Metamorphosis and Life-history of Gnathia maxillaris.

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With plate 18.

The Gnathiidae or Anceidae have been the subject of an excellent memoir by Hesse (1), who discovered the relationship of the larval form, Praniza, to the adult, while Dohrn (2) added a valuable morphological essay. Sars (3) has also made some observations on the Norwegian species. While investigating the secondary sexual characters of certain Crustacea at Naples I became struck with the extraordinary variability in size of the single species of *Gnathia* inhabiting the Bay of Naples, and to this further reference will be made when we come to consider the life-history: but first, since I have on numerous occasions successfully observed the final metamorphosis of this Crustacean, and some doubt still exists as to certain points, it seems worth while to give as complete an account as possible of these remarkable changes.

1. Final Metamorphosis of Praniza into Adult.

The Praniza larva lives ecto-parasitically on various kinds of fish; its mid-gut becomes greatly distended with the blood of its host and in consequence the three last thoracic segments (not counting the rudimentary sixth) become fused and lose all trace of segmentation (Pl. 18 fig. 1). The mouth-parts, consisting of mandibles, two pairs of maxillae and two pairs of maxillipeds. are adapted to piercing and clinging to the flesh of the host (fig. 2). Up to a late stage the Pranizae are sexually indistinguishable, apart from the difference of the sexual elements themselves.

Metamorphosis into the male. The adult male (fig. 3) with its square head and powerful mandibles, in the degeneration of the maxillae and the presence of the two pairs of valve-like maxillipeds (fig. 4), and finally in the complete segmentation of the thorax, differs very greatly from the tumid Praniza larva, and yet the change from the one to the other occurs in a single ecdysis. In a Praniza which is about to undergo metamorphosis into the adult male, it is always to be observed that the neck, instead of being narrow and inconspicuous as in the young Praniza or in one about to change into a female (fig. 5), is much swollen so that there appears to be an extra segment added to the thorax (fig. 6). This swollen region, which corresponds to the segments of the two pairs of maxillipeds is in fact the chief formative region for the square head of the adult male. On examining such a Praniza from the ventral surface the formation of the new valve-like appendages can be observed (fig. 7). Within the case of the larval first maxilliped the definitive appendage can be seen with its hairs folded back upon itself and its base greatly enlarged. The very peculiar valve-like structures which fold externally over the oral region of the adult male can be seen developing in the greatly enlarged basal joints of the larval second maxillipeds. They widen gradually to form the adult structures. It is thus seen that the adult maxillipeds of the male are both formed by an enlargement of the basal joints of the larval appendages, which occurs in correlation with the backward shifting of the formative region of the head.

The formation of the large mandibles of the male has been described by Dohrn (2) who rightly points out that they are not formed within the case of the larval mandibles. He concludes therefore that they are not homologous with the larval mandibles, but it may be suggested that an exaggeration of the process just described in the case of the maxillipeds, i. e. an enlargement of the base of an appendage at the expense of its distal joints, would naturally lead to the condition actually found in the case of the mandibles.

With regard to the rest of the body the segmentation of the thorax completely reappears; the coloured areolation of the front region of the thorax is not completely formed until two days or so after the metamorphosis has taken place. A word must be said with regard to the liver: this in the young Praniza of both sexes consists of two lobes in the anterior thoracic region (fig. 1 *L*). In the female these lobes do not increase in size, but in the male during the period before the final ecdysis, the liver lobes grow downwards and absorb the nutriment from the inflated gut. In the adult they turn blackish brown and appear as conspicuous bodies in the hinder thoracic region. This point is of considerable interest because it gives us a simple explanation of the reacquisition of segmentation in the male and not in the female; for whereas in the male the food in the gut is taken up and compactly stored in special organs for the purpose, in the female the thorax becomes filled with a multitude of embryos which naturally take up more room than the compact liver of the male. But as we shall see the female may reacquire its segmentation if it is not very full of eggs: thin segmented females occuring as rather rare varities. It will be noticed from this account that the statement of Korschelt & Heider (4) that unsegmented Pranizae give rise exclusively to females and that only segmented larvae give rise to males is quite erroneous. The adults of both sexes are derived from swollen Pranizae.

