THE INDUCTION OF LARVAL MOLTS IN DROSOPHILA

DIETRICH BODENSTEIN [1]

(Department of Zoology, Columbia University, New York)

It has recently been shown (Bodenstein, 1943) that a hormone produced by the ring gland controls the growth of the imaginal organ anlagen in Drosophila during the larval period, as well as the growth of purely larval organs. Since molting is mainly a process by means of which the larval insect grows, one might expect it to be governed by the same principle, yet previous experiments were unable to shed any light on this point. It is the purpose of this investigation to provide convincing evidence that the molting of Drosophila larvae is under the control of the larval ring gland.

Material and Methods

The larvae of Drosophila molt twice before they pupate. At each molt they shed their mouth parts, together with their cuticula. The mandibular hooks of the mouth armature, characteristic in size and shape for each larval instar, were used as a criterion for molting. For the experiments the larval head segments, including the complete mouth armature, were cut off from larvae shortly after their emergence from the egg and from 2nd instar larvae. Special care was taken not to include the brain and attached ring gland in the isolated head segments. The brainless head pieces were then transplanted into the body cavity of adult flies or into mature larvae. The transplants, either alone or together, were put with several ring glands into the body cavity of the adult hosts. The hosts were dissected at different times after the operation; the transplants removed *in toto,* stained with orcein, cleared and mounted in diaphane. The number of mandibular hooks present in the transplant could easily be observed in these preparations. In many cases one could also use the spiracles as an indicator for molting, because these structures are shed at each molt and are characteristic for each instar. The majority of experiments was performed on *Drosophila virilis* (wild stock). The experimental animals were kept at a constant temperature of 25° ± 0.5° C.

I am greatly indebted to Dr. L. C. Dunn and Dr. T. Dobzhansky for many stimulating discussions and for their continued interest in the work.

Experiments

The transplantation of larval head segments into adult male hosts

In a series of experiments, larval head segments without brain and ring gland, but containing the complete mouth apparatus, were transplanted into the abdomen of adult male flies and dissected at different times after the operation. These experiments comprise three different experimental groups. In one group the head

[1] Fellow of the John Simon Guggenheim Memorial Foundation.

segments of 1st instar larvae not older than 4 hours were used. In the second group the head segments of the larvae were somewhat older but their age never exceeded 10 hours. In the third group head segments of 2nd instar larvae were transplanted. The experiments are summarized in Table I. They show that none of the transplanted head parts has molted, since only one pair of mandibular hooks is present. Usually there are some brownish spots in the grafts, while the rest of

TABLE I

Transplantation of larval head segments into the abdomen of adult virilis male flies

Age of transplanted head segment	Number of cases	Days transplant remains in host	Number of cases where transplant has only one pair of mandibles, i.e. has not molted
1st instar (4–6 hrs. old)	1	4	1
	4	7	4
	3	8	3
	4	11	4
	10	14	10
	1	15	1
	13	16	13
	3	17	3
	7	18	7
	3	19	3
1st instar (ca. 10 hrs. old)	4	16	4
2nd instar	12	8	12
Total number of cases	65		65

the tissue maintains its larval color characteristics. Grafts which remained very long in the host frequently show some brownish cuticle coloration, which resembles the color of young pupae. Whether this color is an indication of pupation is, however, questionable. Strong muscle contractions of the grafts at dissection demonstrate very well their living condition.

The transplants undergo certain other changes while in their adult hosts. It is often noticed that the cuticle between two adjacent segments becomes somewhat darkened in transplants left for 2 or 3 days in their hosts (Fig. 1). If left longer in the host the larval head pieces exhibit a typical behavior. A fine epithelial membrane begins to appear on the proximal end of the transplant where the body wall of the larvae was cut. This epithelium grows gradually, creeping around the outside of the larval cuticle of the head part until finally the whole transplant is enveloped by a fine transparent tissue sac. Figures 2, 3, 5 and 6 show this condition for some selected cases. It should be explained however that the completeness of this overgrowth does not entirely depend upon the time the implant remains in the host, for in some cases the overgrowth might have been enveloped only one-half, in others the whole of the transplant, although all remained for the

same length of time in the host. The tissue envelope apparently represents the regenerating wound epithelium of the larval epidermis. Its cells are very large and extremely flat, with large nuclei containing polytene chromosomes. In life the space between the epithelium mantle and the larval cuticula appears transparent and empty. In sectioned material, however, it seems to be filled with a laminated deposition (Fig. 6). Whether this deposit is chitin has not been determined.

