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The Central Nervous System of *Leptinotarsa decemlineata* (Say) with Special Consideration of the Brain *

Centralny układ nerwowy *Leptinotarsa decemlineata* (Say) ze szczególnym uwzględnieniem mózgu

Центральная нервная система *Leptinotarsa decemlineata* (Say) с особенным учетом мозга

INTRODUCTION

The central nervous system of *Leptinotarsa decemlineata* was partly described, in terms of general anatomy, by Bruneteau (1928) in the imago, and by Bounhiol (1928) in the larva. These investigations concerned only the general morphology of the central nervous system. Because of its great economic importance, the Colorado beetle is the object of detailed and manifold studies. More exact investigations into the central nervous system, and especially on the histology of the brain, seem therefore to deserve attention.

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I. MATERIAL AND METHODS

Living specimens of various developmental stages of *Leptinotarsa decemlineata* were used. Of the larval form, only the last stage, L4, was studied, the younger larvae being too small. For morphological investigations the central nervous system of the individual developmental stages was prepared in 75 per cent alcohol. Several methods of fixation

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and staining the brain tissues were used in the histological part of the studies. The material was fixed in Bouin's fluid or in 97 per cent ethyl alcohol. Fixation in 10 per cent formol gave unsatisfactory results. All preparations were mounted in paraffin, the melting point of which was between 50 and 52°C, and cut with a crank microtome of the Minot type; the sections were 4 to 6 microns thick. The preparations were then stained, chiefly with iron-haematoxylin according to Heidenhain; some preparations were additionally stained with 0.5 per cent solution of eosin, which gave good results. A number of preparations were impregnated with silver nitrate according to Cajal.

II. EXTERNAL STRUCTURE OF THE CENTRAL NERVOUS SYSTEM

1. The larva

In the central nervous system of the larva there can be distinguished: the supraoesophageal ganglion (brain), the suboesophageal ganglion, three thoracic ganglia, and eight abdominal ganglia (Fig. 1). In the sche-

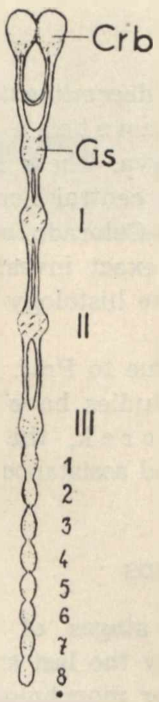

Fig. 1. Central nervous system of the L4; Crb — brain, Gs — suboesophageal ganglia, I, II, III — thoracic ganglia, Ga (1—8) — abdominal ganglia.

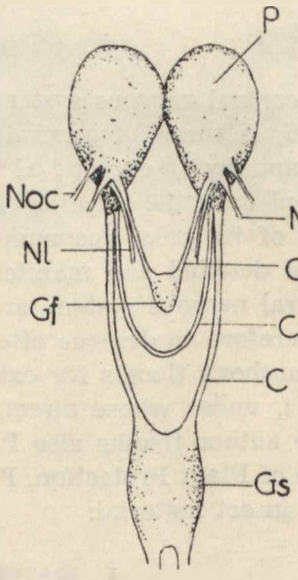

Fig.2. Brain of the larva L4 seen frontally; P — *protocerebrum*, Noc — *nervi ocelarii*, *Nl* — labral nerve, Gf — frontal ganglia, Na — *nervus antennalis*, Cf — frontal commissure, Ct — tritocerebral commissure, C — circumoesophageal connective, Gs — suboesophageal ganglia.

matic drawings published by Beier (1927), the nervous system of the Colorado beetle most resembles that of *Chrysomela menthastri* Suffr.

In comparison with the whole head, the brain of the larva is very small. It consists of two pear-shaped hemispheres united by a small common area (Fig. 2). The thicker part of the protocerebral bulging is bent posteriorly, the thinner one (deutocerebrum and tritocerebrum) anteriorly. This can be seen in Fig. 3, which gives a lateral view of the brain of the larva L4.

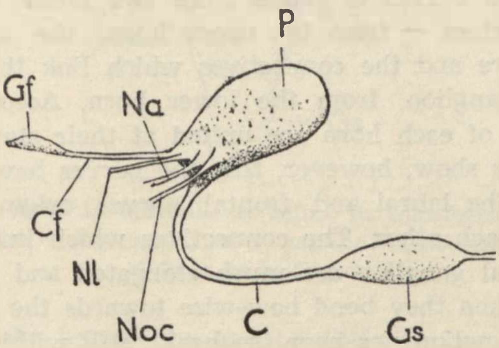

Fig. 3. Brain of the larva L4 seen laterally; abbreviations as in Fig. 2.

The following pairs of nerves originate from the anterior part of the brain:

1. The ocellar nerve, growing in a more upward and lateral direction (Fig. 2, 3, Noc).

2. The antennal nerve *(nervus antennalis)*, thinner than the foregoing one; it originates from a point situated a little lower and more central (Fig. 2, 3, Na). Both these nerves originate from the area where the deutocerebrum is located.

3. The frontal commissure, thicker than the previous ones, takes its origin from a point located even more centrally (Fig. 2 and 3, Cf); it unites with the homologous structure of the other half of the brain, and at the point of their union there is a small ganglion of the stomodeal system, the frontal ganglion (Fig. 2, 3, Gf).

4. The labral nerve originates in the closest vicinity to the frontal commissure (Fig. 2, 3, NI), so that it seems to be its lateral branch. It is the thinnest of all the nerves so far mentioned.

The ocellar nerve in the larva of the Colorado beetle is well developed, but the presence of this nerve in the larva of *Oryctes nasicornis* is disputable. Michels (1880) and Grome (1957) could not find this nerve, whereas Jawłowski (1936) observed its existence in the last-mentioned species.

The tritocerebrum becomes narrower and passes into very thick circumoesophageal connectives which link the brain with the suboesophageal ganglion; (Fig. 2, C). From the same spot originates the tritocerebral commissure (Fig. 2, 3, Cf), which runs under the oesophagus and connects the right and the left part of the tritocerebrum. Bounhiol (1928) did not find this commissure in the larva of the Colorado beetle; nevertheless, he does not deny its existence, but stresses the difficulties he had in observing it. The same author states that all the previously mentioned nerves originate from two horns: the ocellar and antennal nerves stem — from the upper horn, the labral nerve, the frontal commissure and the connectives which link the brain with the suboesophageal ganglion, from the lower horn. According to Bounhiol the nerves of each horn are united at their starting point. More exact observations show, however, that the nerves have different starting points; only the labral and frontal nerves originate from points located close to each other. The connectives which link the brain with the suboesophageal ganglion are much elongated and initially have an anterior course; then they bend bow-wise towards the rear, so that the suboesophageal ganglion lies near the brain, still within the head, close to the border line between it and the thorax (Fig. 3).

The first thoracic ganglion (Fig. 1, I) is located close to the suboesophageal ganglion because the connectives which link these two ganglia are short. On the other hand, connectives linking the thoracic ganglia are much elongated (Fig. 1). The abdominal ganglia are half the size of the thoracic ganglia and the first abdominal ganglion is located in the immediate vicinity of the thoracic ganglion. In the whole ventral nerve cord the ganglia lie close to each other, and their connectives are very short and interconnected. The ventral nerve cord resembles therefore a row of oval beads strung on a thread.

This description of the central nervous system refers to the last stage of the larva, L4, when it is still feeding. After it has descended into the soil, there occur some changes in the structure of the central nervous system in connection with the beginning metamorphosis. The changes concern above all the brain, from the lateral parts of which the optic lobes develop, initially in the form of small bulgings directed frontally and a little laterally. Since the optic lobes grow more in a forward direction, the brain at this stage, when seen from above, has the form of the letter „U"; in the pupa it is straightened and the optic lobes assume a more lateral direction, so that in the imago the brain resembles a very wide open letter „V" (Fig. 12).

