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THE EFFECT OF JUVENILE HORMONE ON THE MATURATION OF THE OOCYTES IN THE COCKROACH, *LEUCOPHAEA MADERAE* (Fab.)

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ABSTRACT

The injection of juvenile hormone analogue or synthetic juvenile hormone into isolated abdomens of female *Leucophaea maderae* initiates the development of the oocytes. The hormone alone applied in single or multiple doses does not sustain the development, and degeneration begins before the oocytes reach half the maximal length. The incidence of degeneration is reduced in alletectomized females treated with juvenile hormone and in isolated abdomens that receive both juvenile hormone and corpora cardiaca. The hormone accelerates the growth of the oocytes in intact virgin females and in isolated abdomens implanted with the corpora allata-corpora cardiaca complex and oothecae are formed in a predictable length of time. The results suggest* that juvenile hormone must be present during most of the developmental period of the oocytes together with corpora cardiaca in order for development to be completed.

INTRODUCTION

Growing evidence supports the view that the juvenile hormone is involved in the regulation of all the major processes associated with the reproductive cycle in cockroaches. These processes include the synthesis of yolk proteins, the growth of the oocytes by the deposition of yolk (Brookes, 1969a; Engelmann, 1969), the activation of the colleterial glands (Willis and Brunet, 1966; Bodenstein and Shaaya, 1968; Shaaiya and Bodenstein, 1969), and the production of pheromones (Emmerich and Barth, 1968). In many other species of insects, a vital role is played by the neurosecretions emanating from the cells of the pars intercerebralis and the corpora cardiaca (CC) (review: Highnam, 1965). Most of the experiments designed to test for neurosecretory activity in cockroaches have been performed on animals in which the glands were not completely removed or destroyed. Abdomens of *Leucophaea maderae,* isolated from the anterior segments that contain the major endocrine centers, complete the development of the ovaries and form oothecae when supplied with corpora allata (CA) attached to a fragment of CC (Brookes, 1969b). Isolated abdomens have been used for some time to explore the effects of various preparations of juvenile hormone on protein synthesis. Although the hormone induces the synthesis of yolk proteins and initiates the growth of the oocytes (Brookes, 1969a), successful development of the ovaries does not take place when only the juvenile hormone is administered. The experiments described in this report show that resorption invariably follows the initial stages of oocyte development when juvenile hormone alone is administered to isolated abdomens; resorption is prevented or delayed when the CC are present, however.

MATERIALS AND METHODS

Procedures for the maintenance of the colony of *Leucophaea maderae*, amputations of abdomens from newly ecdysed females and measurements of the basal oöcytes have been described in detail (Chambers and Brookes, 1967; Brookes, 1969b). Basal oöcytes in isolated abdomens are almost always less than 1.0 mm long and do not grow unless CA or juvenile hormone are present. In this report, as in previous ones, oöcytes are scored as having begun the deposition of yolk when they are 1.1 mm or longer. No statistical analyses to determine the significance of difference in lengths of oöcytes have been made. In oöcytes where extensive resorption has taken place, so much variation occurs in the lengths of oöcytes within one set of ovaries that comparisons amongst animals on this basis have only limited meaning. Where some significance has been attributed to differences in length, the basis of the assumptions are explained.

The degree of abnormality of the oöcytes has also been difficult to score. For the most part, resorption has been described in the tables by the following terms: normal, no apparent abnormality; minor, less than 25% of the group with abnormal ovaries and the remainder with only a few abnormal oöcytes in each set of ovaries; moderate, 25 – 50% of the group with oöcytes in an intermediate or advanced stage of resorption or with most of the group showing some abnormal oöcytes in the ovaries; extensive, most of the group with extensive resorption but many of the oöcytes still large; and resorbed, most of the group with oöcytes reduced in size to that of nondeveloping oöcytes.

Juvenile hormone analogue (JHA) was prepared by a modification (Vinson and Williams, 1967) of the method of Law, *et al.*, (1966). Synthetic DL juvenile hormone (SJH) was a gift from Professor H. Röller. These materials were applied topically in 2 to 5 µl of acetone or mixed with olive oil and injected. Two or 2.5 µl of olive oil solutions were injected through the intersegmental membrane between the 6th and 7th abdominal segment with a 25 µl syringe equipped with a micro-dispenser (Hamilton Company). Corpora allata and corpora cardiaca were removed from adult females through an incision in the membrane at the dorsal region just behind the head. The organs were implanted just beneath the integument through a V-shaped flap cut into the 6th abdominal segment and sealed with wax.