Metamorphosis of the Female. The change from the Praniza into the adult female is not so dramatic as in the case of the male. The mouth parts merely degenerate, except the first maxilliped which resembles that of the male.

The ova begin to develop at a fairly early stage in the Praniza and are recognisable as a narrow strip running down the centre of the back (fig. 1 *o*): they continue to grow at the expense of the nourishment in the gut and come to fill the whole of the body cavity of the mother, when the final ecdysis occurs. Hesse supposed that fertilization took place before the final ecdysis, but this was merely a supposition, and although I have been unable to observe the coupling, the circumstantial evidence seems to show that the supposition is wrong; at any rate Hesse's contention that fertilization is a necessary stimulus for the accomplishment of the final ecdysis is certainly erroneous, because I have succeeded in rearing several Pranizae to the adult female state, but in all cases the eggs failed to develop and subsequently decayed so that it is highly improbable that the Pranizae had been fertilized. We have already mentioned that the female normally has the hind part of the thorax unsegmented (as in fig. 8), but occasionally specimens are found with either one or both constrictions fully present (as in fig. 9) and these specimens are always thinner and contain fewer eggs. They plainly belong to the same species because they do not differ in any other morphological detail and they occur together with only one form of male.

It is a remarkable fact that the embryos develop to a late stage within the body cavity of the mother and completely destroy all her internal organs except the nerve cord and a few shreds of ventral ectoderm. There is no brood-pouch; this is shown in the transverse section fig. 10, where the embryos are seen lying in the body cavity of the mother, all the maternal tissues having degenerated except the nerve cord. The embryos are set free by the cuticle splitting at the points corresponding to the thoracic segments; and after parturition the female appears as a mere cracked shell of its former self; nor can it take any further part in reproduction though it may continue a feeble existence for a few days or even weeks.

2. Life-history.

The young are set free from the body cavity of the mother at a stage which may be called the normal segmented larva (fig. 11). This larva is fully segmented; its body is dotted over with yellow branching pigment cells, and its mouth-parts are essentially the same as those figured for the later Praniza larva (fig. 2). In its thorax are two greenish bodies, diverticula of the gut, which contain the remains of the embryonic food yolk. These larvae can remain alive in this state without taking in food or growing, for a remarkably long time (7 or 8 weeks); for their further developement however it is necessary that they should become attached to fish and when this is accomplished the next larval form, the Praniza, is rapidly assumed; this is proved by the occurrence of small Pranizae not exceeding the average size of the normal segmented larvae (0,8—1,2 mm).

The characteristic form of the Praniza is shown in fig. 1. It lives loosely attached to the fish on which it feeds; after a period of unknown duration it drops off and undergoes the final metamorphosis upon the sea-bottom, whence it can be collected in fair abundance at Naples, together with adults of both sexes, especially among the roots of the weed *Posidonia Carolinii* in 5—30 meters.

Now besides the small normal segmented larvae measuring about 1 millimeter and the non-segmented Pranizae which vary in size from 1—8 mm, another form of larva occurs which may be called the giant segmented larva (fig. 12). All except a few specimens of this form measured about 4 mm[1]; they show no trace of sexual elements; their gut is not inflated and they differ from Pranizae in

[1] Of 29 such larvae 26 measured between 3,75 and 5.5 mm. and 3 measured 2—3 mm. the measurements being symmetrically grouped round 4 mm.