From the lateral parts of the optic lobes develop the optic nerves (Fig. 4, No), which in the larval stage L4 are two or three in number.

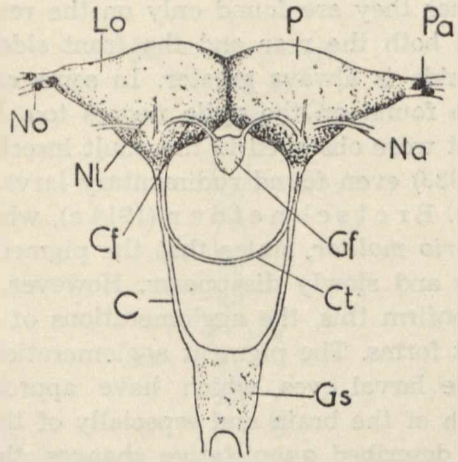

Fig. 4. Brain of the larva L4 immediately before its transformation into the pupa; No — *nervi optici*, Lo — *lobi optici*, Pa — pigment agglomerations. Other abbreviations as in Fig. 2.

These nerves ramify repeatedly, and on their surface there are agglomerations of a dark pigment in the form of small, round spots (Fig. 4, Pa). In young pupae these spots are usually situated on the optic lobes at the base of the optic nerves; and only a small number of them can be found on the optic nerves (Fig. 5 Pa). In older pupae as well as in the adult insects the spots are located on the optic lobes at the base of the optic nerves (Fig. 11, Pa); their distribution shows great individual

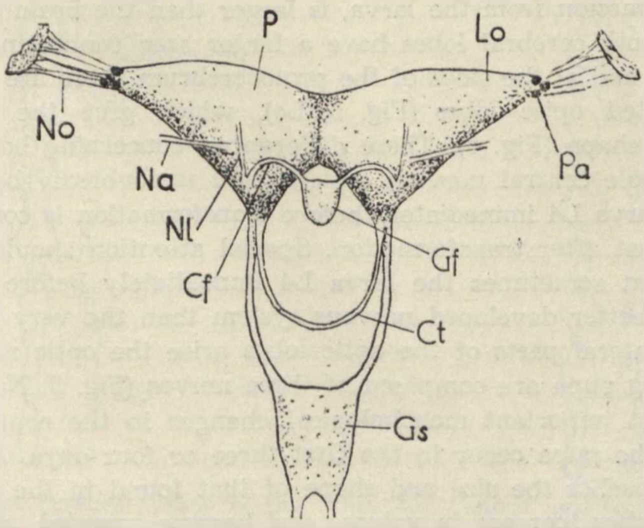

Fig. 5. Brain of the one-day-old pupa; abbreviations as in Figs. mentioned before.

variations. Sometimes they are found only on the rear side of the optic lobe, sometimes on both the rear and the front sides; the number of spots on the rear side is always greater. In some cases, even in the imago, they can be found on the optic nerves too. Similar agglomerations of the pigment were observed in the adult insect by Jawłowski (1936). Holste (1923) even found rudimentary larval eyes in the adult *Dytiscus marginalis*. Bretschneider (1914 a), who saw these agglomerations in *Tenebrio molitor*, states that the pigment is transferred to the compound eyes and slowly disappears. However, the present investigations fail to confirm this, the agglomerations of the pigment being found even in adult forms. The pigment agglomerations might represent the remnants of the larval eyes, which have approached its surface, owing to the growth of the brain and especially of the optic lobes.

Apart from the described quantitative changes, there is both in the brain and in the whole ventral nerve cord an increase of their volume. Marked individual variations of the central nervous system of the larva can also be noted. This concerns the whole central nervous system, but especially the abdominal ganglia. In some cases the latter are much elongated and oval, in others more spherical and less distant from each other. This is probably connected with the later shortening of the nerve cord.

2. The pupa

It is the pupa which shows the greatest metamorphosis of the central nervous system. The brain of the young pupa, immediately after its transformation from the larva, is larger than the brain of the larval stage L4; both cerebral lobes have a larger area connecting them with each other, and at the sides of the protocerebrum there are better developed, pointed optic lobes (Fig. 5, Lo), which give the whole brain a different shape (Fig. 5). These differences, concerning both the brain and the whole central nervous system, will undoubtedly be very small when the larva L4 immediately before transformation is compared with the pupa just after transformation. Special attention should be paid to the fact that sometimes the larva L4 immediately before transformation has a better developed nervous system than the very young pupa. From the lateral parts of the optic lobes arise the optic nerves, which in the young pupa are composed of three nerves (Fig. 5, No).

The most important morphological changes in the central nervous system of the pupa occur in the first three or four days. At that time the brain reaches the size and shape of that found in the adult insect. The optic lobes increase in volume and become rounded, and the optic nerves develop, so that after four days their number increases to six

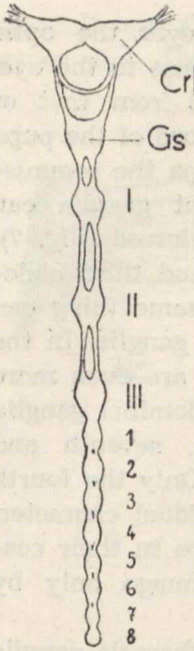

Fig. 6. Central nervous system of the pupa immediately after transformation;

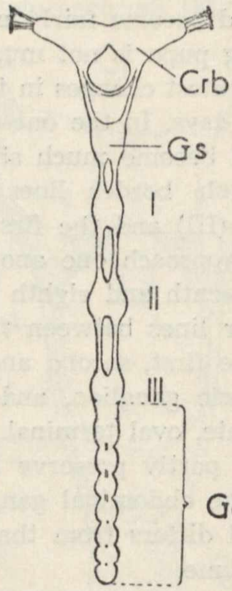

Fig. 7. Central nervous system of the one-day-old pupa

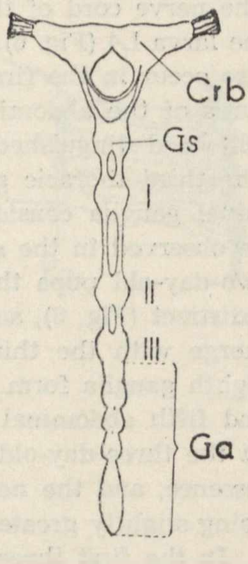

Fig. 8. Central nervous system of the two-day-old pupa

A b b r e v i a t i o n s as in Fig. 1.

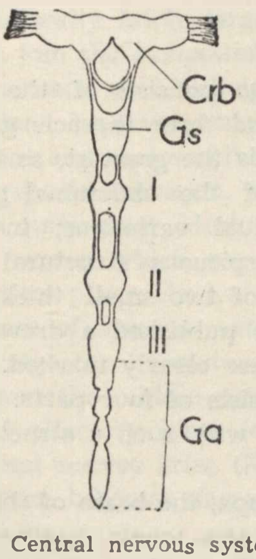

Fig. 9. Central nervous system of the three-day-old pupa

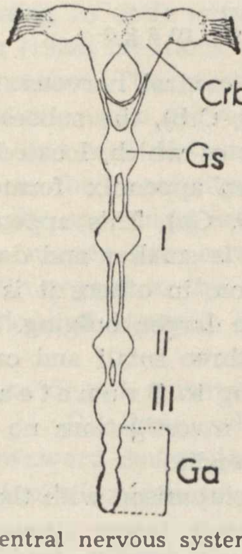

Fig. 10. Central nervous system of the imago

A b b r e v i a t i o n s as in Fig. 1.

