THE FUNCTIONS OF THE CORPUS ALLATUM IN
RHODNIUS PROLIXUS (HEMIPTERA)

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(With Plate 1 and Four Text-figures)

It has been shown in earlier papers (Wigglesworth, 1934, 1936, 1940) that metamorphosis in *Rhodnius* takes place when the corpus allatum ceases to secrete the 'inhibitory' or 'juvenile hormone'. There was no evidence for the existence in this insect of a 'metamorphosis hormone' which promotes the development of imaginal characters. Growth and moulting are induced at all stages of development by a 'moulting hormone' (what is called by Scharrer & Scharrer (1944) a 'growth and differentiation hormone') secreted in the dorsum of the protocerebrum. When this hormone alone is acting, the latent imaginal characters are realized and metamorphosis occurs. When the 'juvenile hormone' from the corpus allatum of the early nymphal stages is present in addition, it causes the preferential development of nymphal characters and thereby suppresses those of the adult.

This conception of growth regulation in insects has proved applicable to Orthoptera (*Dixippus* (Pflugfelder, 1937, 1939); *Melanoplus* (Pfeiffer, 1945a); *Leucophaea* (Scharrer, 1946)); to Lepidoptera (*Bombyx, Lymantria, Galleria* (Bounhiol, 1938); *Ephestia, Galleria* (Piepho, 1940, 1942)); and to Coleoptera (*Tenebrio* (Radtke, 1942)). In the Diptera, on the other hand, the 'ring gland', which is a composite structure with elements representing the corpus allatum, the corpus cardiacum and perhaps the 'pericardial gland' and the hypocerebral ganglion (Poulson, 1945; Thomsen, 1942; Vogt, 1943a), appears actively to induce metamorphosis as though it were secreting a metamorphosis-promoting hormone (Hadorn, 1941).

There is some evidence, however, that the central part of the ring gland, the part representing the corpus allatum, restrains the differentiation of the imaginal disks in the young larva of *Drosophila* (Vogt, 1943a), and it has recently been shown by Vogt (1946) that the corpus allatum of the adult *Drosophila* implanted into the larva will cause a local suppression of adult characters in the resulting fly.

These findings go some way towards bringing the control of metamorphosis in the Diptera into line with that in other insects. It is the object of the present work to see whether the corpus allatum in *Rhodnius*, besides ceasing to produce the juvenile hormone, also plays an *active* part in the causation of metamorphosis.
FUNCTION OF THE CORPUS ALLATUM DURING MOULTING IN THE 5TH-STAGE NYMPH

The secretion of the juvenile hormone by the corpus allatum ceases when the 4th-stage nymph has moulted to the 5th stage (Wigglesworth, 1936). But during the moulting of the 5th-stage nymph to the adult, the corpus allatum again shows signs of renewed activity, the cytoplasm of the cells becoming swollen and dense. At first this was taken as evidence that the gland was secreting the moulting hormone (Wigglesworth, 1934); but since that was disproved and it was shown that the moulting hormone comes from the dorsum of the brain (Wigglesworth, 1940) the meaning of this renewed physiological activity has been obscure.

The question has been studied by comparing the structural characters produced by 5th-stage nymphs moulting in the presence and absence of the corpus allatum. This has been effected in three ways:

(i) 5th-stage nymphs were allowed to develop for 9 days after feeding, by which time they have, for the most part, passed the critical period and can moult after decapitation (Wigglesworth, 1934). Half were decapitated completely with removal of the corpus allatum; half had the head cut through behind the brain but in front of the corpus allatum.

Both groups developed adult characters. No differences could be seen in the structure of the abdominal cuticle. In both, the unexpanded wings were highly crumpled; but here a difference was detectable, the wings being more deeply folded in the second group. Likewise in the genitalia, the adult characters were developed more completely in the second group of insects, those which retained the corpus allatum.

(ii) In the above experiment the corpus allatum was retained in both groups of insects until after the critical period, and may be supposed to have exerted some action by this time. 5th-stage nymphs were therefore decapitated 24 hr. after feeding and were then induced to moult by joining them, as already described (Wigglesworth, 1934), to 5th-stage nymphs decapitated at 10 days after feeding. In six experiments both insects were deprived of their corpus allatum; in six the corpus allatum was retained in both.

The results were more striking than in the former series. The wings were not entirely normal even in the insects which retained the corpus allatum, the folding being slightly less extreme than in a normal adult insect (Pl. 1, fig. 1). But in the insects without the corpus allatum, the wings were in part definitely nymphal. There was considerable individual variation, but in several, although there was some folding towards the base, the apical half was more or less smooth, as in the nymph (Pl. 1, fig. 2).

