Comparison between the brains of the newly hatched larva and the imago of *Pieris brassicæ.*

By

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(With 4 fig.)

Introduction.

Although there are numerous papers dealing with the embryology and the metamorphosis of insects and also some which compare the nervous system of the larva and that of the imago, I have been unable to find in any work a complete comparison between the inner structure of the brain in the larva and the imago of a holometabolic insect. The only attempts to compare the nervous system of the caterpillar and the imago of butterflies which I have been able to find are in the papers of BRANDT ('77 and '79).

BRANDT compared the exterior structure of the nervous system of the larva and the imago of several species of butterflies and stated that a concentration of the larval ganglia takes place during the growth (Fig. 1). But he did not give any account of the changes taking place in the interior of the brain during the metamorphosis. It must, however, be of a special interest to know what parts of the brain of the full-grown insect can be found in the larva and if there are perhaps some centers in the larva, which are not found in the imago. The caterpillar and the butterfly live in a very different manner and also differ in the whole organisation of the head, the body and the appendages. In order to find out this supposed difference in the brain I have sectioned several brains of the larva and the imago of *Pieris brassicæ*.

As is well known, there is a very great difference between the larva and the imago of this animal both regarding their manner of living and their organisation. This difference of organisation corresponds to a quite different manner of feeding and moving. The caterpillar crawls about on the leaves of the cabbage and voraciously consumes them, whereas the butterfly flies among the flowers, sucking their honey. It is obvious that these different manners of feeding and moving must correspond to senses of vision, smell, taste, and touch of a very different type, and it is only natural that a special development of the senses and the sense-organs should be associated with a special development of the different centers of the brain.

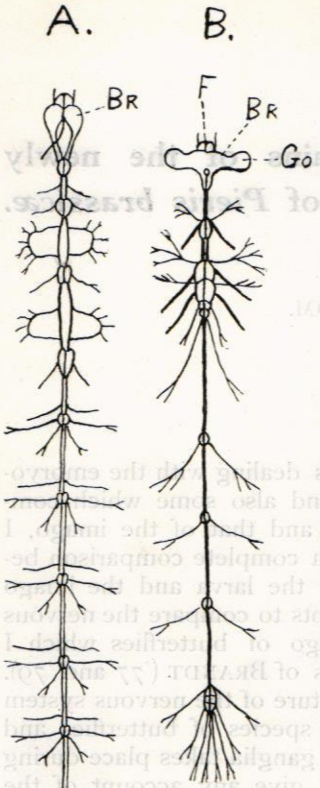

Fig. 1. The nervous system of a full-grown larva (A) and of the imago (B) of *Pieris brassicæ*. From BRANDT. *Br* = brain. *F*=frontal ganglion. *Go*=optic ganglion.

The brain of the butterfly.

The latest papers dealing with the brain of full-grown butterflies are written by BUXTON ('17) and BRETSCHNEIDER ('20—21). The most specialised parts of the adult brain (Fig. 2) are the optic centers, the central body, the protocerebral bridge, the mushroom bodies with their stalks in the protocerebron, and the olfactory glomerulæ in the deuterocerebron. The optic centers and the olfactory glomerulæ are connected with the optic and the antennular nerves, the other parts of the brain being chiefly association centers and not especially concerned with any peripheral nerves.

The optic centers (I, II, III, Fig. 2) in all insects consist of three masses of neuropil, surrounded by small ganglion-cells, which possess very little of plasma but are rich in chromatin. The mushroom bodies (corpora pedunculata) of the brain of most insects consist of the same kind of cells, which send their dendrites into the calyces (glomeruli-masses) and their neurites into the stalks (*S*, Fig. 2; compare KENYON '97!). According to this author the central body (*Cb*, Fig. 2) also possesses special ganglion cells, and as I have found in crustaceans ('24) that the protocerebral bridge even in these animals is connected with small ganglion cells, it is probable that the protocerebral bridge also in insects (*P*, Fig. 2) possesses the same connection.