RESULTS

Resorption of the basal oöcyte

Yolk deposition is initiated and the oöcytes begin to grow when juvenile hormone or one of its analogues is applied to the abdomens of females of *Leucophaea maderae*. As will be described in the following sections, yolk deposition is often followed by resorption and shrinking of the oöcytes. The normal, developing oöcyte is translucent, pale yellow green, and the surface appears divided into platelets (Fig. 1). The first indication of an abnormality is the appearance of opaque areas in the oöcyte. Subsequently, small semitransparent areas are formed and the platelike nature of the surface disappears (Fig. 2). The opaque areas appear as dense white patches within the oöcyte or just beneath the surface. Eventually the white patches consolidate and the remainder of the oöcyte is almost transparent (Fig. 3). Resorption is not uniform and

ovaries may contain normal oöcytes together with those showing all stages of yolk resorption. Later, the abnormal oöcytes begin to shrink in length and the transparent areas disappear. The resorbed oöcytes appear as balls at the end of the penultimate oöcyte and turn a reddish brown.

Abnormal eggs have not been found in the oötheca although oöthecae with less than a normal complement of eggs were an occasional occurrence.

The effect of juvenile hormone analogue on virgin females

Various amounts of JHA were topically applied to virgin females 5 days after imaginal ecdysis (Table 1). Ovarial development was initiated in all animals within 10 days of the application of 134 μg. Larger doses resulted in somewhat larger oöcytes and, with smaller doses, not all female responded in 10 days. Abnormalities were first observed in the oöcytes 20 days after application of 268 μg. Seventeen of the animals so treated had oöcytes in the early stages of resorption; that is, the oöcytes were opaque and slightly transparent. The number of abnormal oöcytes in each female was small, no more than 6 per pair of ovaries. Twenty-six days after a single application, oöthecae were found in three abdomens of a group of eight, three had large, normal oöcytes and in the other two, extensive resorption had taken place although the oöcytes were still large.

Table 1

Effect of Juvenile Hormone on Virgin Females

Treatment (μg)	Females (No.)	Growth period (Days)	Av. length of basal oöcytes (mm ± SD)	Females with developing oöcytes		Resorption
				(No.)	(Oötheca)	
134	15	10	1.62±0.42	15		Normal
201	7	10	2.66±0.33	7		Normal
268	15	10	2.16±0.54	15		Normal
268	24	20	3.37±0.79	24		Moderate
268	8	26	3.54±1.15	3	3	See text
2 x 268*	8	20	4.01±0.43	8		Normal
2 x 268*	13	25–40		3	9	Minor
Control	8	10	1.00±0.01	0		Normal
Control	8	28	2.13±0.89	8		Normal
Control	22	30	3.14±1.5	8		Normal

*Second application 10 days after the first.

When two applications of 268 μg were given 10 days apart, all eight of the animals treated had large, normal oöcytes 20 days after treatment. A group of 13 animals were given two applications of hormone as before and were observed for the formation of oötheca. Five aborted oöthecae with large, normal eggs within 27 days after treatment. A sixth aborted 9 days later. After 40 days, the remaining animals

were opened and the ovaries examined. Of the seven remaining females, three had fully formed oöthecae, one had large normal oöcytes and in two the oöcytes were abnormal. In one female, the oöcytes showed little or no development and she may have aborted a set, although these were not found in the container. Some of the females that had aborted an oötheca and those that retained an oötheca had penultimate oöcytes in the early stages of development. These were often found to be abnormal.

One group of eight animals received two injections of 165 μg of JHA. Two died, but the rest aborted oöthecae with large, normal eggs within 28 days. A second group of eight animals received a single injection of the analogue; two of them also died. After 28 days, two had aborted oöthecae. Two had oöthecae in the genital chamber, one had large, normal oöcytes and one had oöcytes in various stages of resorption.