(Fig. 9). In proportion as they approach the compound eyes, the optic nerves ramify repeatedly and become fairly numerous close to the eye. The nerve cord of the young pupa is not much different from that of the larva L4 (Fig. 6). The greatest changes in the nerve cord of the pupa also occur in the first three days. In the one-day-old pupa the commissures of the abdominal cord become much shorter; eight ganglia can still be distinguished, but their border lines become blurred (Fig. 7). The third thoracic ganglion (III) and the first, second and third abdominal ganglia considerably approach one another. The same thing can be observed in the sixth, seventh and eighth abdominal ganglia. In the two-day-old pupa the border lines between the ganglia are even more indistinct (Fig. 8), so that the first, second and third abdominal ganglia merge with the third thoracic ganglion, and the sixth, seventh and eighth ganglia form a separate, oval terminal ganglion. Only the fourth and fifth abdominal ganglia partly preserve their individual character. In the three-day-old pupa the abdominal ganglia advance in their coalescence, and the nerve cord differs from that in the imago only by being slightly greater in volume.

In the first three days the connectives between the thoracic ganglia also become shorter; the same is true of the connectives which link the supraoesophageal (Crb) and suboesophageal (Gs) ganglia. Only the commissures between the first (I) and second (II) thoracic ganglia remain considerably elongated. The tritocerebral commissure (Ct), on the other hand, also undergoes shortening.

3. The imago

The central nervous system of the imago consists of the brain (Fig. 10, Crb), the suboesophageal ganglion, and three thoracic ganglia, the last of which, located in the metathorax, is the greatest, as it possesses an appendix formed by the fusion of the abdominal ganglia (Fig. 10, Ga). This appendix presents individual variations; in some cases it is smaller and does not show any conspicuous structural differentiation, in others it is larger and consists of two small thickenings and one larger bulging. Bruneteau (1928) published a drawing in which three small and one large thickening are clearly marked. Thus, according to Bruneteau, the appendix consists of four parts. In the present investigations no specimen was found with such a structure of the appendix.

In comparison with that of the larva and pupa, the brain of the imago is much larger, though it does not fill the whole head capsule (Fig. 11), in which there is a great number of muscles and much fat. The brain has the form of a roller and extends from one eye to the other. It is slightly narrower in the middle, and has two bulgings in the upper part. This is the protocerebrum (Fig. 11, 12, P), from which de-

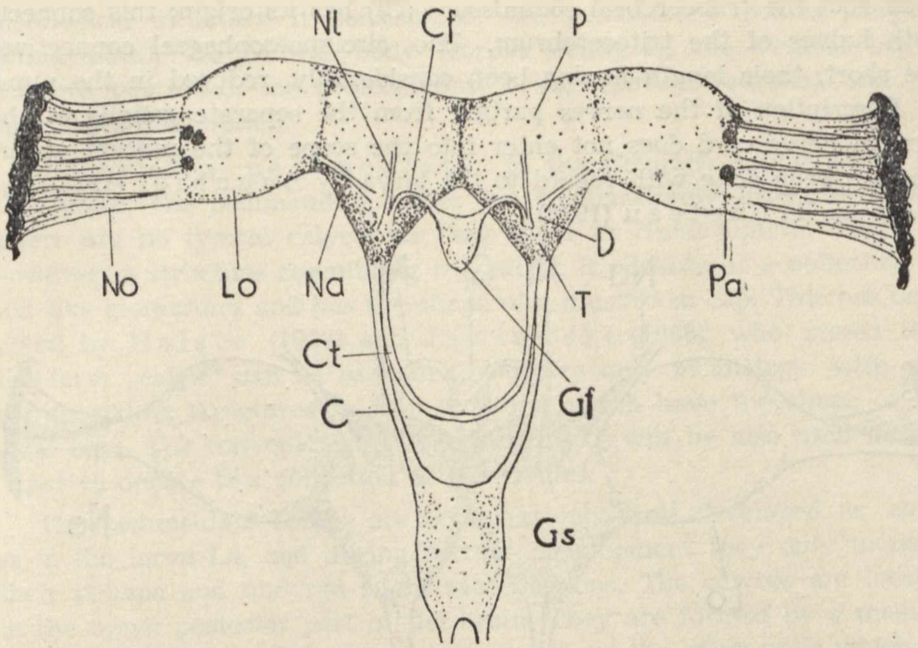

Fig. 11. Brain of the imago seen frontally; D — deutocerebrum, T — tritocerebrum. Other abbreviations as in Figs. mentioned before.

part laterally fairly large optic lobes (Lo) ending in optic nerves (No), which join the compound eyes. B r u n e t e a u (1928) mentions six optic nerves, each of which is divided into two branches. The present investigations, however, show that the number of the optic nerves is not constant and varies between four and six, and that each of them undergoes repeated division, so that their number in the proximity of the eye is quite great. Most branches derive from the uppermost and lowermost nerves, which are thicker. All the optic nerves are arranged in a vertical plane. As has been already said with regard to the larva, at the base of these nerves there are accumulations of pigment, which in the imago can be variously arranged.

From the middle part of the protocerebrum depart downwards the paired olfactory lobes (deutocerebrum) (Fig. 11, D), from which the antennal nerves arise (Na). In its further downward course the deutocerebrum becomes narrower and passes into the tritocerebrum (Fig. 11, 12, T).

From the tritocerebrum there arises the thick frontal commissure, at the base of which departs the rather thin labral nerve (Nl). The tritocerebrum becomes narrower and passes into circumoesophageal connectives (C) which link the brain with the suboesophageal ganglion; at their root the tritocerebral commissure (Ct) has its origin; this connects both halves of the tritocerebrum. The circumoesophageal connectives are short, their length having been considerably reduced in the pupa.

Description of the nerves parting from the separate ganglia of the ventral nerve cord does not enter into the scope of the present paper; this has been done with regard to the larva by Bounhiol (1928) and imago by Bruneteau (1928).

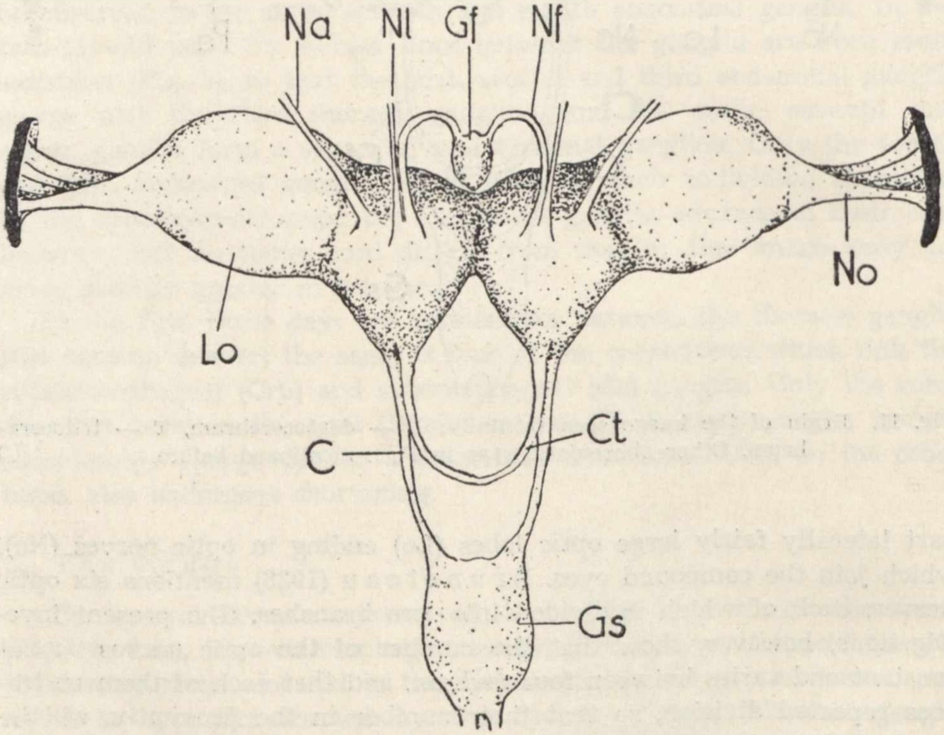

Fig. 12. Brain of the imago seen from below; abbreviations as in Figs. mentioned before.

