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Z badań nad mózgiem owadów

To Prof. Dr Henryk Raabe,
the founder and Rector of the
Maria Curie - Skłodowska University
in Lublin.

The last war has hindered me in gathering the histological materials in order to explain some problems in connection with the structure of the insect brain. A part of these materials has been completely destroyed during the war. The same has happened to the indispensable literature. Such a state caused great difficulties in the farther studies I have done. The present paper regards mainly the nerves coming out from the brain (the oesophageal ganglion) of insects as well as the olfactory lobes (*lobus olfactorius*) and their connection, and partially it regards also the tritocerebrum *). All the histological preparations I have now, have been fixed from the following insect species: the *Hymenoptera* - *Apis mellifica*, *Bombus div. spec.* (Poland), *Xylocopa violacea*, *Vespa germanica*, *Vespa crabro*, *Scolia haemorrhoidalis*, *Ichneumonidae sp.* (Poland), *Formica rufa*, *Camponotus sp.* (Białowieża — Poland), *Lasius sp.* (Poland); the *Diptera* - *Eristalis tenax*, *Tabanus bovinus*; the *Heteroptera* - *Notonecta glauca*, *Mesocercus marginatus*; the *Coleoptera* - *Geotrupes silvaticus*, *Lucanus cervus*, *Orictes nasicornis*, *Tenebrio molitor*; the *Lepidoptera* - *Sphinx ligustri*, *Antheraea pernyi*; the *Saltatoria* - *Trixalis nasuta*; the *Blattariae* - *Periplaneta americana*, *Periplaneta orientalis*. The saved histological

*) The present paper does not consider the suboesophageal ganglion. I have studied only the parts of it, which were quite close to the brain in *Hymenoptera*. The nerves given off from the farther parts of the suboesophageal ganglion in the bee are repeated after Ionescu.



material has not been sufficient, however, to allow for the minute investigations on all the species mentioned above, but only on few of them. These species are: *Periplaneta americana*, *Periplaneta orientalis*, *Vespa germanica*, *Vespa crabro* and *Apis mellifica*. The histological preparations of the brains of all other insects have been used by me as the main comparative material.

In my previous papers I have already explained, in part at least, the technic of my investigations. Now I should like to add, moreover, that in applying the alcohol fixing it is necessary to look for a certain period of time, when brain can be excised from the chitin case most easily. The earlier or later excising may cause some considerable damage. This time depends on the dimensions of the investigated object as well as on the proportion of dimensions of the head muscles and of the brain. As I have previously explained, the head should be put into alcohol with its chitin having been cut off on both sides. For instance, the brain of the ant can be excised almost immediately after it has been dropped into 96% alcohol; the brain of the bee, on the other hand not sooner than 20 to 30 minutes have passed. After one or two hours the damages are very difficult to be avoided by preparing. This time of the optimal convenience for the preparation of the brain depends on the solution used, and may be different for various chemicals. I have stained the preparations by means of the iron-haematoxylin; I have used also the Cajal's method of impregnation. Very good results can be obtained in proceeding after Pflugfelder's method. A few preparations are stained according to Golgi's method.

The nerves coming out from the brain.

The brain in *Periplaneta americana* was exactly examined by Bretschneider. On my preparations of *Periplaneta orientalis* and *Periplaneta americana* too, I have found one pair of nerves which hitherto has not been described. These nerves come out almost on the margin of the deutocerebrum, (figs. 1 and 2, NM). They are given off from the median parts of the brain, on its anterior side; just for that reason I call them „*nervi medii*“ (the median nerves). The roots of these nerves take their beginning in the tritocerebrum, close to the tritocerebral glomeruli (figs 2 and 3, NM). I did not find, unfortunately, up to where the very nerves go. The dimension of these nerves probably shows some fluctuations, and probably are larger in females than in males. It is very interesting that the location of the roots of these nerves resemble, in some points at least, the nerve tracts proceeding from the X-organs described by H a n s t r ö m

in *Petrobius* (fig. 33 and 36, Hanström, 1940). The tegumentary nerves („Scheitelnerven“ after Bretschneider) in *Periplaneta* (fig. 2 and 4, NT) are not as thin as the author has suspected. The roots of these nerves arise not in the deutocerebrum, but in the suboesophageal ganglion as I have stated in my paper (1936) describing analogous nerves in *Coleoptera*. The tegumentary nerves are in *Trixalis nasuta*, too. Via l-