There were differences also in the cuticle of the abdomen. In those with the corpus allatum, the ‘hinge-line’ was fully formed, the pigmentation was of the normal adult type (as represented in Wigglesworth, 1940, Pl. I, fig. 8) and the folding of the epicuticle was shallow and transverse as in the adult. In those without the corpus allatum the ‘hinge-line’ was incompletely formed over the middle and
Functions of the corpus allatum in Rhodnius prolixus (Hemiptera)

Anterior abdominal segments, the pigment spots had a partially nymphal distribution tending to extend towards the postero-lateral angles of the segments, and over much of the abdomen the epicuticular folds showed some change towards the stellate type characteristic of the nymph. The whole appearance resembled that shown in Wigglesworth (1940, Pl. I, fig. 6), which represented an insect that had been switched over from adult development to nymphal development on the thirteenth day after the commencement of moulting.

(iii) In the third series, moulting in the complete absence of the corpus allatum was secured by decapitating a number of 5th-stage nymphs at 24 hr. after feeding and implanting into the abdomen the dorsum of the brain from other 5th-stage nymphs which had been fed 12 days previously.

The results were like those obtained in the preceding series. The characters in the main were those of the adult. But the wing lobes, the genitalia (Text-fig. 1B), and the abdominal cuticle still showed vestiges of nymphal characteristics.

![Text-fig. 1. A, external genitalia of normal adult female; B, genitalia of an adult female decapitated in 5th stage 1 day after feeding and caused to moult by the implantation of another 5th-stage brain without the corpus allatum. viii, eighth sternite; vi, v, and v, the first, second and third pairs of valvulae.](image)

The second type of experiment (series (ii) above) was repeated with 4th-stage nymphs decapitated at 24 hr. after feeding and joined to 5th-stage nymphs which had passed the critical period, with and without the corpus allatum. The results were not so striking as with the 5th-stage nymphs. Both groups of 4th-stage nymphs developed adult characters, but once more these were better formed, notably in the folding of the wings, when the 5th-stage nymphs retained the corpus allatum.

It is clear from these results that the corpus allatum of the 5th-stage nymph in Rhodnius is playing at least a small active part in the completion of metamorphosis. There are two ways in which it might be supposed to act:

(a) By the secretion of a 'metamorphosis hormone' which acts on the tissues and favours the production of adult characters (as the 'juvenile hormone' favours the production of nymphal characters).

(b) By the active elimination of juvenile hormone persisting in the blood and tissues.

An attempt was made to differentiate between these alternatives by implanting the corpus allatum from the 5th-stage nymph at varying stages in its development,
into the abdomen of 4th-stage and 3rd-stage nymphs. In these experiments the
host insect in the 3rd or 4th stage retains its own corpus allatum, which we know is
secreting the juvenile hormone and so preventing metamorphosis. We know also
that the corpus allatum of the 3rd- and 4th-stage nymph, implanted into the
abdomen of a 5th-stage nymph, suppresses metamorphosis and leads to the pro-
duction of a 6th-stage nymph. The corpus allatum from the 5th-stage nymph could
scarcely be expected, therefore, to produce a very striking effect when implanted
into the 3rd- or 4th-stage nymph. But if it does indeed secrete a 'metamorphosis
hormone' we might expect to find developed a small patch of imaginal cuticle in
immediate proximity to the implanted gland—just as implants of the young corpus
allatum into the 5th-stage nymph, if they fail to lead to the production of 6th-stage
nymphs, often produce adults with a small area of nymphal cuticle overlying the
implant.

The corpus allatum (together with the corpus cardiacum to which it is closely
attached) was removed from batches of 5th-stage nymphs, unfed, and at intervals
of 7 days, 15 days and 20 days after feeding, and implanted beneath the cuticle of
the abdomen of 4th-stage nymphs at 1 day after feeding. The results were as
follows:

<table>
<thead>
<tr>
<th>Implants</th>
<th>Description</th>
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</thead>
<tbody>
<tr>
<td>11 implants from 5th-stage nymphs, unfed</td>
<td>No effect</td>
</tr>
<tr>
<td>7 implants from 5th-stage nymphs at 7 days after feeding</td>
<td>No effect</td>
</tr>
<tr>
<td>12 implants from 5th-stage nymphs at 15 days after feeding</td>
<td>1 slightly 'adultoid' 5th-stage nymph</td>
</tr>
<tr>
<td>12 implants from 5th-stage nymphs at 20 days after feeding</td>
<td>1 as above</td>
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</tbody>
</table>

The term 'adultoid' nymph is adopted after Scharrer (1946) to describe insects
in which the differentiation of imaginal characters has proceeded further than in
the normal nymph. In these two instances the effect was very small; there was no
detectable change in the wing lobes, but the first pair of valvulae (on the 8th abdominal
segment) in the female was a trifle more widely separated than normally (cf.
Text-fig. 2B). There was no effect on the abdominal cuticle overlying the implant.