III. HISTOLOGICAL STRUCTURE OF THE BRAIN

The analysis of the histological structure of the brain in various developmental stages of the Colorado beetle shows that in the larva the nerve cell bodies, which lie at the peripheries of the brain, predominate, while the fibre mass (neuropile) is less developed. During the metamorphosis the nerve fibres develop intensively, so that in the imago the ratio, cell bodies: neuropile, becomes more favourable for the latter.

1. The protocerebrum

The protocerebrum is the best developed part of the brain. In its histological structure it consists of: the pedunculate bodies *(corpora pedunculata)*, the central body *(corpus centrale)*, the ventral bodies *(corpora ventralia)*, the protocerebral bridge *(pons cerebralis)*, and the optic lobes *(lobi optici)*.

a. Corpora pedunculata. In the Colorado beetle, as in all *Coleoptera*, the pedunculate bodies are comparatively little developed. There are no typical calyces as they occur in *Hymenoptera*. There is, however, a structure resembling the calyx; it consists of a collection of rod-like glomerules and has the shape of a mushroom cap. This has been noted by Holste (1923) and Jawłowski (1936), who stated that the term „calyx" can be used in *Coleoptera* only in analogy with the corresponding structures in *Hymenoptera*, which have the shape of typical cups. For convenience, the term „calyx" will be also used in this paper to denote this collection of glomerules.

The pedunculate bodies are comparatively well developed as early as in the larva L4, and during further development they only increase their volume and undergo slight modifications. The calyces are located in the upper posterior part of the brain. They are formed by a mass of glomerules (Phot. 1, Cg), over which there are the calyx cells which lie in the external layer and form the posterior convexity of the brain. In the larva L4 they are not much different from other cells of the brain, but in the imago they acquire some distinctive features (Fig. 2, Ccl). In the larva the glomerules of the calyx are very small. In the course of the development of the insect the calyx increases and its glomerules become larger. In the imago the glomerules have a roller-like shape and are arranged in two groups (Phot. 2, Cg). This division, however, is not very distinct and can be observed only in the anterior and posterior part of the calyx.

One of the more important connections of the calyx glomerules is the antenno-globular tract, which is very thick and can be seen already in the larva (Phot. 3, Tagl). There are also connections between the calyx glomerules and the optic lobes or the central body. From the calyx depart fibres forming the pedunculus, which in the larva does not show any differentiation (Phot. 1, Pd). In the imago the pedunculus is divided into two parts (Phot. 2, Pd), which immediately below the calyx unite into one pedunculus. This division is not very conspicuous, and both parts, as can be seen in Phot. 2, are very close to each other. Initially the pedunculus runs downwards, then it bends forwards knee-wise and ramifies into two stalks. One of them, the frontal one, runs upwards and forwards. In the larva this stalk becomes narrower before it enters the cell layer, but in the layer itself it has a characteristic bulb-like thickening (Phot. 4 and 5, R). In the imago (Phot. 6), besides the bulb-like thickening, there arises from the stalk an additional ramification which runs laterally and posteriorly, closely approaching the calyx glomerules. This ramification shows a division into three parts (Phot. 7, R). The second stalk, termed the median root, runs towards the centre, and approaches, under the central body, the median root of the other half of the brain. In the adult insect the median root is more differentiated; running under the central body a little more anteriorly, it becomes thicker and characteristically divides into two parts (Phot. 7 and 8, B). In the larva the structure of the median root is not so complex; it becomes complicated in the pupa.

The function of the pedunculate bodies is still obscure. They are usually regarded as centres of association. Vowles (1955) divides the pedunculate bodies of the bee into two parts. To the calyces and the anterior stalk he attributes an associative function; the pedunculus and the median stalk are said to act as motor centres.

b. The central body *(corpus centrale)*. In the Colorado beetle the central body is very well developed, but in the larva L4 only its rudiments can be found. It is very thin and elongated laterally, thus having the shape of a spindle. It has a fairly simple, glomerular structure. In the course of metamorphosis the central body increases its volume and undergoes differentiation. When the larva L4 has descended into the soil to undergo metamorphosis, the central body becomes more egg-shaped and shows a division into two parts. Hanström (1928) states that in older larvae of *Coleoptera* the central body has the same form as in the adult insect. This statement is true as far as the division into two characteristic parts, already existing in the larva, is concerned. With regard to the structure and structural complexity, the central body of the larva, and even of the younger pupa, differs from that of the imago. These data seem to agree with the observations of Jawłowski (1936), who found only rudiments of the central body in the larvae of *Coleoptera*. In view of the fact that the development of the central body is synchronized with the formation of the optic lobes, Bretschneider (1914 a) advances the hypothesis that it is an important centre of the compound eyes. The definitive central body has a typical structure and is comparatively large (Phot. 11, Cc). The rule which says that the size of the central body is in inverse proportion to the size of the pedunculate bodies finds here its full confirmation.

In the imago the central body consists of two elements. The upper part, kidney-shaped, is more like an ordinary neuropile in its structure. The lower, oval part has a typical structure of dark-stained glomerules. Both elements of the central body adhere closely to each other. No ventral tubercles, present in other orders of insects, could be found; the peculiar knots which are seen in some sections and are situated posteriorly under the central body seem to be nothing but the ends of the median roots of the pedunculate bodies, thus having nothing in common with the ventral tubercles.

c. T h e v e n t r a l b o d i e s *(corpora ventralia)*. The ventral bodies lie on both sides of the central body, over the antennal glomerules and a little more centrally. They are fairly well developed in the larva L4, in which their structure is that of an ordinary neuropile (Phot. 10, Cv). During further development their structure becomes more complex, so that in the imago their frontal parts consist of bulb-like glomerules (Phot. 12, Cv). Their posterior parts are lobular and rather homogenous (Phot. 13 and 14, Cv). In the upper parts of the ventral bodies there are small, dark-stained glomerules (Phot. 13 and 14, Cvg). From all these elements of the ventral bodies depart fibres which connect both ventral bodies (the first commissure, Phot. 13, Ccv). This commissure runs just under the central body.

Some investigators, as B e i e r (1927), H o l s t e (1923), or B r e t s c h n e i d e r (1914a), regard the ventral bodies as a part of the deutocerebrum; others, as V i a l l a n e s (1887) or J a w ł o w s k i (1936), link them with the protocerebrum.

B r e t s c h n e i d e r states that the complexity of the ventral bodies is in inverse relation to the development of the pedunculate bodies.

d. *Pars intercerebralis*. *Pars intercerebralis* is a part of the brain located between the pedunculate bodies and the central body (Phot. 9 and 11, Pi), i.e. in the upper median part of the protocerebrum. H o l s t e (1923), B r e t s c h n e i d e r (1914a) and J a w ł o w s k i (1936) have already drawn attention to the large cells occurring there. Now we know that these are the neurosecretory cells (Phot. 9 and 11, Cn). (H a n s t r ö m and C a z a l, according to W i g g l e s w o r t h, 1954). From these cells departs a pair of crossing nerves which innervate *corpora cardiaca*. They appear in all developmental stages of the Colorado beetle. In Photograph 15 such a nerve (Nc) is seen in the larva L4.