Piepho (1938) in his studies on Galleria (wax moth) has observed the same type of behavior. He transplanted small pieces of caterpillar skin into the abdomens of other caterpillar hosts, and found that an epidermal cover (*Umwachsungshypodermis*), originating from the epidermis of the transplant, gradually enveloped the implant. In a careful histological study, Piepho found, moreover, that the differentiation achievements of this enveloping tissue sheath may vary according to the hormonal situation of the host.

The transplantation of larval head segments together with ring glands into the abdomen of adult flies

Head segments of 1st and 2nd instar larvae without brain and ring gland were transplanted into the abdomen of adult flies. Unlike the former series, however,

TABLE II

Transplantation of head segments together with ring glands into the abdomen of adult flies

Age of transplanted head segment	Host and transplanted ring gland	Number of cases	Days transplant remains in host	Number of cases where transplant has formed				
				1 pair of mandibles	2 pairs of mandibles	3 pairs of mandibles	spiracle of 2nd inst.	spiracle of 3rd inst.
1st instar (4 hrs. old)	v. 2RG	4	8	3	1			
1st instar (4 hrs. old)	v. 2RG	2	15	1	1			
1st instar (4 hrs. old)	v. 2RG	6	16	4	2?			
1st instar (4 hrs. old)	v. 2RG	1	5	1				
1st instar (4 hrs. old)	v. 2RG	2	7	2				
1st instar (6 hrs. old)	m. 2RG	3	7		2	(1?)		1
1st instar (10 hrs. old)	m. 2RG	9	15	2(4?)	2	(1?)	3	(1?)
2nd instar	v. 3RG	6	8	4	2			3(1?)
2nd instar	m. 3RG	3	6	2	1			
2nd instar	m. 3RG	3	8	2	1			3
Total number of cases		39			14 positive			

v. = virilis; m. = melanogaster.

RG = Ring gland.

Number in parentheses indicates number of cases where the mandible or spiracle number formed is not clear.

two or three ring glands from mature larvae were transplanted simultaneously with the larval heads into the same hosts. Not only adult males but also adult virilis females were used as hosts. In many cases adult melanogaster females were employed as hosts, for it had been found previously (Bodenstein, 1943) that the ring gland effect in melanogaster females was much stronger than in virilis females. The results of these experiments are summarized in Table II. They show that in the presence of ring glands the larval head segments can be induced to molt, as indicated by the presence of two pairs of mandible hooks in one transplant. Figures 7 and 10 show a 1st instar transplant and Figure 8 shows one 2nd instar transplant after molting has been induced by the grafted ring gland. In only one case (one other questionable), molting had occurred twice. Although only two pairs of mandibles were found in this case, one pair belonging to the 1st and the other to the 2nd instar, a spiracle typical for the 3rd instar was present, proving that the second molt had taken place (Fig. 11). As far as the molting competence of mandibles and spiracles is concerned, it seems that the spiracles react somewhat more readily to the molting hormone of the ring gland than the mandibles. This is indicated by the fact that of six 2nd instar transplants only three possessed two pairs of mandibles, while all six heads had formed 3rd instar spiracles.

Apart from their molting, the developmental behavior of these transplants is very similar to that discussed in the foregoing section. They apparently form the same type of regenerated wound epidermis cover which envelops either part or the whole of the head segments. The cuticular color of the graft under the epidermal

---

PLATE I

FIGURE 1. Head segments of 2nd instar larva transplanted into an adult virilis male host 8 days after the operation. Note darkening of segment borders.

FIGURE 2. Head segments of 1st instar larva transplanted together with two larval ring glands into an adult virilis male host. Transplant remained 15 days in host but has not molted. Note that an epidermal sheath has enveloped about one-half of the transplant.

FIGURE 3. Head segments of 1st instar larva transplanted into an adult virilis male host 14 days after the operation. Note that an epidermis sheath has completely surrounded the transplant.

FIGURE 4. Head segments of 1st instar larva transplanted into an adult virilis male host 14 days after the operation. An epidermis sheath has almost completely overgrown the transplant, leaving only the tip of the head free. At the proximal end of the transplant note the two quite extensively developed eye discs.

FIGURE 5. Section through head segments of a 1st instar larva, transplanted into an adult virilis male host 17 days after the operation. The epidermis has surrounded only one-half of the transplant. Note the large nuclei(n) in the epidermis cover.

FIGURE 6. Section through head segments of a 1st instar larva transplanted into an adult virilis male host 18 days after the operation. The epidermal envelope covers the whole transplant. Note the large nuclei(n) of the epidermal envelope and also the striated material between the transplant and the epidermal sheath.