In the foregoing experiment the newly implanted corpus allatum, without an
established tracheal supply, is competing with the undamaged corpus allatum of
the host. It seemed possible that a more striking effect might be produced if the
corpus allatum from the 5th-stage nymph were implanted into the 3rd-stage nymph
so as to give it an opportunity to become well established by the time the 4th-stage
nymph moulted. In none of these insects was there any detectable effect on the
characters of the resulting 4th-stage nymphs. The effects on the resulting 5th-stage
nymphs were as follows:

<table>
<thead>
<tr>
<th>Implants</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 implants from 5th-stage nymphs, unfed</td>
<td>1 slightly 'adultoid' 5th-stage nymph</td>
</tr>
<tr>
<td>15 implants from 5th-stage nymphs at 7–10 days after feeding</td>
<td>1 as above</td>
</tr>
<tr>
<td>10 implants from 5th-stage nymphs at 15 days after feeding</td>
<td>1 as above</td>
</tr>
<tr>
<td>11 implants from 5th-stage nymphs at 20 days after feeding</td>
<td>3 as above</td>
</tr>
</tbody>
</table>
Functions of the corpus allatum in \textit{Rhodnius prolixus} (\textit{Hemiptera})

\textbf{Text-fig. 2.} A, female genitalia of normal 5th-stage nymph; B, the same in slightly 'adultoid' 5th-stage nymph produced by the implantation of the corpus allatum of 5th-stage nymph 15 days after feeding into a 4th-stage nymph; C, the same in moderately 'adultoid' 5th-stage nymph produced by implanting corpus allatum of adult 1 week after moulting into a 3rd-stage nymph; D, the same in strongly 'adultoid' 5th-stage nymph produced as C. \(v_1\), \(v_2\), and \(v_3\), the first, second and third pairs of valvulae.

\textbf{Text-fig. 3.} A, male genitalia of normal 5th-stage nymph; B, the same in slightly 'adultoid' 5th-stage nymph produced by the implantation of the corpus allatum of an adult 2 days after moulting into a 2nd-stage nymph; C, the same in strongly 'adultoid' 5th-stage nymph produced by implantation of corpus allatum of a newly moulted adult into a 3rd-stage nymph. ix, ninth sternite; cl, rudiments of claspers.
In the most successful experiments of this series, the 'adultoid' change was a little greater. Not only were the genitalia differentiated more than the normal (resembling Text-figs. 2C, 3B), but the wing lobes were slightly broadened (Pl. 1, fig. 6), the costal margin being convex and projecting well beyond the sides of the thorax (Pl. 1, figs. 6, 7), instead of straight or slightly concave as in the normal 5th-stage nymph (Pl. 1, fig. 3). Again there was no local effect over the implant.

The numbers are small and the effects slight, but the figures suggest that the action may be greater when corpora allata are taken from the 5th-stage nymph during the latter half of the moulting process, and greater when they are implanted into 3rd-stage nymphs than into the 4th stage. But there is no doubt that the implanted corpus allatum of the 5th-stage nymph is inducing a partial premature metamorphosis, and this effect is always diffuse. There is no local effect around the implant. That suggests that the implanted gland is acting by the absorption or partial inactivation of juvenile hormone circulating in the blood.

Text-fig. 4. Longitudinal section through a local patch of nymphal cuticle in an adult Rhodnius.

c.a. implanted corpus allatum; a.c. normal adult cuticle, thin with relatively thick exocuticle; n.c. nymphal cuticle, very thick and soft with highly folded epicuticle but no exocuticle. The epidermis below the nymphal cuticle has the nuclei far more densely packed.