The effect of juvenile hormone analogue on alletectomized females.

Females were alletectomized within 6 hours after imaginal ecdysis, and the first injection of JHA or olive oil was given 5 days later (Table 2).

Table 2

The Effect of Juvenile Hormone Analogue on Alletectomized Females

Treatment (μg)	Females (No.)	Growth period (Days)	Av. length of basal oöcytes (mm ± SD)	Females with developing oöcytes (No.)	Resorption
162	5	16	1.70 ± 0.56	4	Minor
162	5	26	1.38 ± 0.12	5	Normal
2 x 162*	4	26	3.09 ± 0.7	4	Normal
2 x 162*	3	34	2.9 ± 1.26	3	Moderate
2 x 162+	4	14	2.29 ± 0.65	4	Normal
3 x 162‡	5	26	3.43 ± 0.58	5	Normal
None	5	21	0.9 ± 0.06	0	Normal
None	5	31	1.09 ± 0.09	0	Normal

* 13 days apart

\+ 9 days apart

‡ 9 and 5 days apart

One group of 10 females was given a single injection of 162 μg JHA. Sixteen days later the ovaries in five of them were examined. In one of the animals, the oöcytes had not developed, two others had ovaries with a few abnormal oöcytes and in the remaining two, the oöcytes were completely normal. The other group of five was examined 10 days later. The oöcytes in all of these females were normal but very little growth had taken place. The length of the terminal oöcytes in these five females ranged between 1.17 and 1.50 mm, with an average of 1.38 mm.

A second group of nine females was given two injections 13 days apart. Two of them had to be discarded because they were injured when a water bottle leaked. No evidence of the formation of oöthecae appeared after 26 days, so four of the

remaining females were examined. The oöcytes were completely normal and ranged in length between 2.25 and 4.17 mm. The remaining three females were examined 8 days later. The ovaries in all three contained oöcytes in advanced stages of resorption. The largest eggs were 4.33 mm long.

The final group of 9 females received two injections 9 days apart. Four of them were examined after 14 days. The oöcytes were normal and the average lengths of the basal ones were 1.67, 1.83, 2.33, and 3.33 mm. The remaining females were given a third injection. Twelve days later, their ovaries were examined. All of the oöcytes were normal. Four females had oöcytes that were 3.4 mm or longer and in one they were 2.5 mm.

Table 3

The Effect of Juvenile Hormone Analogue on Isolated Abdomens
Surface Application

Treatment (µg)	Interval (Days)	Abdomens (No.)	Growth period (Days)	Av. length of basal oöcytes (mm ± SD)	Abdomens with developing oöcytes (No.)	Resorption
1 x 268		4	3	1.08 ± 0.2	2	Normal
1 x 268		10	6	1.28 ± 0.16	9	Normal
1 x 268		26	10	1.37 ± 0.32	24	Minor
1 x 268		7	15	1.73 ± 0.30	7	Moderate
1 x 268		8	20	2.29 ± 0.9	7	Extensive
1 x 268		8	25	1.05 ± 0.39	2	Resorbed
2 x 268	5	17	10	1.55 ± 0.26	14	Moderate
2 x 268	10	10	15	1.40 ± 0.41	9	Minor
2 x 134	5	8	11	1.17 ± 0.23	5	Minor
3 x 134	1	8	10	1.59 ± 0.34	8	Moderate
3 x 134	3	14	15	1.34 ± 0.25	12 (+1 dead)	Minor
5 x 134	3	7	17	1.77 ± 0.37	7	Normal
5 x 134	2	14	16	2.13 ± 0.73	12 (+2 dead)	Moderate
5 x 134	2	9	20	2.77 ± 0.26	5 (+4 dead)	Extensive
10 x 134	2	8	20	3.19 ± 0.23	3 (+5 dead)	Minor

The effect of juvenile hormone on isolated abdomens

The results of experiments in which concentrations comparable to those used with intact females were applied to isolated abdomens, are shown in Table 3. When a single dose of 268 μg was given topically, the ovaries in all but two of the abdomens began development within 10 days. Most of the oöcytes were normal but in only a few abdomens were they over 2.00 mm long. Resorption was moderate 15 days after the application, extensive after 20 days, and by 25 days, much of the yolk had been resorbed. A second application given 5 days after the first did not improve either the growth or the retension of the yolk, but when the second application was given 10 days after the first, degeneration was minor. Smaller doses applied sequentially at 1-, 3-, or 5-day intervals did not succeed in increasing the rate of growth. When the applications were dispersed at wider intervals the retention of yolk seemed to improve. Frequent applications had little effect on increasing the rate of growth but did increase mortality.