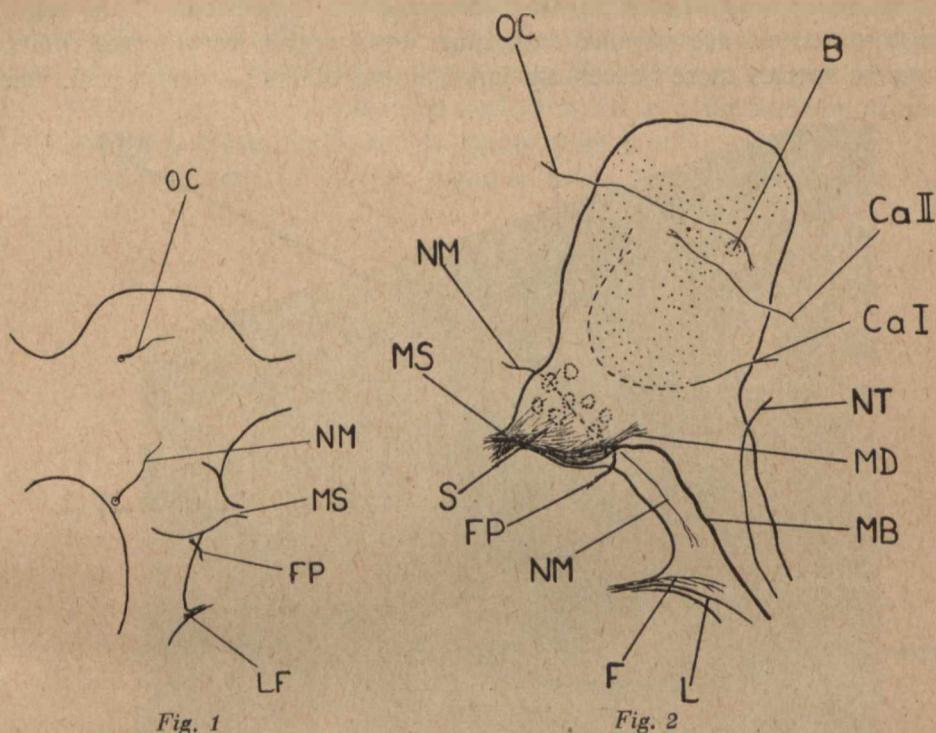


Fig. 1, *Periplaneta americana*: nerves coming out from the anterior part of the brain are visible in one of its half. The nerve (FP) arises from the posterior part of the olfactory lobe, but immediately after the exit turns anteriorly.

Fig. 2, *P. americana*: The scheme illustrating the location of nerves coming out from one half of the brain and the distribution of their roots. The beginning of the median nerve (NM) and part of its root are, of course, on the inner side of this lobus olfactorius, therefore they are marked on this drawing by a broken line. The part of the nerve of the corpora cardiaca I (Ca I) that proceeds in the other half of the brain is marked by a dotted line.

l a n e s describes similar nerves in *Oedipoda coerulescens*. He supposes, however, that they arise from the deutocerebrum. As far as other descriptions of similar nerves in other insects are concerned, it is difficult to state, whether they truly consider just the analogous nerves. Very likely the tegumentary nerves appear also in the species included into many

other insects genera. In *Hymenoptera* I did not find them; other investigators have also not found them. I should like to add here, moreover, that in few individuals of *Vespa crabro* I have found some fibers not overmuch distinct; they come out from the brain, approximately on the level of the dorsal lobe. I cannot maintain, however, whether these fibers appear in all individuals. In one individual I have investigated, the roots reached the suboesophageal ganglion. In *Coleoptera* the dimensions of the tegumentary nerves are various, sometimes even within very broad limits. In some species these nerves are large, in the others — very small. One