EFFECT OF THE CORPUS ALLATUM OF THE ADULT ON THE DIFFERENTIATION OF ADULT CHARACTERS

It seemed possible that the corpus allatum of the young adult insect might continue to exert this same action of eliminating the juvenile hormone. This was tested by implanting the gland (together with the corpus cardiacum as before) from adults of known age into 3rd-stage and 4th-stage nymphs. The results with 4th-stage nymphs were as follows:

13 implants from adults within 2 days after moulting 3 'adultoid' 5th-stage nymphs
15 implants from adults at 1 week after moulting 2 as above
8 implants from adults at 3-4 weeks after moulting No effect

The results with 3rd-stage nymphs were as follows:

13 implants from adults within 2 days after moulting 4 'adultoid' 5th-stage nymphs
30 implants from adults at 5-7 days after moulting 16 as above
9 implants from adults at 2 weeks after moulting 1 as above
12 implants from adults at 3-4 weeks after moulting No effect

A few implants were made into 2nd-stage nymphs with results as follows:

12 implants from adults about 5 days after moulting 3 slightly 'adultoid' 5th-stage nymphs
Functions of the corpus allatum in Rhodnius prolixus (Hemiptera) 7

The corpus allatum of the newly moulted adult clearly has the same effect as that of the 5th-stage nymph in the later stages of moulting; it causes a partial premature metamorphosis in the 5th stage. In the most successful experiments the effect was greater than that following implantation of the gland from the 5th-stage nymph. The wing lobes were broad and crumpled or swollen and distended (Pl. 1, figs. 8, 9); there was a greater degree of differentiation in the genitalia of both sexes (Text-figs. 2D, 3C), and in some the ocelli (which occur only in the adult Rhodnius) were becoming visible. The numbers involved are again rather small, but it appears that this effect is exerted only by the corpus allatum of the young adult; implants from adults 3-4 weeks after moulting had no action.

In one series of experiments, in order to be sure that the corpus allatum is the active part of the implant, brain, corpus cardiacum and corpus allatum were removed from adult insects at 1 week after moulting and implanted separately into 3rd-stage nymphs. The parts were taken from eight adults. The results were as follows:

<table>
<thead>
<tr>
<th>Implant</th>
<th>Survived</th>
<th>Effect on 5th-stage nymphs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brain implanted</td>
<td>6</td>
<td>no effect</td>
</tr>
<tr>
<td>Corpus cardiacum</td>
<td>7</td>
<td>no effect</td>
</tr>
<tr>
<td>Corpus allatum</td>
<td>8</td>
<td>5 'adultoid' 5th-stage nymphs</td>
</tr>
</tbody>
</table>

The action of the corpus allatum of the moulting 5th-stage nymph and young adult in favouring the development of adult characters is thus confirmed. The effect might be due to the gland from the maturing insect acting upon the gland of the young host and weakening its capacity to secrete the juvenile hormone. But we have seen (p. 2) that the action is exerted also in the moulting 5th-stage nymph where there is no young corpus allatum to influence. The failure to obtain in a single experiment any local formation of adult characters around the implant, makes it unlikely that the effect is due to a 'metamorphosis hormone' favouring imaginal differentiation directly. It seems more probable that the gland is either absorbing the juvenile hormone circulating in the blood and so withholding it from its site of action (and that is perhaps the most likely explanation) or it may be producing a secretion which inactivates the juvenile hormone that is in circulation.

SECRETION OF JUVENILE HORMONE BY THE CORPUS ALLATUM OF THE ADULT

The 5th-stage nymphs produced in the last series of experiments, following the implantation of the corpus allatum of the adult into the 3rd or 4th stage, were allowed to moult again. In the most strongly adultoid forms the ecdysial line on the head and thorax had disappeared. Consequently they were unable to split the old cuticle and escape; but apart from this mechanical defect, moulting took place normally in all of them, both normal and 'adultoid'.

The characters of the resulting adults were either normal or 'nymphoid'. In some there was only a small patch of nymphal cuticle immediately overlying the implant (Pl. 1, fig. 5); in others the entire character of wings, cuticle and genitalia might be intermediate between nymph and adult (Pl. 1, fig. 10); others were completely nymphal—6th-stage nymphs (cf. Pl. 1, fig. 12).
Where there was a localized patch of nymphal cuticle over the implant, it could be seen in sections (Text-fig. 4) and dissections that the corpus allatum, richly supplied by tracheae running in from all sides, was rounded and well defined and lay exactly below the centre of the nymphal patch. In some instances the patch was so minute (100\(\mu\) in diameter) that it scarcely exceeded the area of the underlying gland.