FIGURE 7. Head segments of 1st instar larva transplanted into mature larvae 5 days after the operation. Three pairs of mandibular hooks, indicating that the transplant has molted twice.

FIGURE 8. Head segments of 2nd instar larva transplanted into a mature larva 8 days after the operation. The transplant has molted but once, as indicated by the presence of only two pairs of mandibular hooks.

FIGURE 9. Head segments of 1st instar virilis larva transplanted into a mature pseudoobscura larva 7 days after the operation. Note three pairs of mandibular hooks, the third and largest pair somewhat proximal to the others. The transplant has thus molted twice.

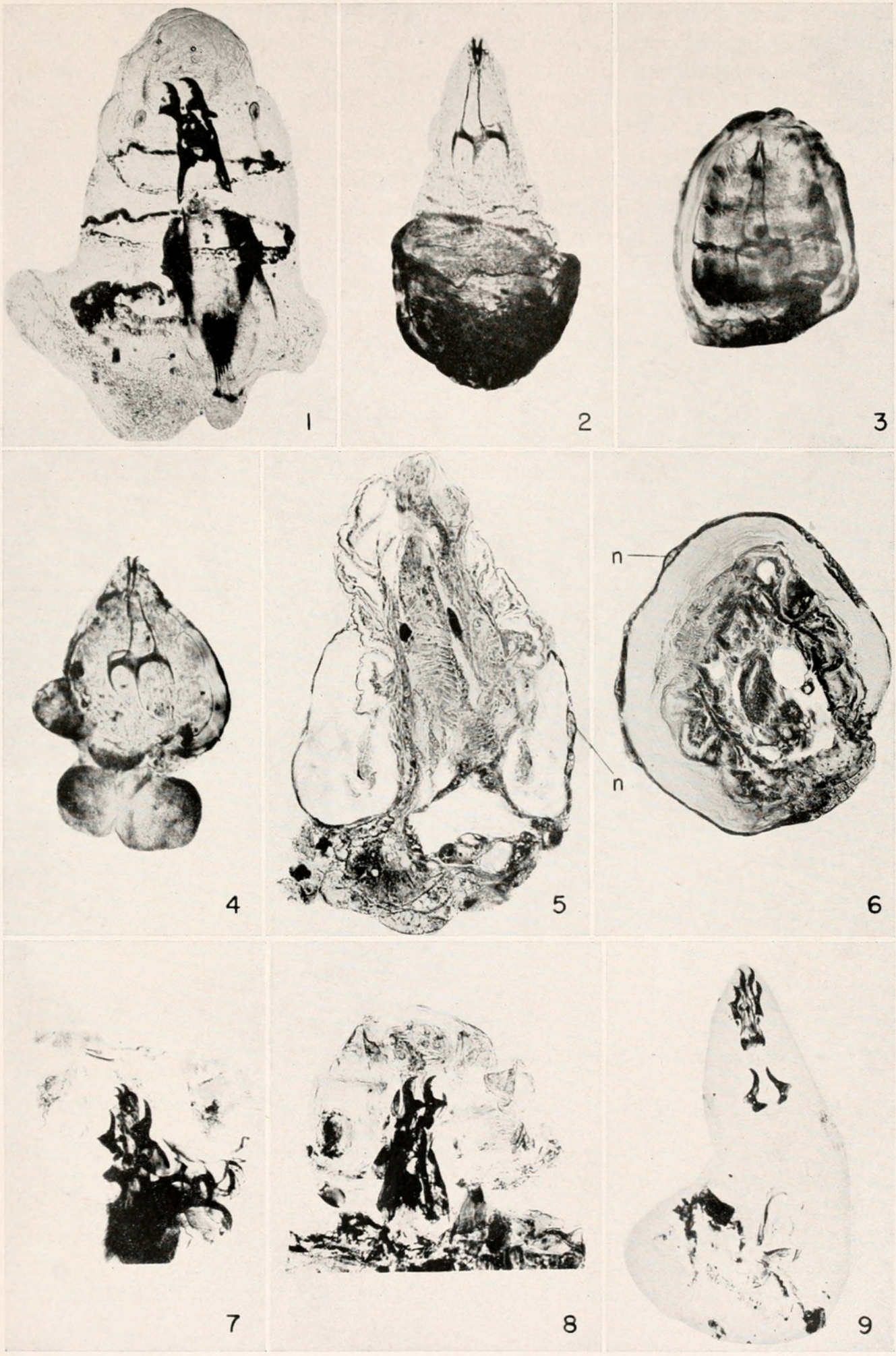

PLATE I

envelope also varies widely, from strictly larval color to darkish spotting or complete browning of the cuticle. Whether or not the browning of the cuticle is an indication of pupation remains questionable. A detailed histological study of the structure of the head parts has not been made. Thus too much emphasis cannot be placed on their apparently similar appearance.

