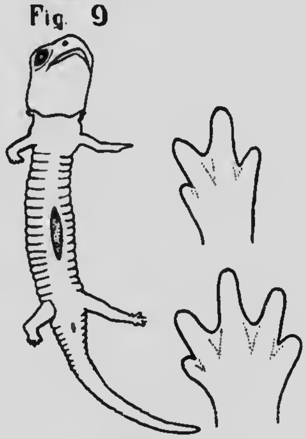
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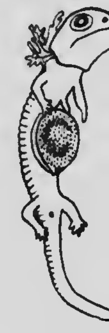
Fig.

ILLUSTRATIONS.

Figures 1 and 9 are camera lucida drawings, 2 and 3 from photographs, 4-8 and 10-14 from projections by Zeiss epidiascope. Figures 4-8 are enlarged to the same extent, which is twice as great as that of figures 10-14. Figures 4 and 5 from eggs of maximum size, 6 and 7 from eggs of minimum size. The outlines of the feet, Figs. 10, 12 and 13, are camera lucida drawings; they are right feet viewed from the dorsal surface under low magnification.

Figure 1. Horizontal section of tail through the proximal wound of an autotomy.
v—centrum of vertebra.
a—perivertebral adipose tissue.
m—myotome.
c. t.—connective tissue.
s—skin.

Figure 2. Cluster of eggs suspended in a large crack in a decaying log.

Figure 3. Cluster of eggs.

Figure 4. Stage 3 mm. Egg viewed from side, the dotted line being the equator of the egg when the latter is in its natural position.

Figure 5. Stage 5 mm. Egg viewed from above.

Figure 6. Stage 5.5 mm. Egg viewed from the side. The outline of the mucous sphere was added from a living specimen.

Figure 7. Stage 6 mm. Egg viewed from above.

Figure 8. Stage 9 mm. Viewed from above, the head and tip of the tail are much bent towards the ventral surface.

Figure 9. Vitelline circulation in larva 10 mm. long.
a—anterior.

Figures 10 and 11. Stage 12 mm.

Figure 12. Stage 16 mm. Taken from a small larva, actual size, 14.5 mm.

Figure 13. Stage 20-25 mm. Actual size of larva 20 mm.

Figure 14. Specimen from the centre of the same bunch of eggs as that of Figure 13, which is one of the outer larvæ.