Clearly the implanted corpus allatum, derived from an adult insect, is now secreting juvenile hormone. A similar result was obtained by Pfeiffer (1945\(a\)) in *Melanoplus*. When the corpora allata from the adult of this grasshopper were implanted into the 5th-stage nymph, the resulting 7th stage instead of being an adult was partially or wholly nymphal; and these insects might moult again to produce an 8th or even a 9th stage.

Now we know that the imaginal tissues, exposed to the combined action of the moulting hormone and the juvenile hormone of the young nymphal stages will revert, in part at least, to the nymphal state (Wigglesworth, 1940). The question arises, therefore, whether the juvenile hormone is a normal secretion of the corpus allatum of the adult; or whether it is produced only when the gland has become 'rejuvenated' by exposure to the secretion of the 3rd- or 4th-stage nymph.

This has been tested in two ways:

(i) By the implantation of the corpus allatum from adults of known age directly into 5th-stage nymphs at 24 hr. after feeding. The results were as follows:

10 implants from newly moulted adults produced:
- 1 6th-stage nymph; 1 nymphoid adult; 5 adults with a small patch of nymphal cuticle over the implant; and 3 normal adults.

10 implants from adults 3 weeks old produced:
- 5 6th-stage nymphs; 2 nymphoid adults; 3 adults with distinct nymphal patches; and 1 normal adult.

Thus the juvenile hormone is being secreted by the corpus allatum removed from the adult without its having been first rejuvenated in the early nymph. Moreover, the production of the hormone would appear to be more active in the mature adult than in the newly moulted insect. This same difference is apparent when implantations are made into the 3rd- or 4th-stage nymph:

13 implants from newly moulted adults into 3rd-stage nymphs gave rise finally to:
- 1 nymphoid adult; 5 adults with small patches of nymphal cuticle; 7 normal adults.

10 implants from adults 3 weeks old into 3rd-stage nymphs gave rise finally to:
- 1 6th-stage nymph; 1 nymphoid adult; 6 adults with well-marked patches of nymphal cuticle; 2 normal adults.

7 implants from newly moulted adults into 4th-stage nymphs produced:
- 3 adults with very minute local patches of nymphal cuticle; 4 normal adults.

6 implants from adults 3 weeks old into 4th-stage nymphs produced:
- 6 adults with well-marked nymphal patches.
Functions of the corpus allatum in Rhodnius prolixus (Hemiptera)

(ii) The second procedure was to allow 5th-stage nymphs to pass the critical period; then to decapitate them at 10 days after feeding with removal of the corpus allatum, and to join them to mature adults (about 3 weeks old; fed 1 day previously) in which the anterior part of the head with the brain were removed but the corpus allatum retained. The moulting 5th-stage nymph was thus deprived of its own corpus allatum and exposed to the secretion of the intact corpus allatum of the adult. And the adult was exposed to the moulting hormone of the 5th-stage nymph and to the secretion of its own corpus allatum.

The 5th-stage nymphs when they moulted developed characters in the wing lobes and in the cuticle of the abdomen that were definitely nymphal. In six experiments out of eight in which the 5th-stage nymphs moulted, the adult also was caused to moult. And in those experiments in which the 5th-stage nymph retained its nymphal characters most distinctly, the new cuticle produced by the adult showed a partial reversion to the nymphal condition. This effect was not so pronounced as in the best examples resulting from the implantation of young corpora allata into the adult (Wigglesworth, 1940, Text-figs. 10, 11), but it was unmistakable. There were areas on the abdomen where the new epicuticle was thrown into folds intermediate in type between those of nymph and adult.

The juvenile hormone must therefore be a normal secretion in the mature adult. Thus the corpus allatum in the adult appears to have a dual function. (a) In the early days after moulting it absorbs or inactivates the juvenile hormone; this function is carried over apparently from the moulting 5th-stage nymph, and is lost in a week or two after the insect becomes adult. (b) It begins to secrete again the juvenile hormone; this activity appears to be slight in the newly moulted adult but to increase markedly in the mature insect.

FUNCTION OF THE JUVENILE HORMONE IN THE NORMAL ADULT

The juvenile hormone is apparently produced in increasing quantity in the adult Rhodnius at the same time as the ‘gonadotropic hormone’, responsible for the formation of yolk in the female and for the activity of the accessory glands in the male, is being secreted by the corpus allatum. Pfeiffer (1945) indeed, has suggested that in Melanoplus the ‘gonadotropic hormone’ of the adult may be identical with the juvenile hormone of the young nymph.