It is interesting that the environment most favorable for molting is apparently that of melanogaster females. Three 1st instar head parts (Table II) which remained in melanogaster females for 7 days molted, while of six transplants which remained in virilis males or in virilis females for 7 to 8 days, only one molted (see Table II).

TABLE III

Transplantation of larval head segments into larval hosts

Age of transplanted larval head segments	Days transplant remains in host	Number of cases	Number of cases where graft has formed		
			1 pair of mandibles	2 pairs of mandibles	3 pairs of mandibles
1st instar (4 hrs. old)	5	6		4(1?)	1
1st instar (4 hrs. old)	6	1			1
2nd instar[a]	2	1	1		
2nd instar[a]	5	3	3		
2nd instar[a]	6	7		1(6?)	
2nd instar[a]	7	3		3	
2nd instar	5	1		1	
2nd instar	6	1		1	
2nd instar	7	6		6	
	Heteroplastic (virilis into pseudoobscura)				
1st instar (0–2 hrs. old)	5	1		1	
1st instar (0–2 hrs. old)	7	5			5
Total number of cases		35			24 positive

[a] Head skin removed, only mouth armature transplanted.

The transplantation of larval head segments into the abdomen of larval hosts

The object of this group of experiments was to test the molting behavior of larval head segments in a larval and pupal environment. For this the brain and ring gland were removed from head segments of 1st and 2nd instar larvae, which were then transplanted into the abdomen of 3rd instar host larvae. The transplanted pieces were dissected shortly before or after the emergence of the fly. Since the pupal life of virilis is about 5 to 5½ days, the head segments dissected 6 or 7

days after the operation were originally transplanted into larvae younger than those which were dissected 5 days after the operation. The head segments in these later dissected hosts therefore had remained longer in a larval environment. A few of the transplants were dissected from younger pupae. The results of these experiments are summarized in Table III, where it can be seen that molting occurred in the majority of the cases. Figure 8 shows such a case. All the head segments in this experimental combination reveal a dark brown cuticle which indeed resembles a pupal cuticle. Unfortunately, however, no special effort was made to determine

