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Studies on the Neurosecretory System in Apterygota

II. Development of the Corpus Allatum in *Ctenolepisma* and its Juvenile Action on the *Philosamia*-Pupa

By

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In the previous paper, the author has dealt with the histological and cytological properties of the corpus allatum and its link in the neurosecretory system of Japanese silverfish, *Ctenolepisma villosa* (YASHIKA, 1960).

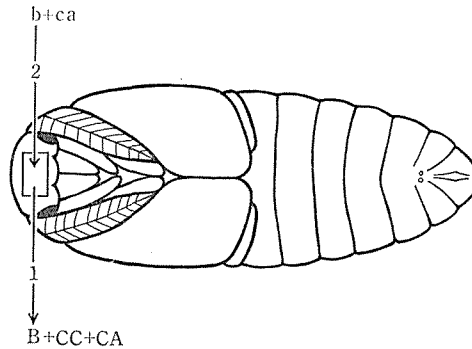
It was found that the corpus allatum of this insect is a small spherical body situated at the base of the maxilla and is innervated by two nerves originating from the neurosecretory cells in the brain and the suboesophageal ganglionic cells respectively. This position of the organ is so different from that of the corpus allatum in other pterygotous insects that it requires to be justified in other respects if this organ is truly the corpus allatum. The present paper is concerned with its organogenesis in embryology and functional activity in adult which was testified by experiment.

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Materials and Methods

Ctenolepisma can be reared on starched paper in a glass-bowl. Full-grown females lay eggs for about 2 weeks at the end of July in the vicinity of Osaka. As for the material for the study of organogenesis of the corpus allatum, eggs were daily collected and kept in a small glass-bowl and fixed at the adequate intervals in reference to the developmental stage. As a fixative, HUETTNER's modification of KAHLE's formol-alcohol-acetic acid mixture was used. Prior to fixation, puncturing was applied to the egg with a fine needle under a stereo-microscope to facilitate a quick penetration of the fixative. Materials remained for one or two days in the fixative. Sections were made at 5 micra and stained with DELAFIELD's haematoxylin.

In order to ascertain whether the organ in question is the corpus allatum, the implantation experiment was carried out together with the brains into the diapausing pupae of *Philosamia* in anticipation of finding its juvenile action on the metamorphosis of the recipient animal. The test pupae were made by means of extirpating the brain, corpora cardiaca and corpora allata within 5 hours after pupation. Such diapausing pupae were proved to remain unchanged for more than a year. Test animals were exclusively males, 1.9-2.0 grams in weight.



Text-fig. 1. Diagram showing the procedure of operation.

Arrow 1; removal of the brain, corpora cardiaca and corpora allata of *Philosamia*.
Arrow 2; subsequent implantation of 10 corpora allata and 10 brains taken from *Ctenolepisma*.

For the experiment, 10 corpora allata taken from the full-grown adults of *Ctenolepisma* were implanted together with 10 brains into each pupa of *Philosamia*. For the control, 2 to 10 brains from the same full-grown adults were implanted alone into a pupa similar to that used in the experiment. The brains and allata to be grafted were dissected out with fine needles in Lock's culture medium under a high magnification of a stereomicroscope. They were inserted deeply into the thorax of the test animal through the hole made on the head on the occasion of extirpating the brain and other organs, after removing the paraffin plug from the hole. Subsequent to implantation, the hole was sealed again with a paraffin plug. The test animals were kept in a humid glass-chamber at 25-28°C after operation.

Observation and Experimental Results

1. *Development of the corpus allatum.*

The rudiment of the corpus allatum begins to invaginate from the ectodermal layer between the mandibular and maxillary segments in the early embryonic

stage, i.e., at 12 days after the egg being laid. In this stage the rudiment is a small body 15 micra in diameter, and it consists of about 10 cells (Figs. 1a and 1b). As the development progresses, the rudiment of the corpus allatum begins to leave the ectodermal layer gradually and to move slightly towards the base of the maxilla (Fig. 2). In the later embryo ready for hatching, the rudiment separates itself completely from the ectodermal layer but stays at the base of the maxilla (Fig. 3). The number of the component cells does not increase by this stage, but in the adult it counts about 50 cells, as is already mentioned in the previous paper. So the mitotic division has to take place after hatching, during the nymphal stages. That the corpus allatum increases the number of its constituent cells in the postembryonic stage is easily acceptable in reference to the finding described by SCHARRER and VON HARNACK (1958) in *Leucophaea*.

The corpus allatum in *Ctenolepisma* locates at the base of the maxilla even in adult, as is already described also in the previous paper. This means that the migration of the rudiment towards the oesophagus should not take place in any stage up to the adult. This point differs much from the case in the pterygotous insects in which the conspicuous migration occurs from the origin to the final position of the organ.

2. Transplantation of the corpora allata.

Ten brains isolated from the adults of *Ctenolepisma* were implanted together with or without 10 corpora allata into each brainless diapausing pupa of *Philosamia*.

In 7 individuals out of 10 hosts in the former experimental series, the imaginal differentiation was restrained evidently in each of them: i.e., the original pupal cuticle was separated from the body surface on the 7-10th day after implantation, so that it was easily shed with a small forceps to expose the new pupal cuticle to the view (Table 1). The new cuticle was coloured brown and just similar to the original one, except for the wings that were white, although they were in pupal form (Fig. 4a). In addition, the section of the new integument revealed that there was no sign of the imaginal differentiation in both of the cuticle and the hypodermis (Fig. 4b).

Table 1.