If that is so, not only should the secretion from the adult restrain metamorphosis in the nymph and induce a reversal of metamorphosis in the moulting adult (as described above), but the secretion from the corpus allatum of the young nymph should induce egg formation in the adult female.*

It was shown in an earlier paper (Wigglesworth, 1936) that the decapitated adult female deprived of its corpus allatum will not develop eggs. If joined to an adult of either sex which retains its corpus allatum, eggs are developed. If joined to

* Vogt (1943b) has already observed that the corpus allatum (that is, the median dorsal region of the ring gland) removed from the first stage larva of Drosophila hydei will induce egg production when implanted into the allatectomized adult female, and has likewise suggested that the secretion responsible may perhaps be identical with the juvenile hormone reported in other groups of insects.
a moulting 5th-stage nymph retaining its corpus allatum no egg development occurs—indeed the adult may be induced to moult by this means. It has now been found that the secretion from the corpus allatum of the moulting 4th-stage nymph will induce egg formation in the decapitated adult female.

Twelve adult females proved by transillumination to have no ripe eggs in the ovaries* were fed, and 24 hr. later were decapitated with removal of the corpus allatum. Each was then joined to a 4th-stage nymph at 7 days after feeding, from which the forepart of the head was removed but the corpus allatum retained. Within 10 and 12 days the 4th-stage nymphs had moulted; and of the twelve adult females, five had developed ripe eggs, some only two or three, others in large numbers.

The small number of successful results is to be attributed probably to the great dilution which the juvenile hormone must suffer when shared with the adult female. In another series of experiments six adult females decapitated 24 hr. after feeding were joined to 4th-stage nymphs retaining the corpus allatum, and at the same time two corpora allata were removed from 4th-stage nymphs at 7 days after feeding and implanted into the abdomen of each female. Of the six adult females four developed large numbers of ripe eggs.

It is worth noting that in those experiments in which no egg development occurred, the characters produced by the moulting 4th-stage nymph were those of the normal 5th-stage nymph. Whereas when active development of eggs took place the characters of the nymphs showed a certain degree of differentiation towards the adult form. This result could be interpreted to mean that the developing eggs were absorbing juvenile hormone and so depriving the tissues of the moulting 4th-stage nymph of the supplies they need.

We have seen that the corpus allatum of the adult or of the late 5th-stage nymph, implanted into the abdomen of the 3rd- or 4th-stage nymph, shows evidence of secretion of juvenile hormone during the moulting of the 5th-stage nymph: in the resulting adult a small area of nymphal cuticle overlies the implant. Five adult females of this sort were decapitated at 24 hr. after feeding. All of them developed ripe eggs.

It is clear, therefore, that the corpus allatum of the adult secretes both yolk-forming hormone and juvenile hormone, and that of the 4th-stage nymph both juvenile hormone and yolk-forming hormone; while in the 5th-stage nymph neither hormone is produced. Isolation and chemical characterization of the substances in question will be necessary to prove the matter, but it appears probable, as Pfeiffer and Vogt have suggested, that the juvenile hormone and the yolk-forming hormone are one and the same substance.

DETERMINATION OF THE SECRETORY FUNCTION OF THE CORPUS ALLATUM

The experiments described earlier in this paper show, among other things, that the corpus allatum of the adult, particularly the very young adult, when implanted into the abdomen of another insect, may vary in its activities. It may secrete juvenile

* As described before (Wigglesworth, 1936, 1943) the ripe eggs contain parahaematin, the red colour of which is readily visible if the abdomen of the insect is examined against a bright light.
Functions of the corpus allatum in Rhodnius prolixus (Hemiptera) 11

hormone; it may inactivate juvenile hormone; and either of these functions may predominate.

That raises the question of the control and determination of the normal function of the corpus allatum. It may be that the normal secretory function is ensured only when the integrity of the central nervous system—corpus allatum complex is unbroken, and that the timing of the activities of the corpus allatum is controlled by the brain. A few observations that bear upon this important question will be reported here.

It was suggested in a previous paper (Wigglesworth, 1936) that the characters in the early nymphal stages of Rhodnius are determined by the level of secretion of the juvenile hormone (inhibitory hormone). It was shown that a 4th-stage nymph deprived of its corpus allatum and caused to moult by joining it to a 3rd-stage nymph which retains its corpus allatum, again develops the characters of the 4th stage. It has now been found that if the corpus allatum of a 3rd-stage nymph is implanted into the intact 4th-stage nymph, this develops into a normal 5th stage. In other words, the corpus allatum of the host appears to control the level of concentration of juvenile hormone.