Table 4

The Effect of Juvenile Hormone Analogue on Isolated Abdomens-Internal Application

Treatment (μg)	Abdomens (No.)	Growth period (Days)	Av. length of basal oöcytes (mm)	Abdomens with developing oöcytes (No.)	Resorption
166	6	10	1.92	6	Minor
166	17	14	1.76	16	Moderate
166	10	15	2.46	9	Moderate
166	12	20	1.40	5	Extensive
166	17	25	1.73	8 (+6 dead)	Extensive
207	7	10	2.06	7	Moderate
207	7	15	3.07	5 (+1 dead)	Extensive
2 x 207*	8	15	2.50	5 (+1 dead)	Extensive
415	8	15	1.97	6 (+1 dead)	Moderate

*5 days apart

Ten days after 166, 207 or 415 μg of JHA were injected most of the abdomens had oöcytes that were over 2.00 mm in length (Table 4). About half of the abdomens had ovaries with normal oöcytes. After 15 days, many of the oöcytes were over 3.0 mm long but much variation occurrred within the ovary. The figures in Table 4 represent the average of the largest oöcytes found in an experimental group. Most of the oöcytes showed some signs of resorption; in many abdomens, resorption was advanced and only a few had completely normal ovaries. Development was not improved by two injections.

Table 5
The Effect of Synthetic Juvenile Hormone on Isolated Abdomens

Treatment (μg)	Abdomens (No.)	Growth period (Days)	Av. length of basal oöcytes (mm ± SD)	Abdomens with developing oöcytes (No.)	Resorption
1	17	10	1.29 ± 0.19	15	Minor
1	12	15	1.23 ± 0.23	6	Normal
1	7	25	0.96 ± 0.24	2 (+2 dead)	Minor
2 x 1*	14	10	1.43 ± 0.32	11 (+2 dead)	Minor
2 x 1+	18	25	1.75 ± 0.61	13 (+3 dead)	Minor
3 x 1*	13	20	1.75 ± 0.52	11 (+2 dead)	Moderate
5	8	10	1.57 ± 0.26	8	Minor
5	10	25	0.93 ± 0.04	0	Resorbed
2 x 5+	9	20	2.32 ± 0.86	6 (+3 dead)	Minor

*5 days apart *10 days apart

Yolk deposition was initiated within 10 days in 15 of 17 abdomens injected with only 1 μg of SJH (Table 5). Smaller amounts in single or multiple doses were without effect. With only 1 μg, growth of the oöcytes was not sustained and the data suggest that the yolk was gradually resorbed over a period of 25 days. Little evidence of resorption was seen in the oöcytes, however.

With two doses of 1 μg, only a minor incidence of resorption occurred but with only slight growth between 10 and 25 days. After three injections of 1 μg, the oöcytes were about the same average size at 20 days as they were at 25 days after two injections. A moderate incidence of resorption appeared, with 7 of 13 abdomens each containing a few abnormal oöcytes.

When 5 μg were injected, growth at 10 days was about the same as when 1 μg was used. Prolonged exposure to a single injection of this amount of hormone did not sustain the oöcytes. Twenty days after two injections of 5 μg, large oöcytes were found, three of the six living abdomens had oöcytes 2.75 mm or longer. A 30% mortality occurred in this group, however.

Comparable amounts of SJH applied topically failed to initiate development of the oöcytes in 10 to 15 days.