The ganglion cells of the central body and the protocerebral bridge, however, do not form distinctly circumscribed areas of the ganglionic cover and thus never form especially prominent parts of the brain. The glomerulæ of the olfactory center (*Ag*, Fig. 2) are of a globular form, consisting of dense neuropil masses, connected with ganglion cells, which, in decapod crustaceans, are small and rich in chromatin but, in butterflies, more resemble the average ganglion cells.

The development of the brain in an insect with incomplete metamorphosis.

Comparing the complicated structure of the adult butterfly brain described above with the much simpler brain of the larva

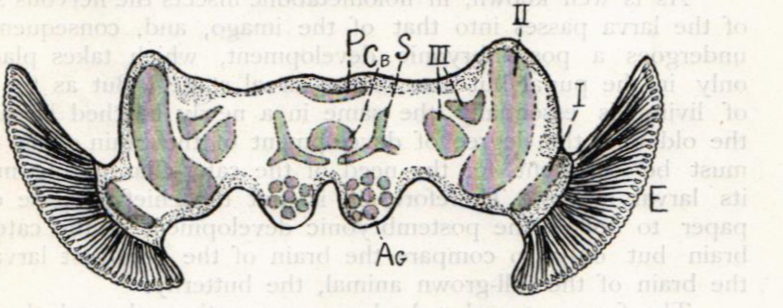

Fig. 2. Diagram of the brain of *Pieris brassicæ*, viewed from the anterior side. *Ag*=Glomeruli olfactorii. *Cb*=central body. *E*=aggregated eyes. *P*=protocerebral bridge. *S*=stalks of mushroom bodies. *I*, *II* and *III*=the first, second and third optic center (optic mass).

one must ask: »How much of the complicated sensory and associative centers of the butterfly can be found in the brain of the larva?» In this connection it may be of some interest to take notice of what is known about the development of the brain of an insect which has an incomplete metamorphosis, namely *Mantis religiosa*.

According to VIALLANES ('91) the ectodermal stripes which give origin to the central nervous system, coalesce one with the other along the medial line and in their anterior part form three ganglions, the proto-, deutero- and tritocerebron.

The lateral part of the protocerebron gives origin to the optic ganglion; the median one joins with the opposite part forming the corpora pedunculata (mushroom bodies), the protocerebral bridge and the central body.

The deuterocerebral ganglions likewise coalesce along the median line and communicate through a supraoesophageal commissure, whereas the tritocerebral ganglions communicate through a suboesophageal commissure. The neuropil of the deuterocerebron develops into the glomeruli olfactorii, whilst the tritocerebron remains relatively small, according to the non-development of appendages in this segment of insects.

Now — because the caterpillar is a larval stage of the butterfly, it must begin its ganglionic development somewhere along the above mentioned path, and it is the aim of this paper to ascertain at which point this event takes place.

The brain of the young caterpillar.

As is well known, in holometabolic insects the nervous system of the larva passes into that of the imago, and, consequently, it undergoes a postembryonic development, which takes place not only in the pupal but also in the larval stage. But as the mode of living is essentially the same in a newly hatched larva as in the old one, the degree of development of the brain of the former must be sufficient for the need of the caterpillar during most of its larval stages. Therefore, it is not the chief purpose of this paper to follow the postembryonic development of the caterpillar brain but only to compare the brain of the youngest larva with the brain of the full-grown animal, the butterfly.

The figures 3 and 4 A show cross-sections through the brains of two caterpillars which were about 2 ½ millimetres in length and less than 24 hours old. At this stage the brain is relatively big compared with the space within the head. The two halves of the protocerebron are not yet united thoroughly along the median line but only communicating through a small opening in the separating neurilemma-sheath (Fig. 4 A).