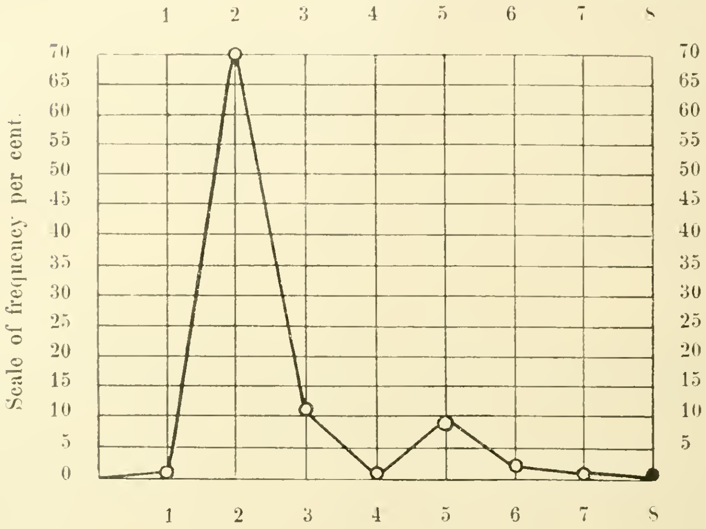
having the thorax completely segmented. These larvae plainly must have been derived from the Praniza form, because the normal segmented larvae are incapable of growth until they assume the parasitic mode of life: the only hypothesis that accounts for the existence of these forms is that they are derived from Pranizae which have been brushed off their hosts at a period when they could not perform the final metamorphosis into the adult. This hypothesis is substantially confirmed by two Pranizae measuring 4,5 mm in my collection which are about to undergo an ecdysis, and underneath their cuticle can be seen the cuticle of a giant segmented larva.

We will now turn to the variation in size of the adults. The adult males vary in size from 1—8 mm and the adult females from 1—7 mm. This is an immense range of variation, and it will be at once suggested that these sizes do not represent the definitive adult size of the animals but are different stages in growth. But this argument cannot apply to the females which produce broods and die when they measure anything from 1—7 mm, and as a matter of fact it applies just as little to the males, because I have reared adult males from Pranizae varying in size from 2—7 mm; so that it is clear that the size of the adult male is dependent on the size of the Praniza that undergoes metamorphosis. Nor is it at all likely that the adult males go on growing to any appreciable extent after they have assumed the adult form, because firstly their mouth-parts are adapted merely for causing a current in the water and possibly driving small Diatoms and Infusoria into the mouth, and secondly the gut ends blindly. It is therefore an absurd supposition that animals with these means of nutrition can go on growing to three or four times their original bulk, especially when the difference in size of the adults has been proved in numerous cases to be due to the great differences in size of the Pranizae which undergo metamorphosis. Furthermore no one has ever seen an adult male exuviate.

In table 1 is presented a curve which shows the frequency per cent with which the various sizes occur in 465 males. The measurement in millimeters was taken from the anterior level of the eyes to the base of the telson.

Table 1.

Frequency distribution per cent of Sizes in Male *G. maxillaris.*



It will be seen from this curve that the modal or most frequent size is 2 mm, but a closer inspection of the curve shows that it is not at all normal in its shape, being decidedly skew in the direction of the larger measurements with the tendency to establish another mode at 5 mm. Out of the 465 males examined only 12 measured 4 mm while 43 measured 5 and 15 measured 6 mm [1]. Now it is a most remarkable fact that out of 29 giant segmented larvae 26 measured approximately between 4 and 5 mm. Putting these facts together it appears that there are two chief critical periods at which the male (and probably also the female) Praniza metamorphoses into the adult: firstly when it has attained to about 2 mm and secondly when it has attained to about 5 mm. If it is brushed off its host when it measures between 4 and 5 mm it cannot assume the adult state but undergoes retrogressive metamorphosis into the giant segmented larvae which must become attached to a fish again and go on growing before arriving at sexual maturity. By this hypothesis only do we obtain an explanation of the bimodality of the frequency curve of sizes and of the occurrence of giant segmented larvae which

[1] The most probable error of the frequency at 4 mm is ± 2,306.

correspond to the mediocre size of least frequency in the adult males, i. e. circa 4 mm.

