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On the Structure of the Brain in some Diptera \*

O budowie mózgu u niektórych Diptera

О строении мозга у некоторых Diptera

Investigations on the internal structure of the brain of Diptera were conducted by J. Cuccati (1888) with regard to *Somomya erythrocephala*. H. Hertweck (1931) studied the anatomy and the variability of the nervous system and sensory organs in *Drosophila melanogaster*. The external and internal structure of the brain of *Drosophila melanogaster* was also the subject of investigations carried out by Power (1943).

The present studies concerned specimens belonging to four genera: *Calliphora* (Robineau-Desvoidy), *Sarcophaga* (Meigen), *Tubifera* (Meigen) and *Eristalis* (Latrali). The insects were caught in the environments of Lublin: their genera were determined by mgr Trojan and his co-workers in the Diptera Department of the Polish Academy of Science. The determination of the species presented great difficulties because the material sent to the Department consisted of the thorax and abdomen only, the head having been destroyed during the preparation of the brain.

The studies concerned the imago only. The brain was removed from the chitin capsule by Jawłowski's method, and fixed in 96 per cent alcohol. Two staining methods were used: staining with iron-haematoxylin and impregnation according to Cajal. The brain was sectioned in three planes to facilitate the observation of all its parts.

The brain of Diptera is a body devoid of conspicuous bulges, it is laterally elongated and terminates in large optic lobes. From the dorsal part of the brain arises the single ocellar peduncle, on which there are

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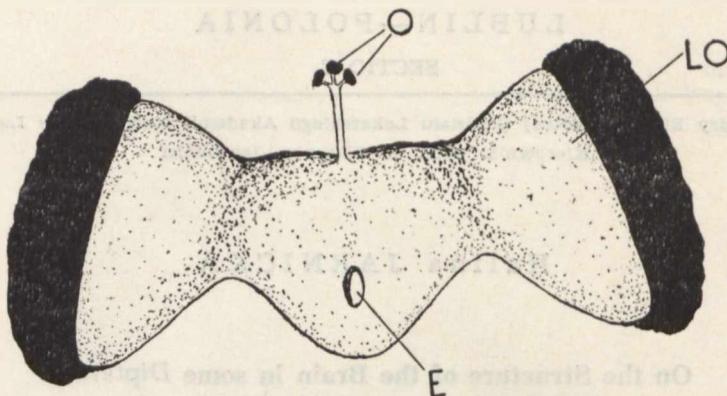


Fig. 1. Schematic drawing of the brain of *Calliphora* (external view); E — oesophagus. O — ocelli, LO — Lobi optici

three dorsal ocelli O (Fig. 1). A similar arrangement of the ocelli can be found in the Rhynchota species *Dundubia rufivena* (Pflugfelder 1937). The oesophageal opening has the form of a narrow channel E (Phot. 9). The three parts of the brain: protocerebrum, deutocerebrum and tritocerebrum are united with each other, so that it is difficult to draw a demarcation line between them.

The central complex (Power 1943) consists of the central body CC, ellipsoid body CE and the pair of circular ventral tubercles VT. It lies in the centre of the brain and is limited from above by the cells of the pars intercerebralis, from the ventral side by the tract which connects the medullae internae of the two opposite sides, and by the oesophageal opening, from the postero-lateral side by the paired olfacto-globular tracts.

The central body CC of convex-concave shape with the convex part directed dorso-laterally is the largest (Phot. 1). The ellipsoid body CE is kidney-shaped in *Calliphora* (Phot. 2), in other studied specimens its shape was ellipsoid. The ventral tubercles VT consist of a delicate fibrous mass and are connected with the ellipsoid body by crossing fibres F (Phot. 1). Hertweck (1931) found four ventral tubercles in the brain of *Drosophila*, while Power (1943) observed there only two. All sections obtained during the present investigations confirm the statement of Power (1943).

In the studied specimens the pedunculate bodies are little developed. The peduncle is divided into two stalks: one is directed anteriorly, the other centrally. The anterior stalk R is at the end partly split into two (Phot. 3). The median stalk B is single and rod-shaped (Phot. 3). According to Power (1943) in *Drosophila* the median stalk is composed of two parallel, closely united parts.