The deuterocerebral ganglions, which contain no glomerulæ, lie in the anterior part of the brain as small rounded neuropil-masses at the lateral sides of the oesophageal connectives.

The antennal nerves enter the deuterocerebral ganglions at the anterior side of the brain, whereas the optic nerves enter the brain at its posterior lateral sides, though the eyes themselves lie at some distance before the brain. At the point, where the united nerves from the three simple larval eyes (described by PANKRATH '90 and HESSE '01) enter the protocerebron, there is a small lateral neuropil mass which represents the optic center (*Sm*, Fig. 3). This neuropil mass does not possess the dense structure, which distinguishes the optic masses of the adults, and its cover of ganglion cells is of the same kind as in the rest of the brain.

The opening in the median neurilemma-sheath does not only let the commissure of the protocerebron pass, but also permits the antennal commissure to pass through its lower part.

The average position of the central body in crustaceans and insects is between the commissural bundles of the protocerebron. In this portion of the larval brain there is, at this stage, nothing which indicates the future central body. I was not able to find any traces of the protocerebral bridge either.

The ganglion-cell layer of the brain seems to be of the same kind everywhere, and I was thus unable to find any traces of the cells of the mushroom bodies. Nevertheless I discovered some dense parts in the neuropil on both sides of the commissure which, according to their position and form, must represent the first indications of the stalks of the mushroom bodies (Fig. 4 A).

The brain of the youngest caterpillar is thus much simpler than the brain of the butterfly. The former completely lacks the protocerebral bridge and the central body. The optic center contains only one optic mass instead of three in the butterfly, and this one is of much simpler structure. The only representatives of the mushroom bodies are the small stalks, and the antennal lobes lack the glomerulæ, on account of the slight development of the antennæ and the olfactory hairs.

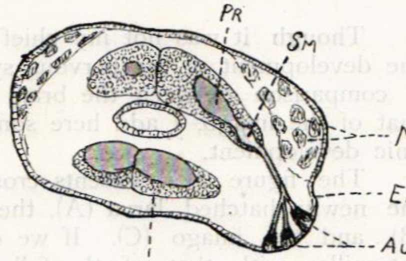

Fig. 3. Oblique cross-section through the brain of a newly hatched larva of *Pieris brassicæ*. *Au*=simple eyes. *Ep*=hypodermis. *M*=muscles. *Pr*=protocerebron. *Sm* = optic mass. *Us* = suboesophageal nerve-center.

Whereas the higher crustaceans and all insects have three optic centers and the associative centers just now enumerated, the same centers in the larva are only slightly differentiated and the reflex arcs in the brain of the latter animal consist of a smaller number of neurons. Consequently, the possibilities for a certain stimulus to change its way along one or another reflex path are much smaller in the caterpillar than in the butterfly. Thus the brain of the larva with its imperfectly developed association-centers reflects the simpler mode of food-procuring and motion, the simpler kind of responding to outer stimuli, and, in general, the simpler actions characteristic of this animal.

If we compare the brain of the caterpillar with the brain of other arthropoda, it is evident that no full-grown arthropod possesses so simple a brain as the young larva of the butterfly. Even the higher annelids have a more highly developed brain, though, according to HOLMGREN ('16), it consists of only one neuromer. But this ganglion, the »proto-deuterocerebron» of HOLMGREN, contains, in higher annelids, well-developed mushroom bodies with glomerulæ and stalks, antennal glomerulæ and a commissure (»die Nuchalkommissur»), representing the future central body of arthropods. As to the optic center in annelids, it is of the same morphological structure as in the larva of *Pieris* and contains only one optic neuropil mass.

The post-embryonic development of the brain.

Though it was not my chief intention to give an account of the development of the nervous system of the caterpillar but only a comparison between the brain of the newly hatched larva and that of the imago, I add here some remarks upon the postembryonic development.