In the *pars intercerebralis* is also located the protocerebral bridge *(pons cerebralis)*. During metamorphosis it undergoes, like the central body, far-reaching changes. In the younger larva L4 it is very thin and slightly bent upwards like a horseshoe (Phot. 3, Pc). It is slightly thickened at the ends and very thin in the middle, where it consists of a few fibres only. It develops quickly during metamorphosis; in the last moments of the larva L4 it already resembles the bridge of the adult insect and has the shape of a rather thick, plaited ribbon resembling the letter M. Its ends are directed downwards and slightly posteriorly. Photograph 16 shows the protocerebral bridge (Pc) of a very young pupa.

Bretschneider (1914a) is of the opinion that, like the central body, the protocerebral bridge is a centre of activity for the compound eyes because its development is parallel with that of the optic lobes.

e. *Tuberculum opticum. Tuberculum opticum* is located in the front part of the protocerebrum, a little aside from the end of the anterior stalk of *corpora pedunculata* (Phot. 21, To). It was first described by Viallanes (1887), and Jawłowski (1936) first found it in *Coleoptera*. In the larva L4 *tuberculum opticum* could not be found; in the young pupa its rudiments could be observed (Phot. 17, To). It is a small, oval body connected with the *medulla interna* by a nerve tract (Tm). In the adult form *tuberculum opticum* consists of two parts, a fact noticed by Jawłowski (1936). In the Colorado beetle the upper part of *tuberculum opticum* has a structure resembling the ordinary neuropile (Phot. 18, Ton); the lower part consists of glomerules (Phot. 18, Tog).

f. The optic lobes *(lobi optici)*. The Colorado beetle has fairly well-developed compound eyes. Accordingly, the optic lobes are of considerable size. They do not occur in the brain of the larva; instead, there are small optic masses (Phot. 3, 5, 10, Op) which lie at the sides of the protocerebrum. They are composed of small condensations of the neuropile substance, which is surrounded by a great number of dark-stained neuroblasts (Phot. 3, 5, 10, N). This condensation of the neuropile has a distinct connection with the protocerebrum (Phot. 3). The development of the optic lobes begins in the larva L4 after its descent into the soil. The original optic mass (neuropile) increases intensively, and towards the end of the L4 stage a small neuropilar plate *(lamina ganglionaris)* appears on the external side of this mass (Phot. 19, Lg). At the same time on the internal side of the original optic mass a third optic mass appears *(medulla interna)*, so that in the young pupa, and sometimes already in the larva L4, there are present three elements of the optic lobes *(lamina ganglionaris, medulla interna*, and *medulla externa)*. During this process the number of neuroblasts decreases slowly, and there appear the slightly smaller cells of the globuli. In the first days of the pupa, the optic lobes and all their elements increase considerably. The *medulla externa* increases the most quickly and finally reaches the form of a large, oval body. The growth of the *medulla interna* is also fast; in the four-day-old pupa it is already divided into two distinct parts, which Jawłowski (1936), following the example of Sanchez, calls

„Foco ovoideo" and „Foco laminar". In the young pupa there is a distinct connection between the *medulla interna* and the optic tubercle (Phot. 17, Tm). In the adult insect this tract sends off a branch which runs downwards in the direction of the deutocerebrum; its further course could not be ascertained (Phot. 20, Tx).

In the immediate vicinity of the *medulla interna* there is in the imago a small body of a glomerule-like structure, with distinct glomerules (Phot. 12, Co). Jawłowski (1957) observed a thickening of the neuropile near the *medulla interna* of the bee and supposes that this might be a structure analogous to that described by Hanström (1940) in *Petrobius* as *corpus opticum*. In the Colorado beetle, these bodies, as compared with those described by Hanström, lie nearer the *medulla interna;* they have a distinctly glomerular structure.

2. The deutocerebrum

The deutocerebrum lies under the protocerebrum and its lobes adhere to that part of the latter where the ventral bodies are located. In the front part of the deutocerebrum there are ball-shaped bulgings known as olfactory lobes *(lobi olfactorii)*. They consist of antennal glomerules surrounded by large nerve cells. As mentioned before, the olfactory lobes send off the antennal nerves. In the young larva L4 the deutocerebrum is very rudimentary, and the antennal glomerules are small (Phot. 10, 3, and 5 Lol). This is connected with the rudimentary state of the antennae in this developmental stage. During the further development of the insect the olfactory lobes grow larger, and their glomerules increase their mass. In the imago the antennal glomerules are comparatively large (Phot. 12, Lol). The antennal glomerules are distributed in the whole olfactory lobe, but they become much larger and more densely grouped near the surface. In the centre of the lobe they are smaller and more distant from each other, while the space between them is filled by a substance of the structure of the ordinary neuropile. Of the more important connections there should be mentioned those which connect the deutocerebrum with the calyces of the pedunculate bodies, and the connection between the two olfactory lobes (2nd commissure) which runs above the oesophagus. Jawłowski (1948) found sex differences in the structure of the *lobus olfactorius* of *Hymenoptera* and *Blattaria*, but he failed to observe such differences in *Saltatoria* (1953). Similarly, the present writer could not find any sex differences in the structure of the olfactory lobe of the Colorado beetle.

3. The tritocerebrum

This is the smallest part of the brain and lies under the deutocerebrum. Jawłowski (1936) found in *Coleoptera* small tritocerebral glomerules. In the larva of the Colorado beetle the tritocerebrum is very small and consists of a completely undifferentiated neuropile. In the pupa there appear tiny glomerules, in the imago they increase a little, but they are still very small and cannot be compared with the smallest antennal glomerules.

RESULTS

1. The most essential changes which occur in the brain during metamorphosis begin at the moment when the larva descends into the soil and end in the four-days-old pupa.
2. During metamorphosis the changes in the central nervous system occur so quickly that a single day can play a decisive part.
3. The shortening of the ventral nerve cord occurs in the young pupa in the first three days.
4. The pedunculate bodies are quite well developed towards the end of the last larval stage and already possess the essential elements; during metamorphosis they undergo only slight modification.
5. In the imago the anterior stalk of the pedunculate body has a characteristic branch, which runs laterally and posteriorly, slightly approaching the calyx of the pedunculate body.
6. The protocerebral bridge, which in the young larva L4 is small and horseshoe shaped, assumes the form of a plaited ribbon.
7. In the young larva L4 the compound eye centres are absent; they develop in the later larval stage and in the young pupa.
8. The principal changes observed during the development of the olfactory lobe concern its size, as well as the size of the antennal glomerules, which in the larva are very small and in the imago comparatively large.
9. No sex differences were found either in the structure of the olfactory lobes or in the whole brain.
10. The optic tubercle could not be found in the larva. It appears in the young pupa. The tract which connects it with the *medulla interna* produces in the imago a ramification which runs downwards towards the deutocerebrum.
11. In the adult form there occurs near the *medulla interna* a body which is probably analogous with the structure described by Hanström and Jawłowski as *corpus opticum*. In the younger stages of development this body could not be found.

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EXPLANATIONS OF THE MICROPHOTOGRAPHS

Phot. 1. Sagittal section through the brain of the larva L4; the area of *corpora pedunculata* (× 230).

Phot. 2. Frontal section through the calyx of the pedunculate body of the imago (× 255).

Phot. 3. Frontal section through the brain of the larva L4 (× 145).

Phot. 4. Sagittal section through the brain of the larva L4 showing the anterior stalk of the pedunculate body (× 230).