We have so far only considered the variability of the males: the females are very much rarer than the males, a fact which has been noted by Sars in the Norwegian species. From a study of 260 adult ovigerous females I have determined that the variation in size extends from 1 to 7 mm: the curve of frequency distribution is bimodal, the modes being at 2 and at 4 mm (thus in 260 females 13 measured 3 and 33 measured 4 mm). It is probable that these two modes correspond in reality to the two modes in the males; the bodies of male and female not being strictly comparable with regard to length because the female when distended with eggs is stretched transversely and loses in stature. The modal condition of 2 mm is of far commoner occurrence than that of 4 mm, just as the small males preponderated in numbers over the large. It is therefore of interest to find that the large females always produce a far greater number of eggs[1]. Consequently to account for the persistently and greater frequency of small adults in general we must either suppose that there is a much greater selective death-rate among the offspring of the large adults or else the numbers of the small adults are continually being supplemented from the offspring of the large forms. A definite answer to this question can only be obtained by rearing the larvae from the youngest stage upwards, and besides that one would have to know at least both the parents of the brood; but at present my efforts to get the adults to pair in captivity and the young to infect fish in aequaria have been in vain. So we may proceed to inquire from other evidences what it is that determines the size to which any Praniza may attain. Is this a purely hereditary character or does it depend upon the individual experience of each larva? Certain facts point strongly to the conclusion that although inheritance may play a part in determining the size of the adult yet an equally important rôle must be allowed to the direct action of nutritional conditions upon the larva during its parasitic life. For firstly it must be noted that although the larger females produce slightly larger segmented larvae than the smaller females, yet this initial difference in size is not sufficient to account for the immense variability of the adults, and so the differentiation in sizes must occur

[1] Females spanning 2 mm had a mean number of 50 eggs, those spanning 4 mm a mean number of 104 eggs.

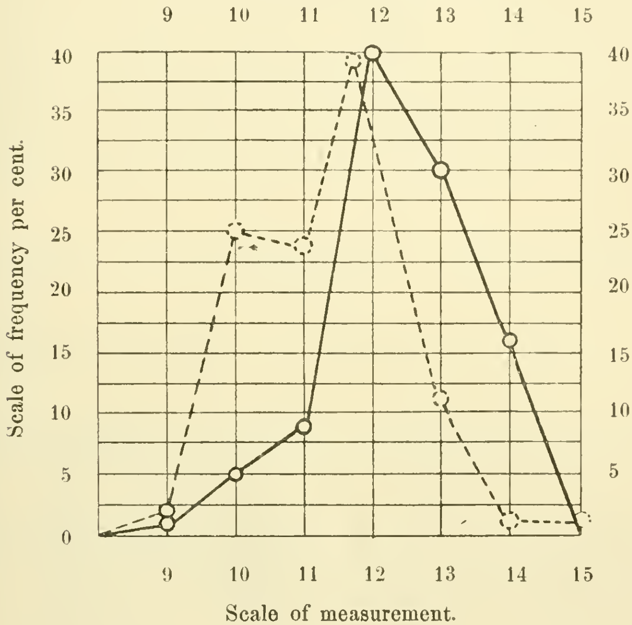
during the Praniza stage when the animal is following its parasitic mode of life. Now we know that this mode of life is highly irregular, for their is no particular species of fish to which the attentions of the larvae are confined and they may attach themselves to the gills or to any part of the body or fins indifferently. Then they are only loosely attached and can be brushed off with the greatest ease.

Combining these facts with the evidence that was produced to show that the bimodality of our curve was due to the existence of two critical periods for the final transformation, the presumption is strong that the size to which any larva may attain is chiefly due to the conditions of nutrition it meets with, and its fortune in being brushed off its host at an early or late stage of growth. In this way we obtain a rational explanation of the immense range of variability in the animal, which would be correlated according to our view with the great irregularity of the conditions met with during the Praniza state. But whether the size of the adult is influenced greatly by hereditary tendencies or not, it is at any rate certain that the larger adults owe their size to the length of time spent and the amount of nutrition acquired during the Praniza stage, because the difference in size of the segmented larvae from variously sized females is not sufficient to account for the differences in size of the adults.