Other evidence is derived from the action exerted by implanted corpora allata at subsequent moults. When the corpus allatum of the 5th-stage nymph is implanted into the 4th-stage nymph it usually causes no visible effect (p. 4); the corpus allatum of the 4th-stage host determines the level of concentration of the juvenile hormone. Occasional slightly adultoid 5th-stage nymphs are produced. When the 5th-stage nymphs moult again they usually turn into normal adults. But, occasionally, adults are produced which are nymphoid to a varying degree. Pl. 1, fig. 11, for example, shows a nymphoid adult with short wings, intermediate genitalia, ocelli, thorax, etc. The abdominal cuticle is mostly of adult type and pigmentation but it has evenly distributed bristles as in the nymph.

It is not possible to decide in this experiment whether it is that the implanted 5th-stage corpus allatum has now become adult and is secreting the juvenile hormone again for that reason; or whether, as the result of implantation into a 4th-stage nymph, it has recovered nymphal characters and continued to secrete juvenile hormone for that reason. But in any case it is clear that the implanted corpus allatum is out of step with that of the host.

Sixth-stage nymphs can be produced by the implantation of the corpus allatum either from a young nymph (1st–4th stage) or from a mature adult. When the 6th-stage nymphs moult again their characters are variable and bear no strict relation to the stage from which the implanted corpus allatum was derived (Wigglesworth, 1936). Pl. 1, fig. 12, shows a 6th-stage nymph which was produced by the implantation of the corpus allatum from a 2nd-stage nymph into a 4th stage. When this insect moulted again it developed wholly adult characters (Pl. 1, fig. 13)—although the implanted corpus allatum had passed through only four nymphal stages. The corpus allatum of the host appears to have overcome the activity of the implant.

On the other hand, in one series of experiments in which the corpus allatum of
the 3rd-stage nymph was implanted into the 4th-stage nymph, a 6th-stage nymph was produced which gave rise to a 7th stage which was entirely nymphal and showed no further differentiation towards the adult form—although the implanted corpus allatum had by that time passed through five nymphal stages and the gland in the 5th-stage nymph does not normally secrete juvenile hormone.

From these examples it is clear that the functional activity of the corpus allatum is not determined wholly by humoral means; nor is this determination wholly autonymous: it does not, for instance, produce juvenile hormone for a definite number of moulting stages. In other words, it is not the corpus allatum itself which 'counts the instars'. The mechanism responsible for this presumably resides in the central nervous system or in some part of the stomato-gastric nervous system. From the standpoint of experimental method it is obvious that the transplantation of the corpus allatum alone may give a misleading impression of its function; it is well to combine such experiments with the transfusion of haemolymph from intact insects (so-called 'parabiosis').

**DISCUSSION**

It was suggested in the introduction to this paper that there might be two factors involved in the control of metamorphosis in insects: (i) the corpus allatum ceases to secrete the juvenile hormone and thus permits the latent imaginal characters to be realized. (ii) Some part of the endocrine system may actively promote metamorphosis and the differentiation of the characters of the adult. The former factor has been demonstrated in Hemiptera, Orthoptera, Lepidoptera and Coleoptera, and there is some evidence for its existence in *Drosophila* (Vogt, 1943a, 1946). The latter factor has been regarded as characteristic of the Diptera.

In the present paper it has been shown that in *Rhodnius* the corpus allatum of the mature 5th-stage nymph not only ceases to secrete the juvenile hormone but also plays an active part in the promotion of metamorphosis. The results, however, are interpreted as indicating an active elimination by the corpus allatum of those quantities of juvenile hormone still persisting in the blood of the 5th-stage nymph.

If the corpus allatum in *Dixippus* is removed from the 3rd stage, the insect undergoes two moults and then gives rise to a diminutive egg-laying female in the 5th stage (instead of the 7th stage) (Pflugfelder, 1937). And in the cockroach *Leucophaea*, extirpation of the corpus allatum in the young nymph is followed by the appearance of a 'preadultoid' instar before the final diminutive 'adultoid' is produced (Scharrer, 1946). This presumably means that a certain amount of juvenile hormone remains in the blood from one stage to the next. There must normally be some provision for the elimination of this hormone.

It is possible, therefore, that the active removal of juvenile hormone by the corpus allatum is a general phenomenon in the metamorphosis of insects. What appears to be a 'metamorphosis promoting hormone' in the Diptera (Hadorn, 1941) may in fact be nothing more than 'inactivation of juvenile hormone'.