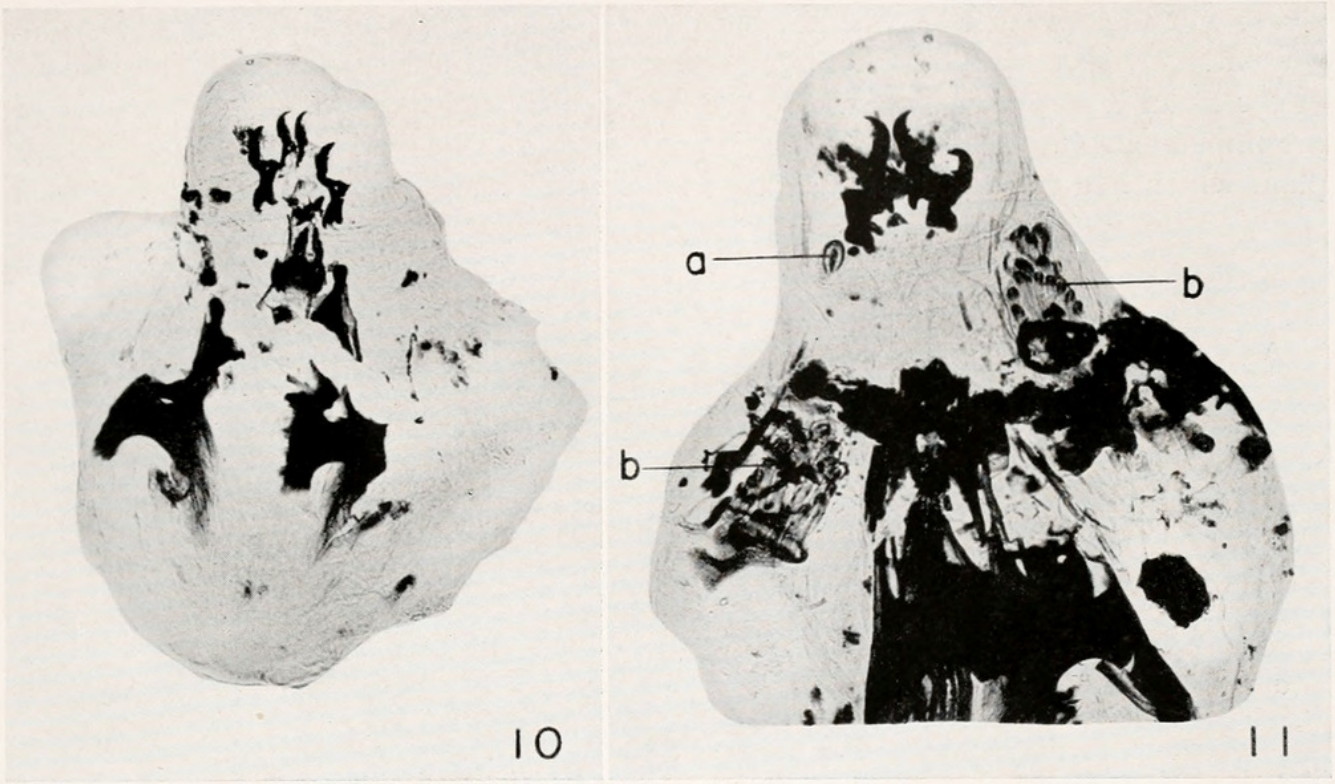

FIGURE 10. Head segments of 1st instar larva transplanted together with two larval ring glands into the abdomen of an adult melanogaster female; 7 days after the operation. The transplant has molted once. Note the two pairs of mandibular hooks.

FIGURE 11. Head segments of 1st instar larva transplanted together with three larval ring glands into an adult melanogaster female 8 days after the operation. The transplant has molted twice. Note the two pairs of mandibular hooks and the spiracles of the 2nd instar (a) and of the 3rd instar (b).

whether or not any epidermal overgrowth surrounded the transplant. Some of the 2nd instar head segments were transplanted after the skin around the mouth parts was removed, with the exception of a very small piece of skin left near the distal end. Such naked mouth parts are also able to molt (see Table III).

The molting factor is not species-specific. This is demonstrated by the transplantation of head segments of 1st instar virilis larvae without brain and ring gland into 3rd instar pseudoobscura larvae. From six cases available in this series, five had formed three pairs of mandibular hooks, revealing that they had molted twice (Fig. 9). One transplant, however, dissected somewhat earlier, had molted only once (see Table III).

The growth of young organ discs in adult hosts

Some of the organ discs such as eye, legs and antennae for example, may be left behind in the transplant after the removal of the nervous system, for these organ anlagen are too minute in size to be recognized in the dissection of the 1st instar larval transplants. Nothing has been said about their developmental fate while they remained in the adult fly. Larval organ anlagen are unable to develop in the abdomen of adult male hosts in the absence of larval ring glands (Bodenstein, 1943). Nevertheless we find in the experiments reported on page 114 that young eye discs left behind in the anterior part of 1st instar larvae develop quite extensively when transplanted into adult male hosts, although no larval ring glands were present. By their growth the discs are usually forced out through the cut surface of the small transplant so that they are finally placed almost or entirely outside of the implant itself. In Figure 4 are shown the two developed eye discs of a transplant which had remained for 14 days in the adult male host environment.