In all the investigated specimens the calyx-like TAK structures are little developed. They consist of a layer of contacts which in *Tubifera* and *Eristalis* are coarsely punctate WK (Phot. 4, 5, 6). In *Eristalis* the structures analogous to calyces are partly divided into two condensations of contacts (Phot. 6). A similar structure of the calyx-like bodies is seen in *Calliphora*, though they are less clearly divided into two parts, and the contact layers are finely punctate (Phot. 7, 8, 9).

In the posterior part of the brain there is located the protocerebral bridge PC. In *Calliphora* and other studied genera it is slightly bent posteriorly and ventrally, and is undivided (Phot. 4, 9). According to Power (1943), in *Drosophila* the protocerebral bridge is divided into two lateral parts by a fissure which corresponds to the median line of the brain. Cuccati (1888) described the protocerebral bridge in *Sarcophaga* as undivided. The inner part of the bridge is composed of delicate fibres, the surrounding fibres being thicker. Fibres which pass through the pons cerebralis run further towards the central body and ramify there (Phot. 10), as observed in other insects (Bretschneider 1914). There is probably a connection between the bridge and the fibres of the olfactorio-globular tract FP (Phot. 11).

On both sides of the oesophageal opening are symmetrically located condensations of the antennal glomerules, which are all that can be recognised as the „deutocerebrum” of Viallanes (1884). They are situated in front of the central complex, but their upper surface reaches its level. The glomerules are inter-connected by a distinct tract TLO (Phot. 12), which in other insects, e.g. in the bee (Jawłowski 1958) is hardly visible. In *Calliphora* and *Eristalis* the lobus olfactorius LOL is composed of small glomerules (Phot. 10, 13). In *Sarcophaga*, which has a well-developed olfactory sense, the glomerules are large (Phot. 12).

Near the optic lobes there can be observed a darker stained neuropile, bilaterally connected with a tract TCO (Phot. 14). This may be a structure homologous to the „corpus opticum” described by Hansström (1940) in *Petrobius*, and by Jawłowski (1958) in the bee.

The lower part of the protocerebrum contains the well-developed corpora ventralia CV, which are formed of a network of fibres, and are connected by a distinct tract TCV (Phot. 2). On the same level, in the lateral parts of the protocerebrum, are located the optic tubercles TO (*Tuberculum opticum*, Phot. 15). The tract TM which connects the medulla interna and the optic tubercle (*tractus opticum anterior*), as in other insects, is thicker than other tracts (Phot. 15, Jawłowski, Viallanes, and others). The tract CN links the right and left medulla interna (Phot. 16). The fibres of the ocellar stalk OF are the thickest, as can be also observed in the bee (Jawłowski 1958); they

disappear in the lower part of the brain (Phot. 17). Some fibres cross each other. Only one pair of olfactory-globular tracts TAG connects the olfactory lobe with bodies analogous to the calyces in other insects (Phot. 16, 18). According to Jawłowski (1948), only in Hymenoptera occur two pairs of tracts which connect the olfactory lobe with the calyces. Like other investigators, the present writer failed to find direct connections between the antennal glomerules and the optic lobes. There may, however, exist indirect connections through the pedunculate bodies and central complex.

#### RESULTS

1. The brain of Diptera contains an ocellar peduncle with three dorsal ocelli.
2. Only two circular ventral tubercles were found in the central complex.
3. In all specimens the pedunculate bodies are little developed. In specimens of the genera *Tubifera* and *Eristalis* formations analogous to the calyces in other insects are coarsely punctate, but in individuals of the genus *Calliphora* they are finely punctate. In *Eristalis* the calyx-like formations are partly divided into two condensations of contacts.
4. The anterior root is divided into two at the end, the median root is single.
5. The protocerebral bridge is not divided.
6. The ventral bodies are well developed.
7. In all studied specimens the antennal glomerules are connected with each other by a distinct tract.
8. Large glomerules can be observed in *Sarcophaga*: this is probably connected with the well-developed olfactory sense in this genus.