If we suppose that these two factors, cessation of secretion of juvenile hormone and active elimination of this hormone, differ in their relative importance in
Functions of the corpus allatum in Rhodnius prolixus (Hemiptera)

different insects, we may perhaps have the basis for a theory of metamorphosis applicable to all groups of insects.

The cessation of secretion of the juvenile hormone by the corpus allatum of Rhodnius, which is the chief factor that causes metamorphosis in the moulting 5th-stage nymph, is a temporary phase only. Once metamorphosis has taken place the corpus allatum begins once more to secrete the juvenile hormone. Since the juvenile hormone from the young nymphal stages will induce egg formation in the adult female and the secretion from the adult female will inhibit metamorphosis in the nymph, it seems highly probable that in Rhodnius, as was suggested by Pfeiffer (1945a) for Melanoplus, the juvenile hormone and the yolk forming hormone are identical.

If that is so, the hormone has quite different functions in the two stages. In the young moulting nymph it favours the intracellular system in the tissue cells which lays down nymphal structures (Wigglesworth, 1940). In the adult female it is necessary for the normal function of the follicular cells and the continued life and nourishment of the oocyte after the separation of the nutritive cords (Wigglesworth, 1936). Associated with the development of eggs in the adult female there is a much more rapid digestion of the intestinal contents. Whether this is a direct effect of the hormone on digestion and metabolism (Day (1943) and Pfeiffer (1945b) regard the ‘gonadotropic hormone’ as a ‘metabolic hormone’) or whether it is an indirect effect consequent upon the demands of the developing ovaries, has not been determined.* In the male it is necessary for the full activity of the accessory glands.

This dual function of what appears to be a single hormone recalls the multiple actions of thyroxin, which on the one hand has a general effect on metabolism, and on the other, has specific effects such as the induction of metamorphosis in the Amphibia.

SUMMARY

Two factors are involved in the control of metamorphosis in Rhodnius: (a) The corpus allatum of the 5th-stage nymph no longer secretes the juvenile hormone (inhibitory hormone). The latent imaginal characters can thus be realized, (b) The corpus allatum in the 5th-stage nymph, particularly in the later stages of moulting, actively favours the production of imaginal characters.

The evidence suggests that this activity (b) consists, not in the secretion of a metamorphosis promoting hormone favouring adult differentiation in the tissues directly, but in the elimination of the small quantities of juvenile hormone persisting in the blood and tissues.

If we suppose that these two factors differ in relative importance in different insects we may perhaps have the basis for a theory of metamorphosis applicable to all groups of insects.

* It may be worth putting on record that if the ovaries of the adult female Rhodnius are removed there is a hypertrophy of the corpus allatum—as was first shown by Thomsen (1942) in Calliphora and confirmed by Day (1943) in Lucilia although not in Sarcophaga. The normal corpus allatum of a fed Rhodnius adult measured 71 μ; in an adult from which the ovaries had been removed 101 μ.
V. B. Wiggleworth

The corpus allatum of the mature adult *Rhodnius* again begins to secrete the juvenile hormone; and the juvenile hormone of the 4th-stage nymph will induce egg development in the adult female. It is probable that the yolk-forming hormone and the juvenile hormone are identical.

The sequence in the secretory activities of the corpus allatum, and so the number of instars, is controlled by some other centre, perhaps in the central nervous system.

REFERENCES


EXPLANATION OF PLATE 1

Fig. 1. Unexpanded wing developed by 5th-stage nymph which retained its corpus allatum.

Fig. 2. Unexpanded wing developed by 5th-stage nymph deprived of its corpus allatum.

Fig. 3. Normal 5th-stage nymph.

Fig. 4. Normal adult.

Fig. 5. Small patch of nymphal cuticle on the abdomen of an adult *Rhodnius*, overlying the implanted corpus allatum.

Figs. 6-9. 5th-stage nymphs showing "adultoid" characters in varying degrees, following the implantation of corpora allata from late 5th-stage nymphs or young adults into 3rd- or 4th-stage nymphs (fuller explanation in text).

Fig. 10. 'Nymphoid' adult (explanation in text).

Fig. 11. 'Nymphoid' adult (explanation in text).

Fig. 12. 6th-stage nymph.

Fig. 13. 7th-stage adult; the same insect as fig. 12.
WIGGLESWORTH—THE FUNCTIONS OF THE CORPUS ALLATUM IN RHODNIUS PROLIXUS (HEMIPTERA)