The effect of implanting endocrine glands together with the injections of juvenile hormone analogue in isolated abdomens

In the experiments shown in Table 6, endocrine organs were implanted alone or together with a single injection of 162 μg of JHA. The principal finding in these experiments was that abdomens implanted with CC responded to hormone treatment with far fewer abnormal oöcytes than had been found in those that had received hormone alone. Only one abdomen had abnormal oöcytes 15 days after receiving both CC and the analogue. The range in lengths, 1.33 to 3.75 mm, was about the same as in

those abdomens that had received the analogue alone. After 20 days, four abdomens were normal and the remaining four had less than four abnormal oöcytes each. In most of the abdomens, the oöcytes were over 3.0 mm long and, in two, they were over 4.0 mm. The results were not as good after 25 days. Three of the abdomens had normal oöcytes, but, in three of the others, many of the oöcytes were transparent. Resorption must not have started until the oöcytes were quite large, because most of them were over 3.0 mm long and many were over 4.0 mm.

Implantation of both CC and CA together with 162 μg of JHA resulted in the formation of oöthecae in four abdomens. In each of the remaining five, no more than four oöcytes showed signs of resorption. In all of these, the penultimate oöcytes were also in the early stages of yolk deposition, many showed the early indications of resorption.

Table 6

The Effect of Corpora Allata – Corpora Cardiaca and Juvenile Hormone Analogue on Isolated Abdomens

Treatment (μg)	Abdomens (No.)	Growth period (Days)	Av. length of basal oöcytes (mm ± SD)	Abdomens with developing oöcytes (No.)	Resorption
2 pr CC–CA	10	25	3.02 ± 0.46	8	Normal
2 pr CC	8	25	0.92 ± 0.11	0	Normal
162	8	15	2.39 ± 0.42	8	Moderate
162 + CC	8	15	2.43 ± 0.83	8	Minor
162 + CC	8	20	3.43 ± 0.90	8	See text
162 + CC	8	25	3.2 ± 1.14	7	See text
162 + CC–CA	9	25	4.12 ± 0.33	9	See text

Activation of the colleterial glands.

During the development of the ovaries, the colleterial or accessory glands become filled with a material that makes them large, turgid, and pale blue. The enlargement of the glands begins at about the same time that the oöcytes begin to increase in length. In the experiments performed during the course of this work, in intact females and in isolated abdomens, the activation of the glands was always observed where there were ovaries with developing oöcytes. The glands remained enlarged and blue during the advanced stages of resorption, but in those abdomens where the yolk was more or less completely resorbed, the glands were small and not blue. Occasionally glands were found that were large but milky, rather than blue. This condition was rare and could not be correlated with a stage of degeneration in the oöcyte.

DISCUSSION

Bell and Barth (1970) have shown that four major events associated with the reproductive cycle in *Byrsotria fumigata*–yolk protein synthesis, yolk deposition, activation of the colleterial glands, and pheromone production-- are all initiated by the

juvenile hormone in the absence of neurosecretory glands. In isolated abdomens of *L. maderae,* SJH and JHA likewise initiated the early stages of oöcyte development. The hormone induces the synthesis of yolk protein in the fat body (Brookes, 1969a) and growth of the oöcytes entails deposition of this material as yolk (Brookes, unpublished observations). Along with the growth of the oöcytes, the colleterial glands develop in a characteristic way. Isolated abdomens will produce oöthecae when implanted with CC-CA, but they failed to do so in response to single or multiple applications of juvenile hormone, and the oöcytes were eventually resorbed.

Under normal conditions, mated female *L. maderae* produce the first egg case, which contains 40 eggs, about 25 days after mating. Abnormal oöcytes are rarely found but, if the CA are removed during the period of vitellogensis, the eggs degenerate completely (Brookes, unpublished observations). The development of the ovaries is erratic in virgin females and oöcytes of all sizes are found even after 65 days (Roth and Stay, 1962). Virgin females of the species *B. fumigata* may oviposit, or the eggs may undergo degeneration. The eventual fate of the oöcytes in *Leucophaea* is unclear. Only two of a large number of virgin females dissected had degenerating oöcytes and 47 formed oöthecae prior to examination (Roth and Stay, 1962). The formation of the oöthecae in virgin *Leucophaea* begins 25 to 30 days after the topical application or injection of JHA. Some degenerating eggs were found in many of the females receiving a single topical application, but the incidence was reduced with two applications. The oöcytes do not develop in virgin females from which the CA had been removed within 6 hours after imaginal ecdysis. Growth was induced with JHA, but multiple injections were required to sustain the oöcytes. No oötheca were formed in 26 days.