The figure 4 represents cross-sections through the brains of the newly hatched larva (A), the old larva, ready for suspension (B), and the imago (C). If we compare the brain of the young caterpillar with that of the fullgrown (A and B), we notice that the changes are not restricted to the structure but also affect the form of the brain. At the same time they show that the head has grown faster than the brain, the space between the cuticula and the brain in the old larva being much wider than in the younger one.

Regarding the inner structure the most noticeable differences are perhaps shown by the optic ganglions. In this region the neuroblasts soon — during the first days — form real imaginal discs (*D*, Fig. 4 B), which give origin to the complicated optic centers of the adults. It is very characteristic that, in butterflies, the optic centers begin their development earlier than the aggregated eyes, whereas in the diptera the eyes appear at the same time as their optic centers.

A histological research of the developing optic ganglions in butterflies is done by SANCHÉZ ('20), and the embryology of their eyes is described by JOHANNSEN ('93). A description of the development of the optic centers in *Culex pipiens* will appear in a future paper of me (»Über die Augen und Sehzentren von Turbellarien, Anneliden und Arthropoden»), but, in butterflies, I was unable to follow in detail the metamorphosis of the optic centers. According to SANCHÉZ ('20) and my own, more detailed observations in *Culex* the larval eyes and their centers degenerate and the optic imaginal discs form a quite new center for the aggre-

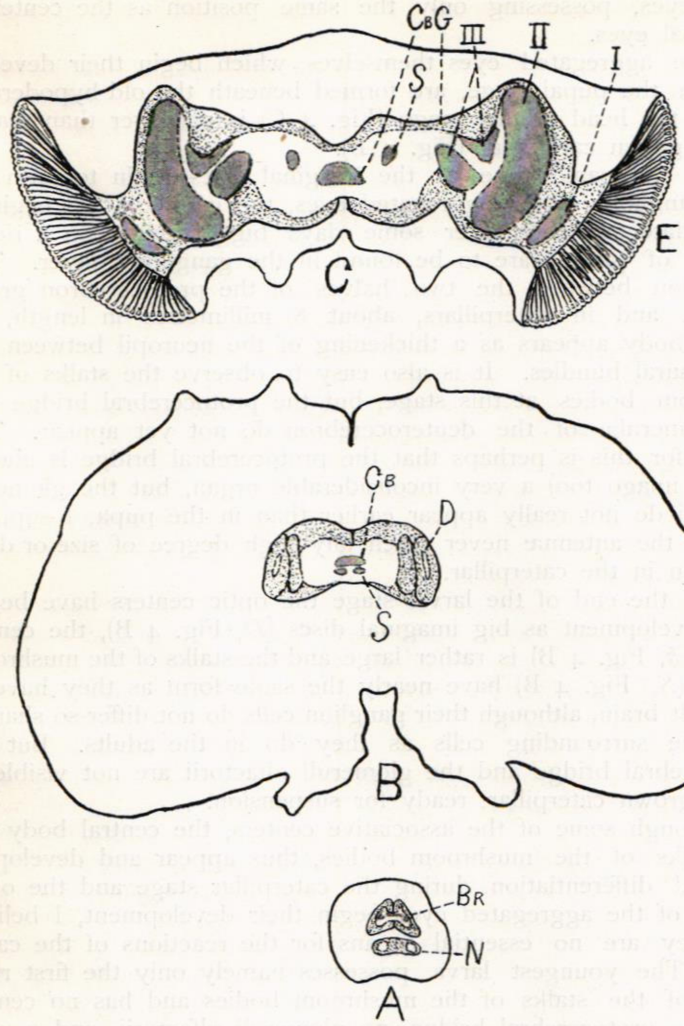

Fig. 4. Cross-sections through the heads of a newly hatched larva (*A*), a fullgrown larva (*B*) and the imago (*C*) of *Pieris brassicæ*. The sections are cut through the region of the protocerebral commissures and the central body and are drawn with aid of micro-projection. The sections *B* and *C* are equally magnified, whereas the section *A* is somewhat too big. *Br*=brain. *Cb*=central body. *D*=imaginal discs of the aggregated eyes. *E*=aggregated eyes. *G*=ganglion cell layer. *N*=suboesophageal nerve-center. *S*=the stalks of the mushroom bodies (the figure represents the medial, cross-sectioned parts of the stalks). *I*, *II* and *III*=the first, second and third optic mass.

gated eyes, possessing only the same position as the center of the larval eyes.