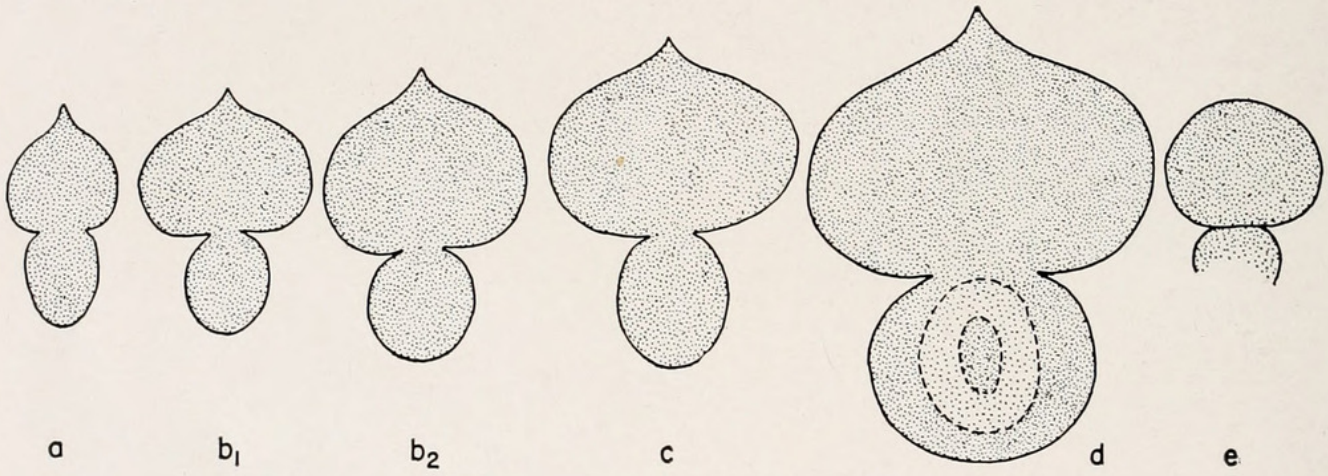

FIGURE 12. a. Eye-antenna disc of a 2nd instar larva shortly before the second molt. b_1 and b_2. Eye-antenna disc which had been transplanted into an adult male host at stage a. Note the increase in growth. c. Eye-antenna disc of very young 3rd instar larva. d. Eye-antenna disc of mature larva. e. Eye disc which had been transplanted at 1st instar stage into an adult male host. (For further explanation, see text.)

Since we know that eye discs of 3rd instar larvae are unable to develop in adult male hosts and find, as described above, that eye discs of 1st instar larvae are able to develop in the same environment, there must be one definite stage in development beyond which the discs are unable to develop. In order to find this critical stage one further experiment was designed and is semi-diagrammatically represented in Figure 12. The size relationships in this figure are based on camera lucida drawings of the same magnification. Figure 12 a shows an eye disc of a 2nd instar larva shortly before the second molt. One may observe that at this stage the distal portion of the disc, the eye disc proper and the posterior portion, the antenna disc, are separated only by a small constriction. Although the eye and antenna discs are bound up together during the whole of the larval life, they become more distinctly separated from one another as development proceeds. A few hours after the second molt the eye and antenna discs have become two definite structures, as illustrated in Figure 12 c. At this stage there is no differentiation recognizable in the antenna discs in total mounts. The eye disc of a mature larva

is shown in Figure 12 d. The considerable increase in size of the eye during the third larval instar is evident if one compares Figure 12 c with Figure 12 d. Moreover, histological differentiation has taken place during this time in both discs. In the mature eye discs the cells have arranged themselves into a definite pattern, which is however scarcely perceptible in total mounts, whereas the differentiation processes in the antenna are visible as oval concentric folds within the disc.

If eye discs of young 3rd instar larvae (Fig. 12 c) are transplanted into the abdomen of adult male flies it is noticed that these discs are unable to grow further. Yet eye discs of old 2nd instar larvae (Fig. 12 a) transplanted in the same manner reach the stage of growth shown in Figure 12 b_1 and b_2 but apparently do not develop further. In comparing the discs in Figures 12 b_2 and c, it may be noticed that both discs are almost the same size. From the foregoing consideration this should be expected, for since the discs of stage "c" are unable to grow in an adult male environment, the younger discs should cease growing in this environment when they reach stage "c." Thus the critical period for the cessation of growth of the eye discs lies between stages "a" and "c," i.e. at about the time the larvae undergo their second molt. Therefore the growth of eye discs transplanted at stages younger than "a" (see experiments above) should never surpass the growth stage "c." This expectation has been fulfilled, for one finds (Fig. 12 e) that the final growth stage of the largest eye disc shown in Figure 4 lies somewhere between the stages of growth represented in Figures 12 a and b.

Discussion

The results described in this paper emphasize the important part played by the ring gland in the larval molting of Drosophila. The molting of larval parts *in vivo* in the abdominal cavity of adult flies is possible only when larval ring glands are added. The speed with which the molts occur is, however, much slower than in normal development, where the two larval molts are accomplished during 4 days. In only one case has the transplant molted twice during the 7 days it remained in the adult host, while the majority of the cases molted only once, although some of them had remained as long as 15 days in the adult host. The slow developmental progress of larval structures in an adult environment was also observed in earlier experiments, and is apparently due to the different metabolic situation within the adult environment (Bodenstein, 1943). In this connection it is of interest to note that the transplant, which had molted twice, was a virilis head part transplanted together with two ring glands into a melanogaster female. It has been established (Bodenstein, 1943) that the melanogaster female environment is much better suited for the growth of organ discs than either melanogaster male or virilis female or male environments. It seems that the same applies to the molting of larval structures. This observation supports a suggestion (Bodenstein, 1943) that the ring gland does not act directly, but rather indirectly in affecting the metabolic level of the host, which then in turn is responsible for the various developmental achievements of the transplanted structures. This hypothesis also assumes that the larval or pupal level is much higher than the highest level induced by ring glands in the adult host (see Bodenstein, 1943, p. 56). If this is correct, it should follow that larval head parts of the first instar should always molt twice in a larval or pupal environment, and that the successive molts should proceed in more rapid succession