The results suggest that juvenile hormone must be present during most of the period that the oöcytes are developing. A similar interpretation was presented by Bell and Barth (1970) on the basis of results obtained with *B. fumigata.*

The amount of hormone necessary to initiate the development of the ovaries in isolated abdomens of *L. maderae* was a function of the chemical structure and the mode of application. Growth seemed to depend on the presence of a minimal amount, and larger doses had little effect on the rate. The oöcytes began to degenerate between 10 and 15 days after a single application. Multiple doses of JHA applied topically and at appropriate intervals delayed the onset of degeneration. Multiple injections of SJH also delayed the onset of degeneration but the injection of the analogue did not. The amount of growth induced by the subsequent applications was not great and mortality increased amongst abdomens so treated.

Under normal conditions, oöcytes grow in excess of 5 mm before the formation of the egg case. In isolated abdomens implanted with CC-CA, the eggs are smaller, about 4.0 to 5.0 mm long at the time of oviposition. In all of the experiments where JHA or SJH alone were applied, oöcytes betweem 3.00 and 3.75 mm in length were found only occasionally and usually showed some signs of resorption. No oöcytes 4.00 mm or longer were found. This suggests that the incidence of degeneration may increase with the increasing size of the oöcyte. Degeneration may begin at any stage of development whenever the hormone becomes limiting. As long as the hormone is not limiting, growth continues until the oöcyte reaches a critical size when resorption increases.

A single injection of JHA is all that is required to bring about oviposition in virgin females with intact CC-CA and in isolated abdomens implanted with CC-CA. At

first glance, the improved growth may seem solely the result of additional hormone secreted by the CA. Considering that resorption rarely occurs in untreated virgin females and in implanted abdomens despite a very slow rate of growth, the oöcytes seem to respond to the titre of hormone produced by the CA. Some balance must exist between the titre and the size of the developing oöcyte. When the balance is upset by the administration of extraneous hormone, the oöcytes grow at an accelerated rate and, if the hormone titre becomes limiting as may occur when it is applied topically, resorption begins. If JHA were the only factor controlling the development of the oöcytes, however, better results would have been expected with multiple injections of JHA or SJH into isolated abdomens without CC-CA. Instead, some degeneration was apparent 10 days after the injection of one of several levels of JHA. Twenty days after, degeneration was in an advanced stage and could not be prevented by a second dose of hormone. Another mechanism must depend upon secretions from the CC, because abdomens that receive an implant of CC and a single injection of JHA contained oöcytes 3.0 and 4.0 mm long, most of which were normal 20 days after treatment. Even after 25 days, the amount of resorption was much reduced when compared with that in abdomens that had received JHA alone.

Neurosecretions have been implicated as controlling factors of the reproductive cycle of a number of different species of insects. Highman and his associates have argued that, in *Schistocerca,* neurosecretions control the synthesis of proteins (Hill, 1962) and CA the deposition of protein as yolk (Highman, *et al.,* 1963). Minks (1967), working with *Locusta,* has suggested that secretions from the CA modify protein synthesis so that yolk-specific proteins are produced. The induction of the synthesis of proteins specific to the yolk has been clearly shown in several species of cockroaches (Brookes, 1969a; Engelmann, 1969; Bell, 1969). A role for neurosecretions in cockroaches has not been demonstrated. Engelmann (1965) failed to prevent vitellogenesis by cauterizing the pars intercerebralis. The formation of oöthecae in isolated abdomens implanted with CA led to the conclusion that neurosecretions played no direct role in development of the ovaries (Brookes, 1969b). Davey (1968) has pointed out that complete isolation of the CA from the CC is difficult, if not impossible. Most implantations of CA in cockroaches, of necessity, include a fragment of the CC. This fragment can no longer be ignored.