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#### EXPLANATION OF MICROPHOTOGRAPHS

- Phot. 1. Frontal section through the brain of *Calliphora*: the central body is visible  $\times 200$ .
- Phot. 2. Frontal section through the brain of *Calliphora*  $\times 126$ .
- Phot. 3. Frontal section through the brain of *Calliphora*: the frontal and median roots of the corpora pedunculata are visible  $\times 120$ .
- Phot. 4. Frontal section through the brain of *Tubifera*: formations analogous to calyces are visible  $\times 50$ .
- Phot. 5. Frontal section through the calyx-like formation of the pedunculate body in *Tubifera*  $\times 400$ .

- Phot. 6. Frontal section through the calyx-like formation in *Eristalis*  $\times 340$ .
- Phot. 7. Frontal section through the calyx-like formation in *Calliphora*  $\times 480$ .
- Phot. 8. Frontal section through a part of the brain in *Calliphora*  $\times 95$ .
- Phot. 9. Frontal section through the brain of *Calliphora*: the protocerebral bridge is seen  $\times 80$ .
- Phot. 10. Frontal section through the brain of *Calliphora*: condensations of antennal glomerules are seen  $\times 85$ .
- Phot. 11. Frontal section through a part of the brain of *Calliphora*  $\times 95$ .
- Phot. 12. Frontal section through the brain of *Sarcophaga*; the olfactory lobe is seen  $\times 90$ .
- Phot. 13. Frontal section through the brain of *Eristalis*: the olfactory lobe is seen  $\times 80$ .
- Phot. 14. Frontal section through the brain of *Calliphora* showing the corpus opticum  $\times 85$ .
- Phot. 15. Horizontal section through the brain of *Calliphora* showing the optic tubercle  $\times 85$ .
- Phot. 16. Frontal section through the brain of *Tubifera*  $\times 70$ .
- Phot. 17. Frontal section through the brain of *Calliphora*: the ocelli are visible  $\times 150$ .
- Phot. 18. Frontal section through the brain of *Calliphora* showing the olfacto-globular tracts  $\times 85$ .

#### EXPLANATION OF SYMBOLS

B — median root of *corpus pedunculatum*; CC — central body; CE — ellipsoid body; CN — tract connecting the right and left *medulla interna*; CO — *corpus opticum*; CV — *corpora ventralia*; E — *oesophagus*; F — fibres connecting ventral tubercles with the ellipsoid body; FMC — fibres passing through the protocerebral bridge; FP — fibres departing from the olfacto-globular tract; LOL — *lobus olfactorius*; MI — *medulla interna*; OF — *ocellar fibres*; PC — *pons cerebralis*; R — anterior root of the pedunculate body; T — *tritocerebrum*; TAG — olfacto-globular tract; TAK — formations analogous to the calyces; TCO — tract connecting the *corpora optica* of the two opposite sides; TCV — tract connecting the ventral bodies; TLO — tract connecting the right and left olfactory lobes; TM — tract connecting the *medulla interna* and the optic tubercles; TO — optic tubercle; WK — coarsely punctate contact layer; VT — ventral tubercles; X — artefact.

#### STRESZCZENIE

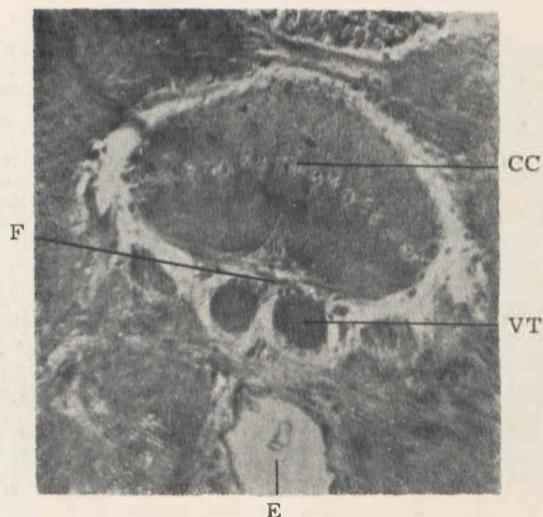
Mózg Diptera jest ciałem bez wyraźnych wypukłości, wydłużonym w kierunkach bocznych, zakończonym dużymi płatami wzrokowymi. Z grzbietowej części mózgu wystaje pojedyncza łodyżka oczelarna, na której znajdują się trzy grzbietowe przyoczka. Trzy części mózgu: *protocerebrum*, *deutocerebrum* i *tritocerebrum* złączone są ze sobą tak, że trudno jest odgraniczyć te struktury od siebie. U badanych okazów *corpora pedunculata* są słabo rozwinięte. Twory analogiczne do kielichów u innych owadów są podłużnego kształtu i małych rozmiarów. U *Eristalis*