The great variability in size of the male and the bimodal frequency of the sizes led me to suppose that we had here an instance of »high« and »low« dimorphism, the occurrence of which has been noticed in Lamellicorn beetles, and the Earwig by Bateson & Brindley (5) and according to Fritz Müller (6) in the Tanaidae and Orchestiidae. I therefore proceeded to make a series of measurements upon two hundred males of *G. maxillaris* to see if there was any difference of structure in the mandibles of large and small individuals. The result of this investigation is set out in Table 2 and is of some interest.

Table 2.

Frequency distribution per cent in 200 males of *G. maxillaris* (150 small and 50 large), as regards mandibular index. Dotted curve refers to small males, continuous curve to large males.



The measurements taken are explained in figure 13. From the two measurements AB and BC an index was determined for each mandible, the index being $\frac{AB \times 10}{BC}$; this gives the relation between the length and breadth of the mandible.

The dotted curve in table 2 shows the frequency distribution per cent of the index in »low« males of stature below 3 mm, the continuous curve refers to »high« males of 5 mm and upwards. Now it is seen that the modal condition of the index taken is the same for large and small males, viz. 12, but a low index occurs much more frequently among small males than among large and vice-versa, the difference in frequencies being well without the limit of their probable errors. This means that on the whole small males have mandibles that are broader and shorter than large males: in other words, there is an incipient structural dimorphism in the mandibles, in correlation with the difference in size of the males.

Summary.

We may tabulate the life-history of *G. maxillaris* as follows:—

Normal segmented larvae
0,8—1,2 mm.

Pranizae on fish
1—4 mm.

Small adults on ground.

Giant segmented larvae on ground 4—5 mm. → Pranizae on fish 5—8 mm.

Large adults on ground.

The points that remain uncertain are: (1.) Whether segmented larval stages can be interpolated at various points in the larval history. It is true that this happens to a certain extent, as segmented larvae of various sizes are met with in very small numbers, but it is probable that this is only the general rule when the Pranizae are brushed off from their hosts measuring about 4 to 5 mm. (2.) The fate of the giant segmented larvae remains doubtful, but it is highly probable that if they can succeed in attaching themselves to another fish they will develop into large Pranizae, as indicated by the arrow in the diagram.

The chief theoretical interest of the life-history is that differences in the length of the larval life and in the amount of nutrition taken in during this period, whether under the control of hereditary tendencies or not, lead to very great differences in the size of the adults and to an incipient dimorphism in the secondary sexual characters of the males. Further there is a very decided tendency towards the establishment of two modal conditions corresponding to the two kinds of males.

Naples, Zoological Station, February 1904.

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6. **Müller,** F., Facts for Darwin. 1869 chap. 4.

Explanations of Figures on Plate 18.

Fig. 1. Praniza larva. *L* liver. *G* gut. *O* ovary. × 20.

Fig. 2. Mouth-parts of Praniza from ventral surface. × 65.

Fig. 3. Male *G. maxillaris.* × 12.

Fig. 4. Mouth-parts of male from ventral surface. × 12.

Fig. 5. Female Praniza, dorsal view. × 37.

Fig. 6. Praniza metamorphosing into male, dorsal view. × 37.

Fig. 7. Ventral view of Praniza changing into male. *1* 1st antenna. *2* 2nd antenna. *3* mandible. *4* 1st maxilla. *5* 2nd maxilla. *6* larval 1st maxilliped. *6'* definitive 1st maxilliped. *7* larval 2nd maxilliped. *7'* definitive 2nd maxilliped. × 160.

Fig. 7*a*. Larval 2nd maxilliped before metamorphosis has begun. × 160.

Fig. 8. Gravid unsegmented female. × 40.