Luscher (1968) showed that in *Nauphaeta cinera,* the CC delayed the degeneration of the oöcytes following the removal of the CA. The results presented here suggest that in *L. maderae* both JH and secretions from the CC are necessary for the successful completion of oöcyte development to the stage of oöthecal formation. The formation of oöthecae in alletectomized females has not been accomplished nor has resorption been prevented in isolated abdomens in the presence of CC. In both instances, the reason may be that the amount of JH applied is still insufficient. The abuse that isolated abdomens can take is limited, and increasing the number of injections increases mortality. Experiments are being continued with topical applications on isolated abdomens in the presence of CC and with alletectomized females.

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Freshly dissected normal and degenerating oöcytes:

Degenerating eggs were taken from isolated abdomens 15 days after the injection of 207 µg JHA.

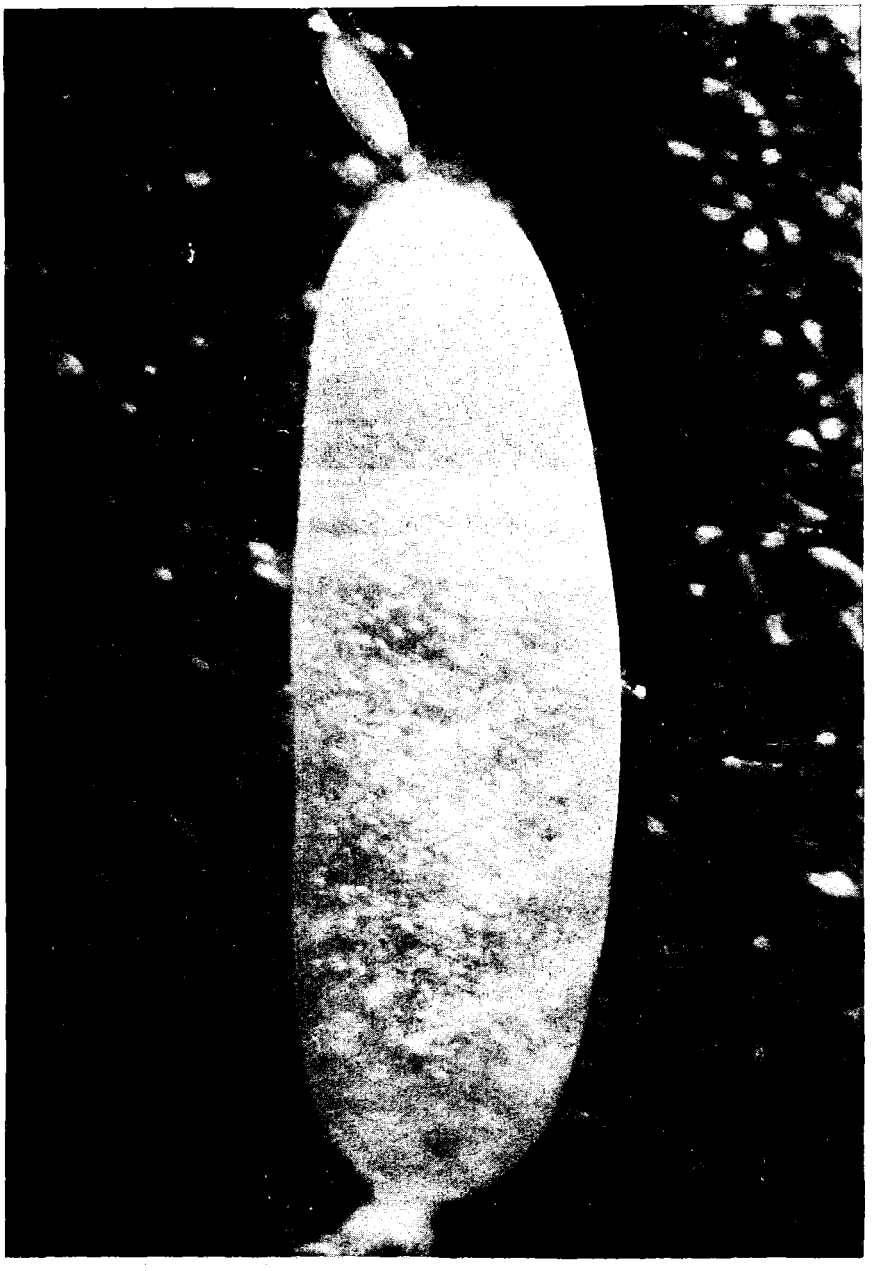

Fig. 1. Normal oöcyte, 3.5 mm long.