lis twory analogiczne do kielichów są grubo punktowane i częściowo rozdzielone na dwa skupienia kontaktów. Podobną strukturę tworów analogicznych do kielichów widzimy u *Calliphora*, chociaż mniej wyraźnie rozdzielają się na dwie części i warstwy kontaktów są drobno punktowane. W zespole centralnym znajdują się tylko dwa koliste guzki brzuszne. Most protocerebralny u wszystkich badanych rodzajów jest nie podzielony. Glomerule antenalne są połączone ze sobą wyraźnie znaczonym szlakiem. W dolnej części protocerebrum znajdują się silnie rozwinięte ciała brzuszne, połączone ze sobą wyraźnym szlakiem.

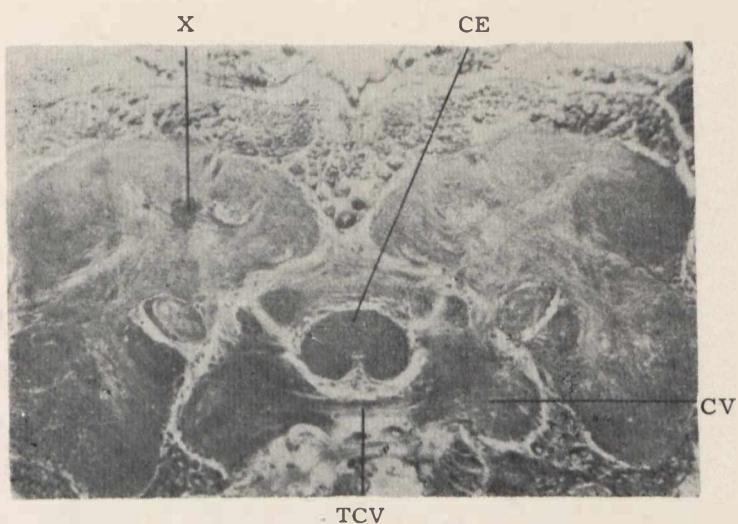
### РЕЗЮМЕ

Мозг Diptera лишен сколько-нибудь заметных выпуклостей, удлинен в латеральных направлениях, законченных крупными зрительными долями. От дорзальной части мозга отходит одиночный оцелярный стебелек, на котором находятся три дорзальных глазка. Три части мозга: протоцеребрум, дейтоцеребрум и тритоцеребрум столь соединены, что весьма трудно их друг от друга разграничить. У всех исследуемых особей *corpora pedunculata* слабо развиты. Образования аналогичные чашам у других насекомых имеют продольную форму и незначительные размеры. У *Eristalis* образования аналогичные чашам крупно пунктированы и отчасти разделены на два скопления контактов. Подобную структуру образований аналогичную чашам наблюдаем и у *Calliphora*, хотя они не так отчетливо разделены на две части и мелко пунктированы. В центральном скоплении находятся лишь два вентральных образования круглой формы. Протоцеребральный мост у всех исследуемых родов не разделен. Антеннальные гломерулы правой и левой стороны соединены между собой отчетливо выраженным трактом. В нижней части протоцеребрума находятся сильно развитые брюшные тела, соединенные между собой тоже ясно выраженным трактом.