in a larval than in an adult environment. The fast rate of normal development, as compared with the very slow developmental rate of the transplanted head parts in adult hosts, is indicative in supporting the "level" conception. The experiments in which larval head segments were transplanted into the abdomen of 3rd instar larvae offer another case in point; for three out of eight cases had already molted twice in 5 to 6 days, while five out of five cases had also molted twice in 7 days. Moreover, in these cases the transplants were under the influence of but one ring gland, that of the host larva, while in the adult hosts two ring glands were present. A similar situation is also found when one compares the second instar larval head transplants in larval and adult host environments. The fact that several transplants in adult hosts had not molted at all, although they had been in their hosts for a considerable length of time, may also be explained by the very low effective level of this environment.

Molting is a process involving many different structures. In normal development there is apparently a marked synchrony between the structural systems involved, in that all of these tissues are ready to perform their molting task at one set time. The same situation, it would seem, prevails in the different organ anlagen systems, as far as their reactions towards pupation are concerned. Yet different organ anlagen vary in their competence to respond to the metamorphosis hormone. These differences, however, are not apparent in normal development, but become noticeable in a modified hormonal environment (see Bodenstein, 1943, p. 55). As far as the molting of head segments in adult flies is concerned, we find the spiracles apparently reacting more readily to the ring gland hormone than the mandibles. For although the spiracles are more difficult to detect, we have cases where it is certain that the mandibles have not molted, while the spiracles have (see Table II). Thus the different systems involved in the process of molting possess different degrees of reacting competence (see Bodenstein, 1943, pp. 53–55).

The number of molts in Drosophila seems to be fixed at two, for 2nd instar head parts transplanted into 3rd instar larvae molt only once, while 1st instar head parts may molt twice although they have remained no longer in the host than the 2nd instar head parts. This seems to be quite unusual in the light of our knowledge of hormone-induced molting in insects (see review Bodenstein, 1942). It might, however, be that the mouth parts used here as a criterion for molting react with greater difficulty than some other structures.

The competence of larval discs

It has been stated previously that in the development of organ discs, the processes of growth as well as of differentiation are controlled by the same hormone. Whether growth or differentiation takes place, depends upon a definite relationship between hormone level and organ competence (Bodenstein, 1943). The observation that young organ discs are able to grow in adult male hosts, but only to a certain stage of growth, still further clarifies the hormone control of Drosophila development. It shows that young discs are very responsive, at least as far as the growth response is concerned, since older discs fail to grow in the same environment. Furthermore these young eye discs grow only to a stage reached by normal eye discs at the time the larva enters the 3rd instar. This fact is decisive, since it shows that the male environment is effective in inducing growth only and does so

solely in very responsive young discs. The question now arises, have these young discs only the competence for a growth response, or are they also able to differentiate under the influence of a very effective hormone level? The answer is provided in an experiment (Bodenstein, 1939a) where young eye discs were transplanted into the abdomen of mature larvae, and thus subjected to a very highly effective level, with the result that they did not reach imaginal completion. Since older eye discs transplanted in the same manner complete their imaginal differentiation in synchrony with the host, it follows that the young discs respond with growth, until they have reached the size above which they can respond with differentiation. By this time, however, the host organs are already so far advanced in their differentiation that the young discs are unable to catch up. In the light of these considerations we might ask what takes place in the eye discs at the time they reach their maximal growth in the adult male fly? The young discs must have acquired the competence to react with differentiation if the appropriate stimulus is present. They are now bi-potent; they react to a low effective level with growth, but might be induced to differentiate, provided the effective hormone level is high enough. That this is the case can be demonstrated experimentally, for an eye disc of a 3rd instar larva will grow considerably before differentiation begins in an adult male environment if supported by two larval ring glands (Bodenstein, 1943). The same eye disc transplanted into a mature larva will, however, cease to grow and begin to differentiate immediately, with the result that finally a small imaginal eye is formed (Bodenstein, 1939a; 1941). This experiment shows clearly that the response of the same organ disc varies according to the hormonal situation. Thus we may conclude that as the eye discs of 3rd instar larvae become older their competence to respond with growth gradually decreases, while at the same time the competence of the differentiation response increases. At the end of larval life the discs are able to respond only with differentiation.