Phot. 5. Frontal section through the brain of the larva L4, central area (× 180).
Phot. 6. Sagittal section through the anterior stalk of the pedunculate body of the imago (× 365).
Phot. 7 and 8. Frontal section through the part of the brain of the imago where end the median roots and the anterior stalks of the pedunculate bodies (× 145).
Phot. 9. Frontal section through the brain of the imago in its posterior part (× 145).
Phot. 10. Frontal section through the brain of the larva L4 showing the central body (× 135).
Phot. 11. Frontal section through the middle of the brain of the imago (× 105).
Phot. 12. Frontal section through a part of the brain of the imago (× 215).
Phot. 13. Frontal and horizontal section through the brain of the imago (× 145).
Phot. 14. Horizontal section through the brain of the imago (× 140).
Phot. 15. Sagittal section through the brain of the larva L4 showing the course of the nerve which runs to *corpora cardiaca* (× 215).
Phot. 16. Frontal section through the protocerebral bridge of the one-day-old pupa (× 130).
Phot. 17. Frontal section showing the optic lobe of a one-day-old pupa (× 205).
Phot. 18. Frontal section showing the optic tubercle in the imago (× 445).
Phot. 19. Frontal section through the optic lobe of the young pupa (× 150).
Phot. 20 and 21. Frontal section through a part of the brain of the imago (× 150).

ABBREVIATIONS

B — median stalk of the pedunculate body
Cc — central body
Ccl — calyx cells
Ccv — protocerebral commissural tract.
Cg — calyx glomerules
Cn — neurosecretory cells
Co — *corpus opticum*
Cv — *corpora ventralia*
Cvg — glomerular part of the *corpora ventralia*
Lg — *lamina ganglionaris*
Lol — *lobus olfactorius*
Me — *medulla externa*
Mi — *medulla interna*
N — neuroblasts
Nc — nerve running from the brain to *corpora cardiaca*
Op — centre of the larval eyes
Pc — pons cerebralis
Pd — *pedunculus* of the pedunculate body
Pi — *pars intercerebralis*
R — anterior stalk of the pedunculate body
Tagl — antenno-globular (olfactory) tract
To — *tuberculum* opticum
Tog — glomerular part of *tuberculum opticum*
Ton — neuropilar part of *tuberculum opticum*
Tm — tract connecting *medulla interna* with *tuberculum opticum*
Tx — tract departing from *medulla interna* towards the *deutocerebrum*.

STRESZCZENIE

Morfologia centralnego układu nerwowego stonki ziemniaczanej podczas metamorfozy ulega znacznej modyfikacji. Skracanie się łańcuszka nerwowego przebiega u poczwarki w pierwszych trzech dniach po przepoczwarczeniu, natomiast modyfikacja mózgu rozpoczyna się już pod koniec ostatniego stadium larwalnego, a kończy się u czterodniowej poczwarki. W budowie histologicznej mózgu larwy stonki ziemniaczanej występują już zasadniczo te elementy, które spotykamy u imago, są one tylko słabiej rozwinięte. Zaznacza się tu jedynie zupełny brak *tuberculum opticum*, którego rozwój przypada na wczesne stadium poczwarki. Poza tym u larwy stonki ziemniaczanej nie występują ośrodki oczu złożonych, a znajdują się tu tylko bardzo małe ośrodki oczu larwalnych. Rozwój ośrodków oczu złożonych, rozpoczyna się pod koniec ostatniego stadium larwalnego, tak że już u młodej poczwarki występują wszystkie trzy elementy płatów ocznych.

РЕЗЮМЕ

Морфология центральной нервной системы колорадского жука во время метаморфоза подвергается значительным изменениям. Процесс сокращения нервной цепочки протекает у куколки в первые три дня после окукления, изменения же в мозгу начинаются уже в конце последней личиночной стадии и заканчиваются у четырехдневной куколки. В гистологическом строении мозга у личинки колорадского жука выступают в основном уже те структурные элементы, которые наблюдаются у взрослого насекомого, но характеризуются лишь более слабой степенью развития. Исключением является лишь полное отсутсвие *tuberculum opticum*, которое начинает развиваться в ранней стадии куколки. Кроме того у личинки колорадского жука не развиты еще центры сложных глаз, а имеются здесь только очень маленькие центры личиночных глаз. Развитие центров личиночных сложных глаз начинается под конец последней личиночной стадии, так, что у молодой куколки выступают уже все три элементы глазных долек.

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STRESZCZENIE

Morfologia centralnego układu nerwowego [illegible]

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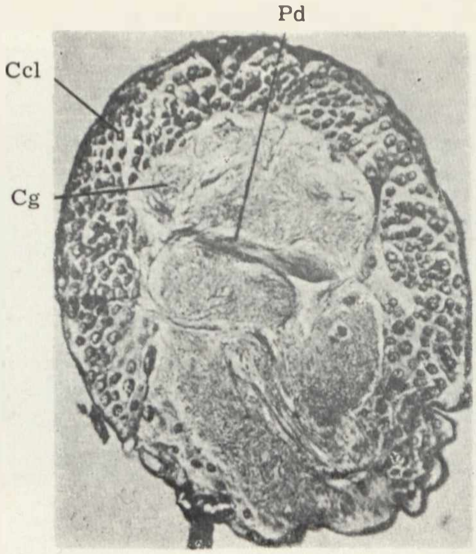

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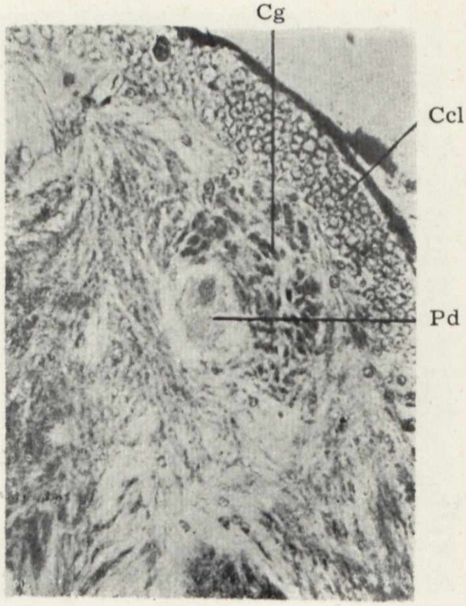

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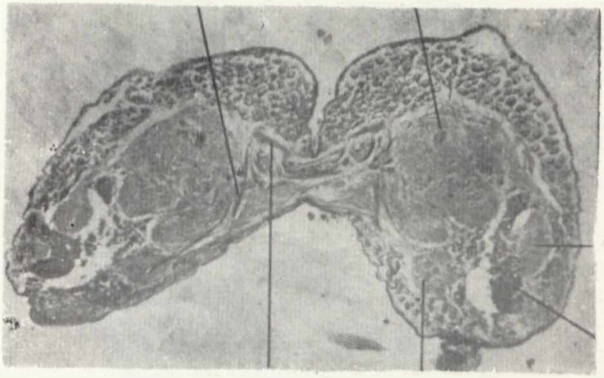

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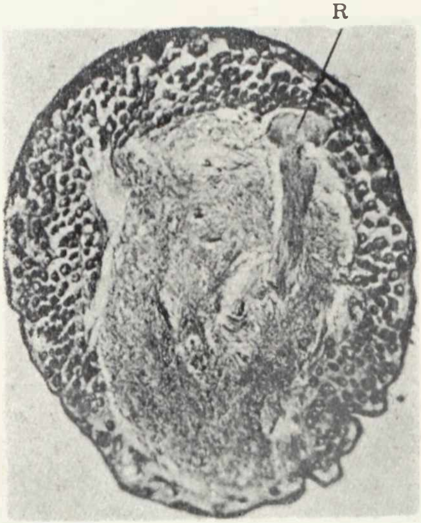