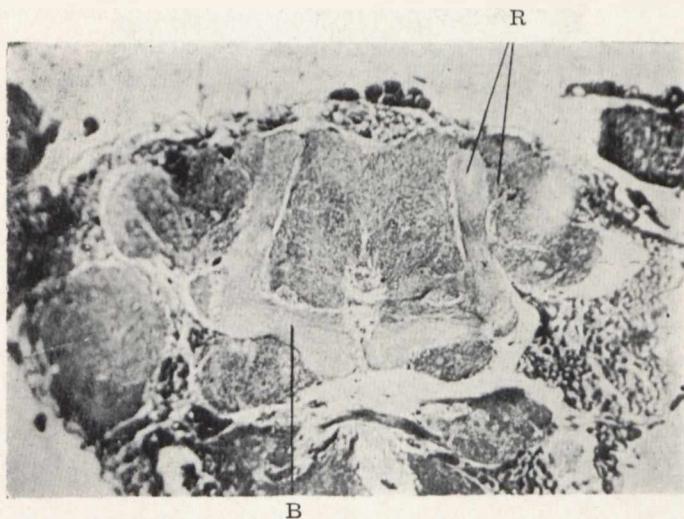




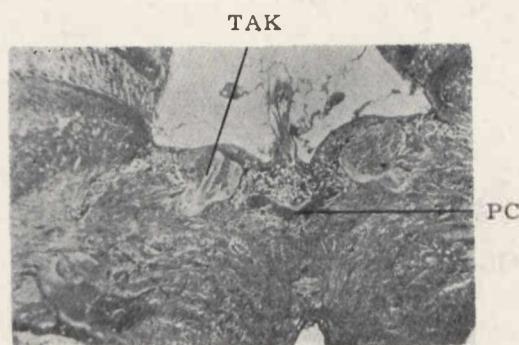
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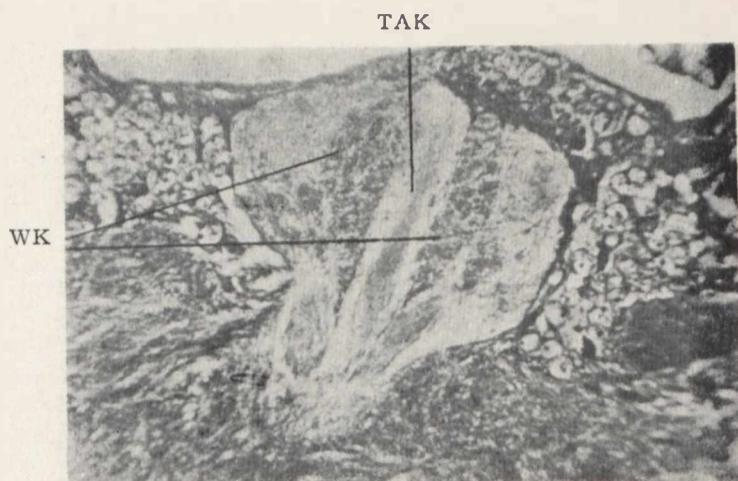
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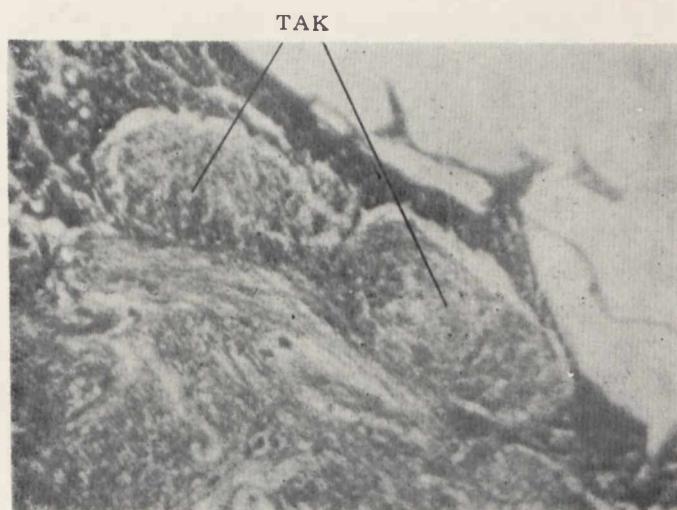
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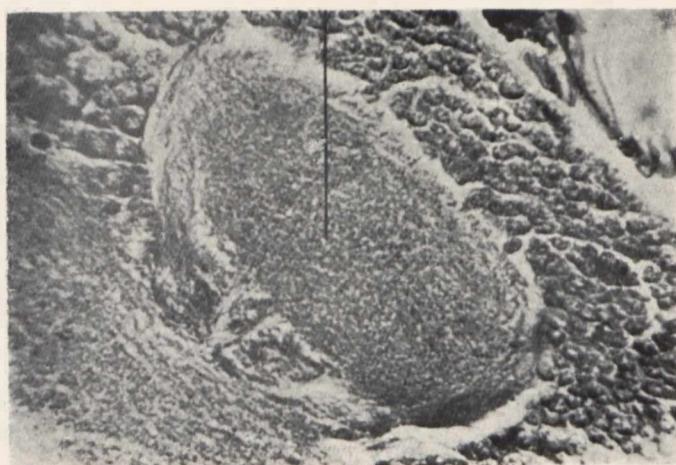