Series	Number of hosts	Results	
		re-pupation	adult formation
Experimental	10	7	3*
Control	14	0	14

* Development of the wings was delayed markedly, so that these moths should be called imperfect adults.

The remaining 3 individuals in the experimental series performed the imaginal differentiation at 20 to 25 days after implantation (Table 1). But this differentiation was subnormal in some respects, i.e., the body was covered by many scales and hairs which indicated the imaginal colour-pattern, but the wings were still white in spite of being covered with some scales (Fig. 5).

Fourteen animals in the latter control series performed, without exception, a complete imaginal differentiation at 20 to 25 days after implantation, regardless of the number of implanted brains (Table 1). The colour-pattern and the number of the scales and hairs were quite similar to those of the normal moth (Fig. 6).

Discussion

In the pterygotous insects, it is a well-established fact that the corpus allatum develops from the ectodermal layer between the mandibular and maxillary segments and migrates towards the oesophagus during the subsequent development as its name implies (TOYAMA, 1902; PFLUGFELDER, 1937). The developmental process of this organ in *Ctenolepisma* is found to be essentially the same as the finding of previous workers, but it differs much in that the migration of the organ towards the oesophagus is checked after it is separated from the ectodermal layer. No reasonable explanation is provided concerning why and how this migration is suppressed in *Ctenolepisma*, but till the time when the same situation is found in other primitive insects belonging to Apterygota and Pterygota to allow us a comparative study, it will be anticipated that the organ in *Ctenolepisma* indicates the primitive form in insects.

We have repeatedly informed that the brain in lepidopterous insects secretes the hormone that can stimulate the prothoracic glands so as to liberate the molting hormone from them by means of transplanting the active brain from other individuals and even from other species into the diapausing pupae of *Luehdorfia* as well as of *Philosamia* artificially induced by extirpation of its own brain before the critical period for adult formation (ICHIKAWA, NISHITSUTSUJI and YASHIKA, 1955; ICHIKAWA and NISHITSUTSUJI-Uwo, 1957, 1959).

In the present control series, all of the brainless pupae of *Philosamia* that received the brains from *Ctenolepisma* were also caused to develop into imaginal form. This indicates that the brain hormone of the apterygotous insect exerts also the stimulating action upon the prothoracic gland of the pterygotous insect. Moreover, it is noteworthy that only 2 brains coming from tiny *Ctenolepisma* can secrete the hormone enough to activate the prothoracic glands of a large pupa of *Philosamia*.

There are several information that the diapausing pupae can molt again into second pupae by the conjoint action of the molting hormone from the prothoracic glands and the juvenile hormone from the corpora allata (WILLIAMS, 1959; ICHIKAWA and NISHITSUTSUJI-Uwo, 1959; ICHIKAWA and TAKAHASHI, 1959). In the present experiment, when 10 brains and 10 corpora allata of *Ctenolepisma*

were implanted into each diapausing *Philosamia*-pupa, about two-thirds of the experimental pupae extramolting into second pupae, whereas the control pupae which received 2-10 brains alone gave rise to the moths without exception. From these results of experimental and control series it is safe to say that the implanted corpora allata from *Ctenolepisma* can restrain the host from differentiating into a moth.

Thus, it is clearly demonstrated that the corpus allatum specified by the histological and embryological examinations of *Ctenolepisma* can secrete actually the juvenile hormone.

Summary

1) The corpus allatum of *Ctenolepisma* develops from the ectodermal layer between the mandibular and maxillary segments in the early embryonal stage. It never migrates to the lateral side of the oesophagus, but remains at the base of the maxilla even in the full-grown worm. It consists of about 10 cells through the larval stages, but increases to some 50 cells up to the time when the worm becomes full-grown.

2) Ten corpora allata and 10 brains of *Ctenolepisma* were implanted together into a diapausing pupae of *Philosamia* whose brain, corpora cardiaca and corpora allata were removed previously. Seven individuals out of 10 recipients extramolting into second pupae, while the remaining 3 individuals proceeded to the imperfect imagines. These results indicate clearly that the corpus allatum of *Ctenolepisma* can secrete the juvenile hormone even in the body of different species.

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Explanation of Plate I

- Fig. 1 a. Longitudinal section of an early embryo, showing the rudiment of the corpus allatum. B, brain; L1, L2 and L3, thoracic limbs; T, tail; Y, yolk-granule; A and P represent the anterior and posterior parts.
- Fig. 1 b. Enlargement of a part indicated in Fig. 1a. CA, corpus allatum; MX, maxilla; MN, mandible; AN, antenna; B, brain.
- Fig. 2. Longitudinal section of an embryo with eyes faintly coloured. Corpus allatum is leaving the ectoderm. CA, corpus allatum; MX, maxilla; MN, mandible; LA, labium.
- Fig. 3. Longitudinal section of an embryo just before hatching. Corpus allatum is situated at the base of the maxilla. CA, corpus allatum; MX, maxilla; MN, mandible.
- Fig. 4 a. Re-pupated specimen induced by implantation of 10 brains and 10 corpora allata. Brown colour appeared on the pupal cuticle except wings.
- Fig. 4 b. Section through the abdomen of a second pupa, showing the new pupal integument and hypodermis. No sign of the imaginal differentiation. CH, new pupal cuticle with a brown exocuticle; H, hypodermis.
- Fig. 5. Moth provided with underdeveloped wings, caused by implantation of 10 brains and 10 corpora allata from *Ctenolepisma*.
- Fig. 6. Perfect moth caused by implantation of 2 brains from *Ctenolepisma*.