Fig. 2 Intermediate state of resorption, 3.85 mm long.

Fig. 3 Advanced stage of resorption, 3.05 mm long.

REFERENCES

Bell, W.J. 1969. Dual role of juvenile hormone in the control of yolk formation in *Periplaneta americana.* J. Insect Physiol. *15:*1279-1290.

Bell, W.J. and R.H. Barth, Jr. 1970. Quantitative effects of juvenile hormone on reproduction in the cockroach *Byrostria fumigata.* J. Insect Physiol. *16:*2303-2313.

Bodenstein, D. and E. Shaaya. 1968. The function of the accessory sex glands in *Periplaneta americana* (L.)--I. A quantitative bioassay for juvenile hormone. Proc. nat. Acad. Sci. U.S.A. *59:*1223-1230.

Brookes, V.J. 1969a. The induction of yolk protein synthesis in the fat body of an insect, *Leucophaea maderae,* by an analog of the juvenile hormone. Devel. Biol. *20:*459-471.

Brookes, V.J. 1969b. The maturation of the oöcytes in the isolated abdomen of the cockroach, *Leucophaea maderae.* J. Insect Physiol. *15:*621-631.

Chambers, D.L. and V.J. Brookes. 1967. Hormonal control of reproduction – I. Initiation of oöcyte development in the isolated abdomen of *Leucophaea maderae.* J. Insect Physiol. *13:*99-111.

Davey, K.G. 1968. The physiology of reproduction: some lessons from insects. In: "Insects and Physiology." Beament, J.W.L. and J.E. Treherne, (Eds.) American Elsevier Publishing Company, Inc., New York. pp. 351-364.

Emmerich, H. and R.H. Barth, Jr. 1968. Effect of farnesyl methyl ether on reproductive physiology in the cockroach, *Byrsotria fumigata* (Guerin). Z. Naturforsch. *23b:*1019-1020.

Engelmann, F. 1965. The mode of regulation of corpus allatum in adult insects. Archs Anat. microsc. *54:*387-404.

Engelmann, F. 1969. Female-specific protein: biosynthesis controlled by corpus allatum in *Leucophaea maderae.* Science *165:*407-409.

Engelmann, F. 1970. The Physiology of Insect Reproduction. Pergamon Press, New York.

Highnam, K.C. 1965. Some aspects of neurosecretion in arthropods. Zool. Jahrb. abt. Physiol. *71:*558-582.

Highnam, K.C., O. Lusis and L. Hill. 1963. The role of the corpora allata during oöcyte growth in the desert locust, *Schistocerca gregaria* Försk. J. Insect Physiol. *9:*587-596.

Hill, L. 1962. Neurosecretory control of haemolymph protein concentration during ovarian development in the desert locust. J. Insect Physiol. *8:*609-619.

Law, J.H., C. Yuan and C.M. Williams. 1966. Synthesis of a material with high juvenile hormone activity. Proc. nat. Acad. Sci. U.S.A. *55:*576-587.

Luscher, M. 1968. Oöcyte protection – A function of a corpus cardiacum hormone in the cockroach, *Nauphoeta cinerea.* J. Insect Physiol. *14:*685-688.

Minks, A.K. 1967. Biochemical aspects of juvenile hormone action in the adult *Locusta migratoria.* Arch. neerl. Zool. *17:*175-258.

Roth, L.M. and B. Stay. 1962. A comparative study of oöcyte development in false ovoviviparous cockroaches. Psyche, *69:*165-208.

Shaaya, E. and D. Bodenstein. 1969. The function of the accessory sex glands in *Periplaneta americana* (L.)- - II. The role of the juvenile hormone in the synthesis of protein and protocatechuic acid glucoside. J. exp. Zool. *170:*281-292.

Vinson, J.W. and C.M. Williams. 1967. Lethal effects of synthetic juvenile hormone on the human body louse. Proc. nat. Acad. Sci. U.S.A. *58:*294-297.

Willis, J.H. and P.C.J. Brunet. 1966. Hormonal control of colleterial gland secretion. J. exp. Biol. *44:*363-378.