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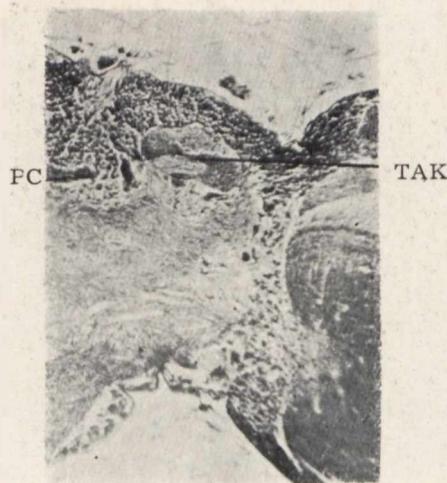


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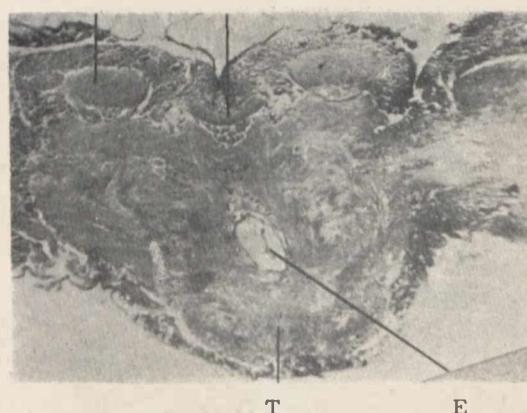


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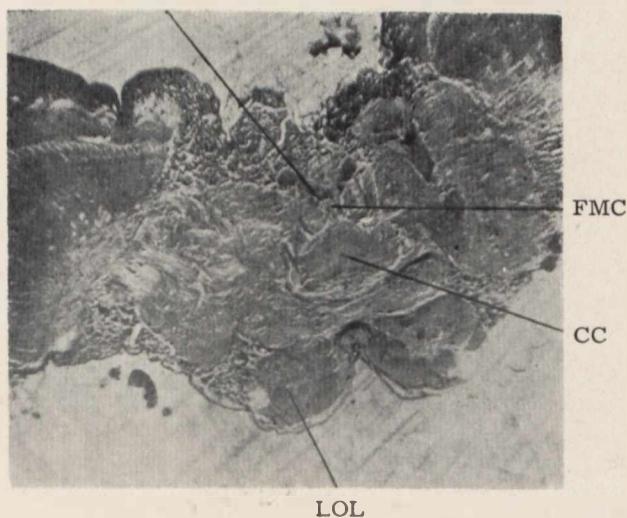
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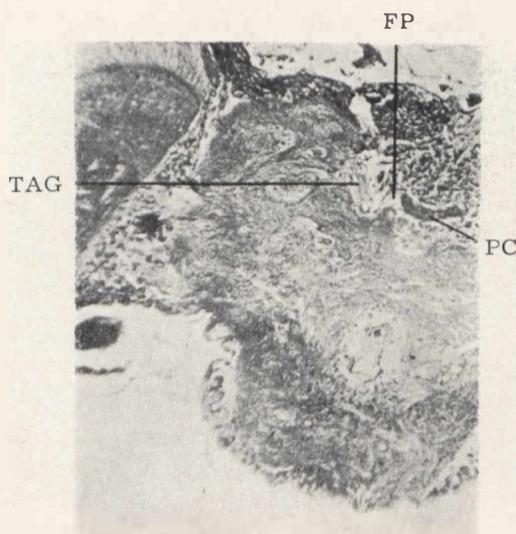