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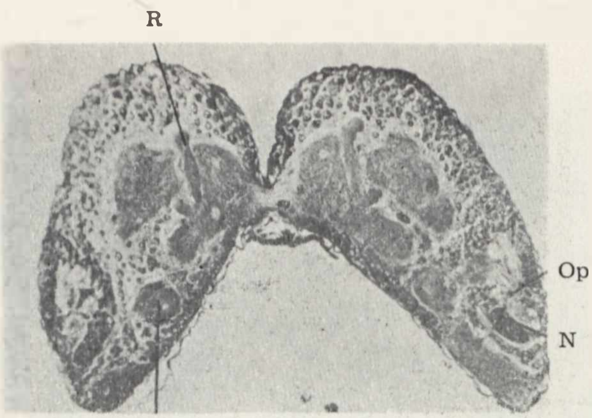

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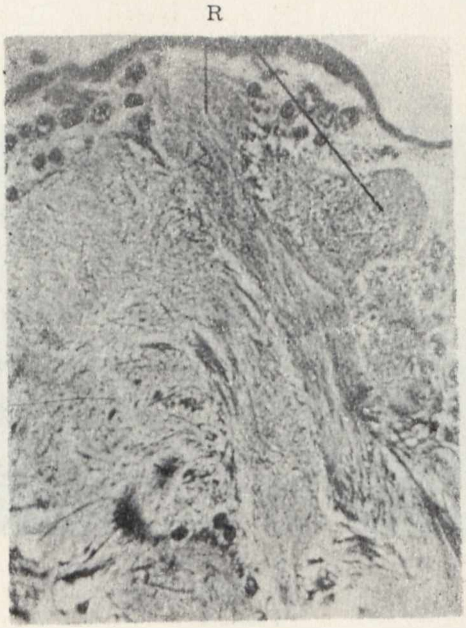

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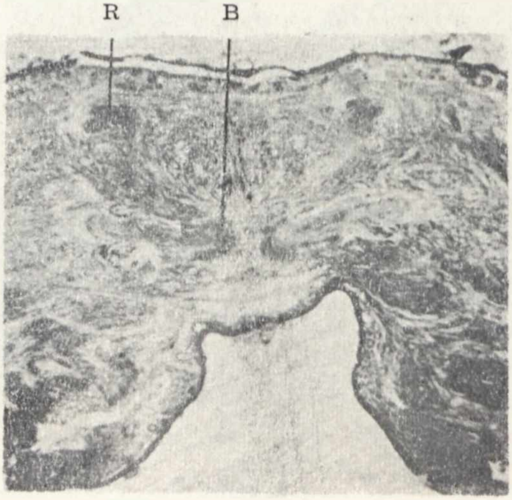

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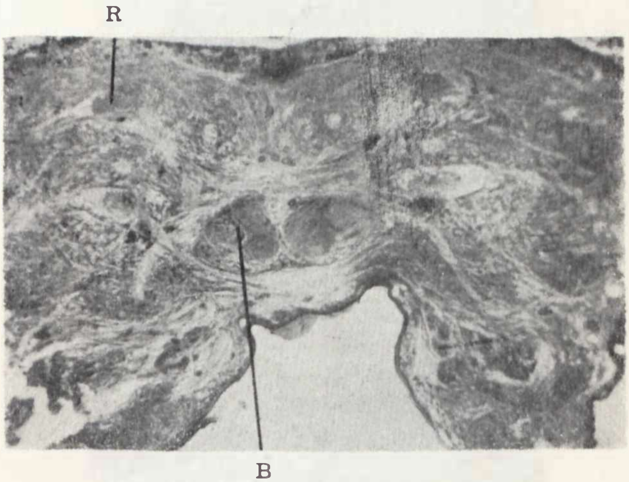

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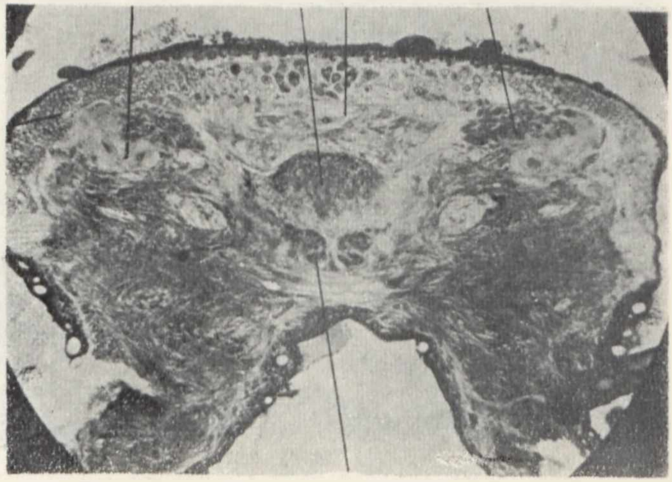

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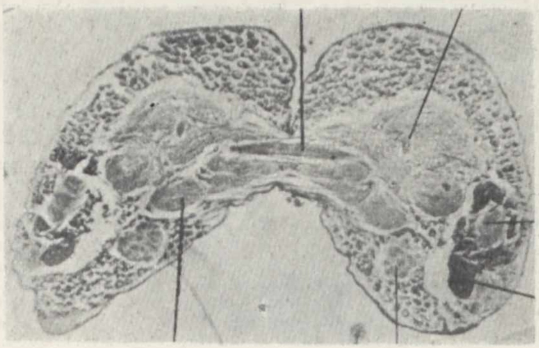

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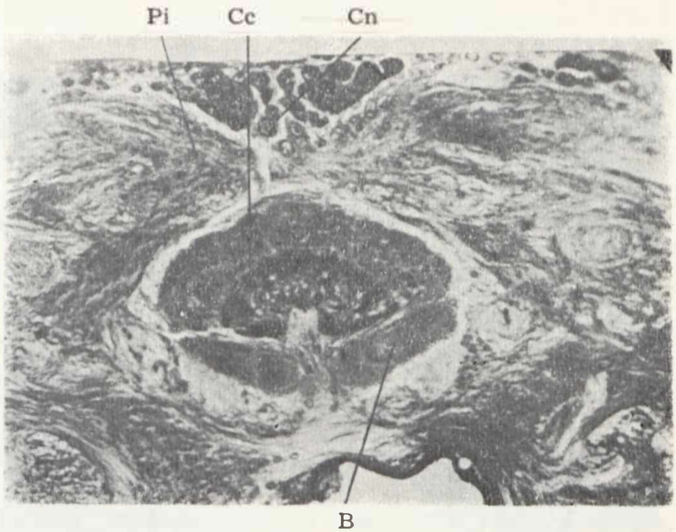

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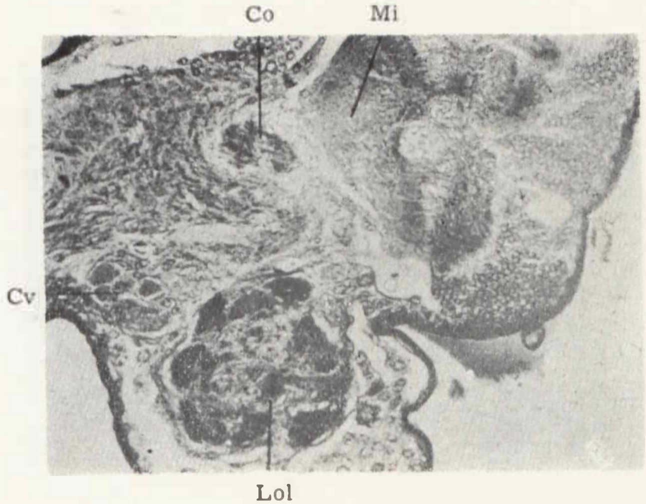