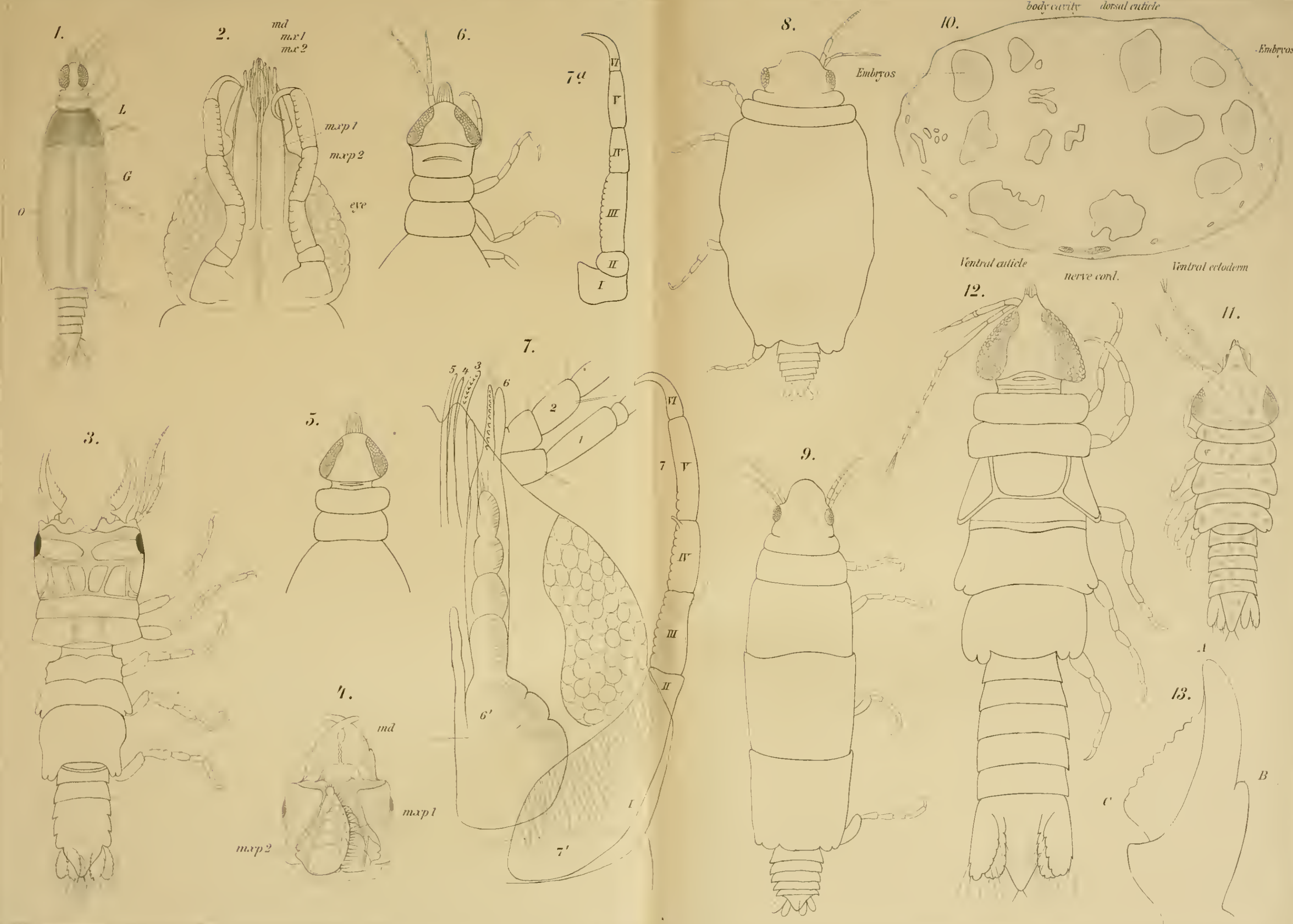
Fig. 9. Gravid segmented female. × 40.

Fig. 10. Transverse section through thorax of gravid female. × 75.

Fig. 11. Normal segmented larva. × 75.

Fig. 12. Giant segmented larva. × 40.

Fig. 13. Dorsal view of mandible. *AB* measurement of length. *BC* measurement of breadth. Index $\frac{AB \times 10}{BC}$. × 130.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md
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eye
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7a
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Embryos
10.
body cavity
dorsal cuticle
Embryos
Ventral cuticle
nerve cord.
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