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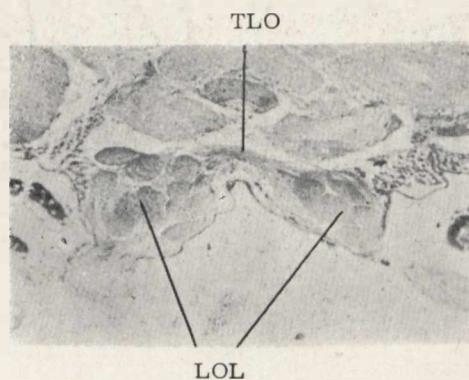
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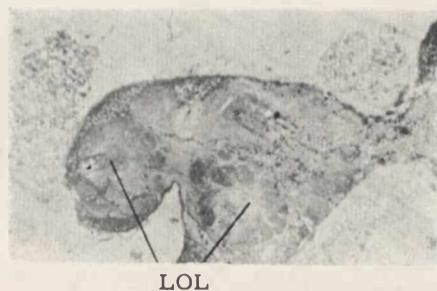
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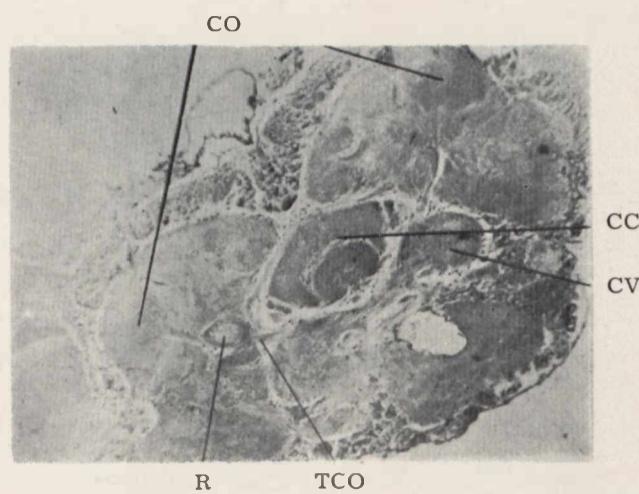
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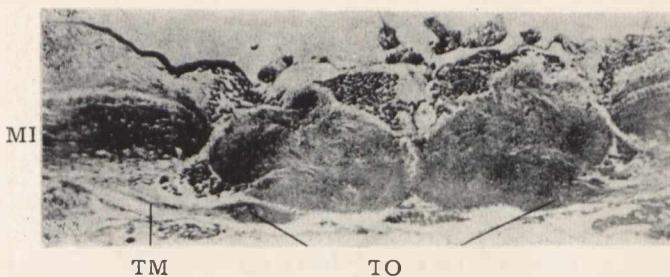
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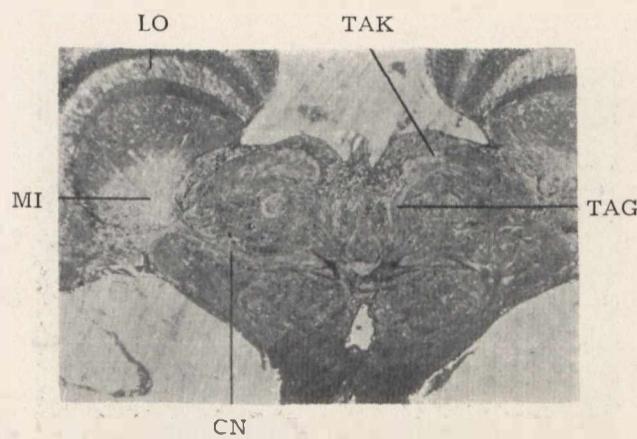
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Phot. 14



Phot. 15



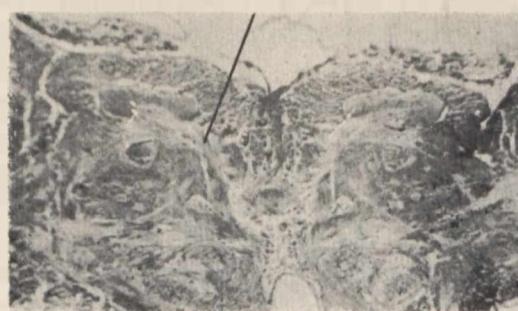
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OF



Phot. 17

TAG



Phot. 18