The aggregated eyes themselves, which begin their development in the pupal stage, are formed beneath the old hypodermis, so that the head of the imago (Fig. 4 C) is narrower than that of the full-grown caterpillar (Fig. 4 B).

At the same time as the imaginal discs begin to form the optic ganglions of the aggregated eyes, the ganglion cells begin to differentiate, so that after some days bigger cells with a richer amount of plasma are to be found in the ganglionic layer. The connection between the two halves of the protocerebron grows broader, and in caterpillars, about 8 millimetres in length, the central body appears as a thickening of the neuropil between the commissural bundles. It is also easy to observe the stalks of the mushroom bodies at this stage, but the protocerebral bridge and the glomerulæ of the deuterocerebron do not yet appear. The reason for this is perhaps that the protocerebral bridge is always (in the imago too) a very inconsiderable organ, but the glomeruli olfactorii do not really appear earlier than in the pupa, I suppose because the antennæ never reach any high degree of size or differentiation in the caterpillar.

At the end of the larval stage the optic centers have begun their development as big imaginal discs (*D*, Fig. 4 B), the central body (*Cb*, Fig. 4 B) is rather large and the stalks of the mushroom bodies (*S*, Fig. 4 B) have nearly the same form as they have in the adult brain, although their ganglion cells do not differ so sharply from the surrounding cells as they do in the adults. But the protocerebral bridge and the glomeruli olfactorii are not visible in the fullgrown caterpillar, ready for suspension.

Though some of the associative centers, the central body and the stalks of the mushroom bodies, thus appear and develop in size and differentiation during the caterpillar stage and the optic centers of the aggregated eyes begin their development, I believe that they are no essential organs for the reactions of the caterpillar. The youngest larva possesses namely only the first rudiments of the stalks of the mushroom bodies and has no central body, no protocerebral bridge, no glomeruli olfactorii, and a small optic center, consisting of only one optic mass. Besides, the manner of behaviour seems to be almost the same during the whole of the caterpillar stage, and even in the full-grown caterpillar these organs have by far not completed their development. The optic ganglions do not even communicate with the ectodermal thickenings of the aggregated eyes, which do not appear until the pupal stage.

Summary.

The chief purpose of this paper is to make a comparison between the brain of the newly hatched larva and that of the imago of *Pieris brassicæ*. The result of the investigation is that the brain of the caterpillar is, morphologically and structurally, of a much simpler form than that of the imago, differing from the latter in the following respects:

1. The original boarder between both the protocerebral and the deuterocerebral ganglions is almost wholly retained in the larva, only being perforated in order to let thin commissures pass between the ganglionic halves.

2. The ganglion cell layer is of a uniform structure, all cells being small and rather rich in chromatin.

3. The central body and the protocerebral bridge do not appear in the newly hatched larva, whereas the stalks of the mushroom bodies are feebly developed.

4. The optic centers of the simple eyes of the caterpillar only contain one optic mass of a uniform structure, whereas the optic centers of the butterfly have three highly specialised optic masses.

5. The deuterocerebral ganglions form slight projections on the lateral sides of the oesophageal connectives, and do not contain any morphologically distinguishable glomeruli olfactorii.

6. The slight development of the associative and sensory centers of the caterpillar brain has resulted in its reflex-arcs being of a much simpler kind than those of the imago. This corresponds to the simple manner of behaviour of the caterpillar when feeding and moving.

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