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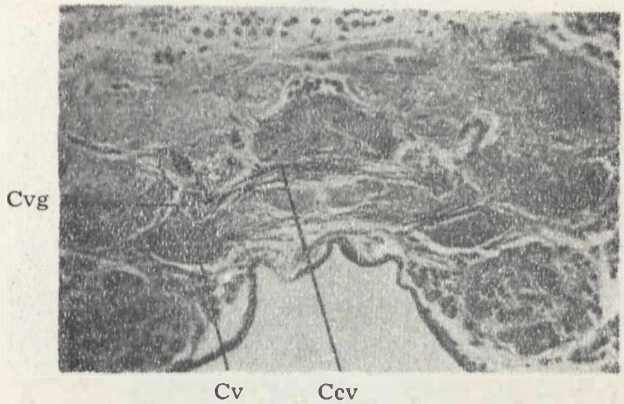

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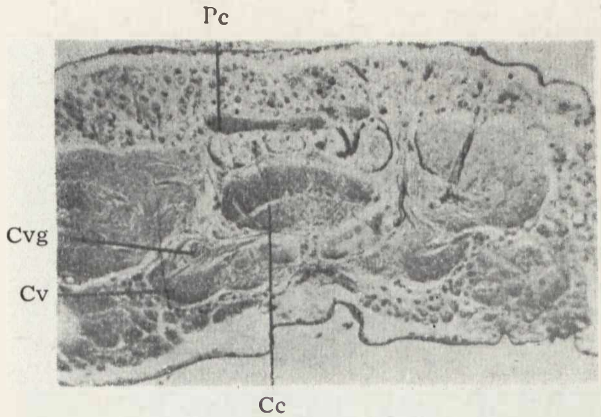

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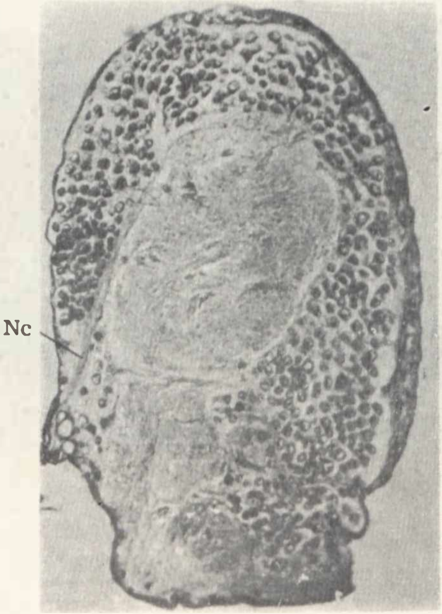

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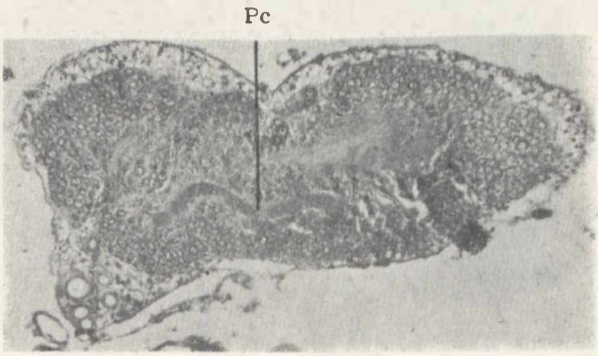

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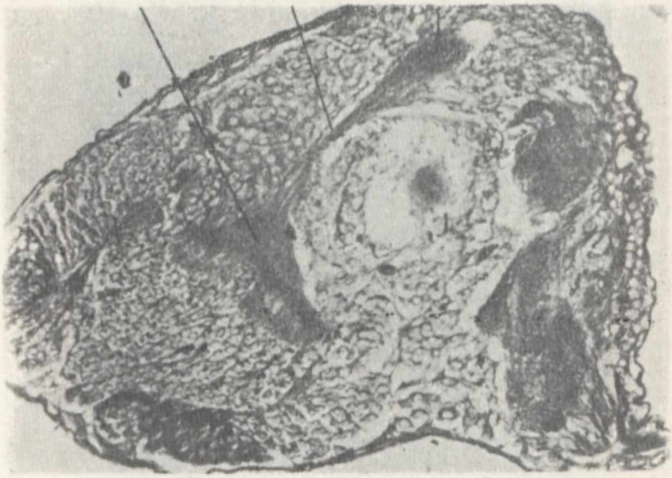

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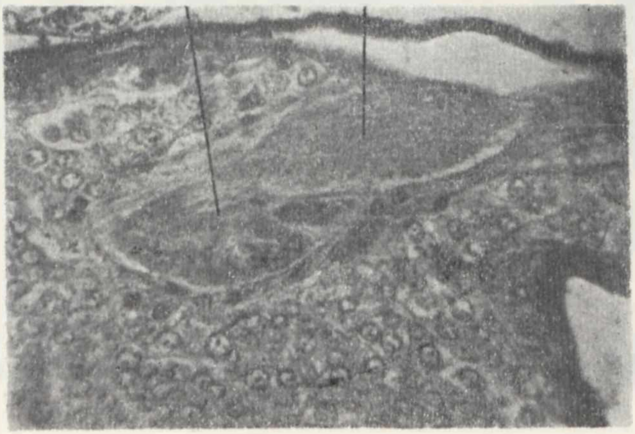

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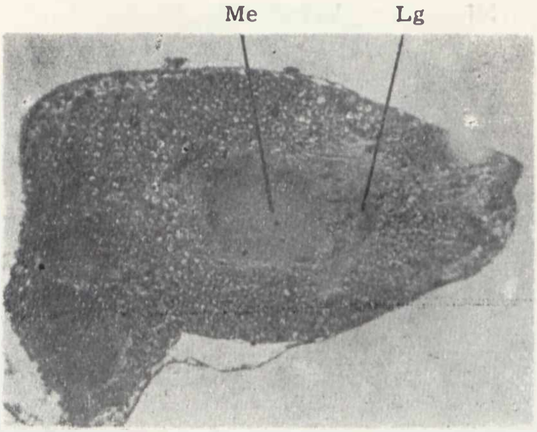

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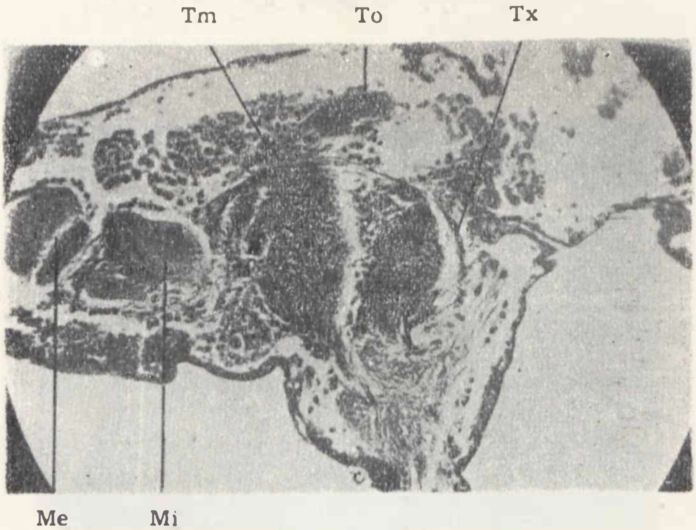

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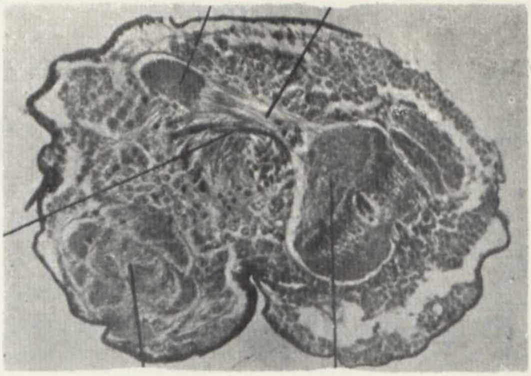

Phot. 21

Rcman Gieryng

Phot. by A. Czerepiński