It is of interest to note that our earlier results (Bodenstein, 1943) and those discussed here are confirmed by recent experiments of Vogt (1943). This author, working with *Drosophila hydei,* approached the problem in a different way experimentally. She used as host the rear part of a 3rd instar larva, after the anterior larval part had been removed by means of a ligature. Into these larval rear parts she then transplanted the eye discs of 3rd instar larvae and simultaneously the eye discs plus the nervous system of very young 2nd instar larvae. She found that the older eye discs remained larval (whether growth occurred is not stated) while the young eye discs developed to a stage equivalent to that of an old 2nd instar larva. When, however, she transplanted six ring glands of the young 2nd instar donors simultaneously, the result was different. The young eye discs had become larger, while the old eye discs had begun differentiation. From this Vogt concludes that growth and differentiation are apparently controlled by the same hormone.

Here attention should be drawn to the fact that this critical stage which occurs at about the time of the second molt corresponds closely to critical periods observed in two other sets of experiments. 1. Beadle *et al.* (1938) and Bodenstein (1939b; 1941) observed that Drosophila larvae (melanogaster and hydei) when starved completely before they are 50 and 100 to 120 hours old respectively, i.e. about the time of the second molt, are unable to pupate. 2. Bodenstein (1939a;

1941) transplanted melanogaster eye discs from donor larvae younger than 50 hours into mature larvae and found that these discs were unable to differentiate completely, while older eye discs transplanted in the same manner differentiate to imaginal completion. From all this it becomes evident that at this time a change occurs in the organ discs of the larvae, the nature of which we have discussed above. Whether all the imaginal discs reach this critical stage at the same time is questionable, since one must remember that the different discs, as well as different regions of the same discs (Bodenstein, 1943), respond differently to the same effective level. Whether all discs have such a critical stage is at present unknown, but seems highly probable.

Summary

1. Larval head parts of 1st and 2nd instar larvae without nervous system and ring glands were transplanted into the abdomen of adult male flies, together with two larval ring glands from mature larvae. The transplanted heads molt once or twice, as indicated by the presence of double or triple mouth parts.

2. Head parts transplanted in the same manner, but without larval ring glands fail to molt. This shows that the larval ring gland hormone induces larval molting.

3. Head parts without their nervous system and ring glands were also transplanted into the abdomen of 3rd instar larvae. The transplantations were performed either homo- or heteroplastically. In either case molting was induced. The molting hormone of the ring gland is thus not species-specific.

4. Very young organ anlagen were transplanted together with anterior larval head segments after the removal of the nervous system into adult male hosts. It was found that these organs were able to develop in their new environment in the absence of ring glands. Older organ discs transplanted in the same manner develop however only in the presence of ring glands. These experiments are discussed in relation to hormone level and tissue competence.

LITERATURE CITED

Beadle, G., E. Tatum, and C. Clancy, 1938. Food level in relation to rate of development and eye pigmentation in Drosophila melanogaster. *Biol. Bull.*, **75**: 447–462.

Bodenstein, D., 1939a. Investigations on the problem of metamorphosis. IV. Developmental relations of interspecific organ transplants in Drosophila. *Jour. Exp. Zool.*, **82**: 1–30.

Bodenstein, D., 1939b. Investigations on the problem of metamorphosis. V. Some factors determining the facet number in the Drosophila mutant bar. *Genetics*, **24**: 494–508.

Bodenstein, D., 1941. Investigations on the problem of metamorphosis. VII. Further studies on the determination of the facet number in Drosophila. *Jour. Exp. Zool.*, **86**: 87–111.

Bodenstein, D., 1942. Hormone controlled processes in insect development. *Cold Spring Harbor Symp. on Quant. Biol.*, **10**: 17–26.

Bodenstein, D., 1943. Hormones and tissue competence in the development of Drosophila. *Biol. Bull.*, **84**: 34–58 (review).

Piepho, H., 1938. Wachstum und totale Metamorphose an Hautimplantaten bei der Wachsmotte Galleria mellonella L. *Biol. Zentralblatt*, **58**: 356–366.

Vogt, M., 1943. Hormonale Auslösung früher Entwicklungsprozesse in den Augenantennen-Anlagen von Drosophila. *Naturwiss.*, **31**: 200–201.