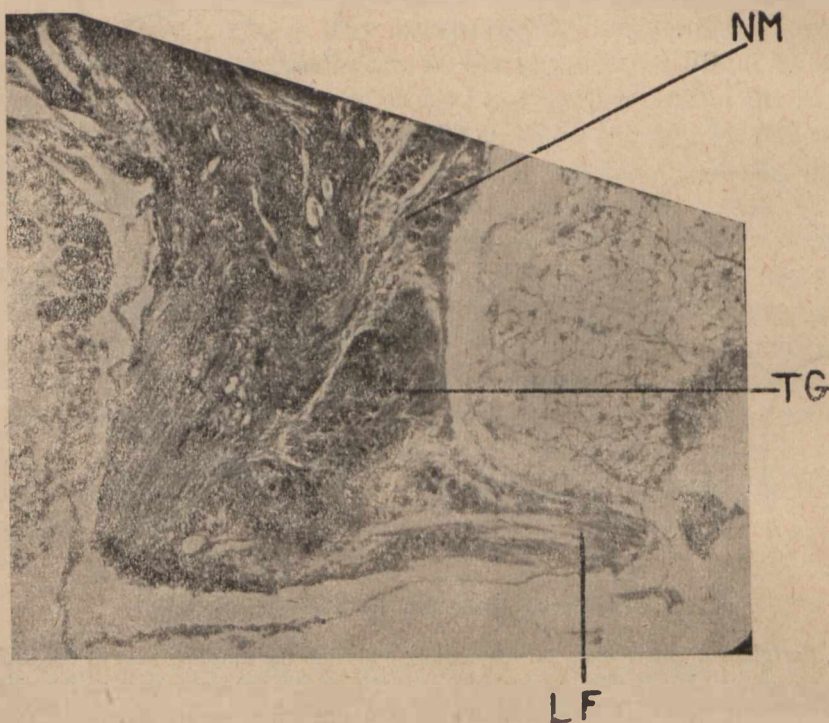


Fig. 3. *Periplaneta americana*: stained with iron-hematoxylin. The ventral parts of the brain, mainly the tritocerebrum, sectioned lengthwise.

may suppose therefore, that the mentioned nerves in *Vespa crabro* are just the tegumentary nerves very weakly developed; in other species of *Hymenoptera* they may be absent altogether. The discussed fibers may be an abnormal phenomenon, too. Farther researches would be necessary to enlighten that problem more precisely.

The antennal nerves in insects are much more complicated than it might be supposed judging by the descriptions heretofore known, especially in the case of *Hymenoptera*. In *Vespa* two main bundles of motor

fibers — the motor nerve tracts — go from different parts of the brain to the antenna. (fig. 5).

One of them (MD) arises from the so called motor part (the dorsal lobe-*lobus dorsalis*) of the deutocerebrum (see further on *Periplaneta*) and gives off the branch (FP) to the first antennal segment. Very likely, that the bunch of the antenno-sensory fibers joins also with the branch (FP).

The other, larger bundle consists, strictly speaking, of two lesser bundles-tracts, one (MB) arises from the suboesophageal ganglion the other one (MO) — from the ocellar bundle. Thus there is a direct connection between the antenna and the ocellar tract, and the suboesophageal ganglion. Both these small bundles approach each other on the level of the deutocerebrum and run further together towards the antenna. It is not

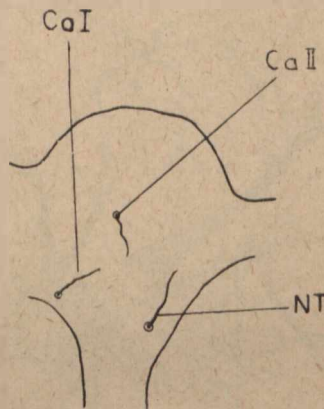


Fig. 4. *Periplaneta americana*: The drawing of one half of the brain, showing nerves coming out from its posterior parts.

impossible, that besides these two main motor nerves tracts some other, smaller ones, enter the antenna, too. I did not find any fundamental difference in the above described nerves in the bee and the wasp. I enclose, too, a drawing, illustrating the course of analogous tracts in the bee (fig. 6). Ionescu, on the other hand, limited the origin of motor-bundles of the bee, exclusively to the deutocerebrum. I also enclose the drawing (fig. 7), showing the nerves of the bee brain, coming out from the anterior part, according to my investigations. The sensory and motor fibers of the nerves (MS), leave the brain together. I did not find the tritocerebral nerve, mentioned by Ionescu.

No less than two bundles of motor fibers (fig. 2) in *Periplaneta* go to the antenna. Like in *Hymenoptera*, one of them (MD) arises in the dorsal lobe, the second one (MB) takes its origin in the suboesophageal ganglion. The first bundle (MD) contains also fibers, coming out from

the protocerebrum (fig. 24 — TP). They run on a different plain than is shown in fig. 2, therefore they cannot be seen on it. The existence of these nerve fibers is mentioned also by Bretschneider. In the protocerebrum they meet bundles running from the compound eyes, and take part in conveying visual impulses similarly to the activity of tracts which convey stimuli from the ocelli, described by me in *Hymenoptera*.

The suboesophageal ganglion (the drawing does not show it) is much more distant from the oesophageal one in *Periplaneta* than in *Hymenoptera*. Just for that reason there is much more easily to trace the fiber tracts proceeding from the suboesophageal ganglion, for they are visible on longer distance. I did not find in *Periplaneta* those fibers,

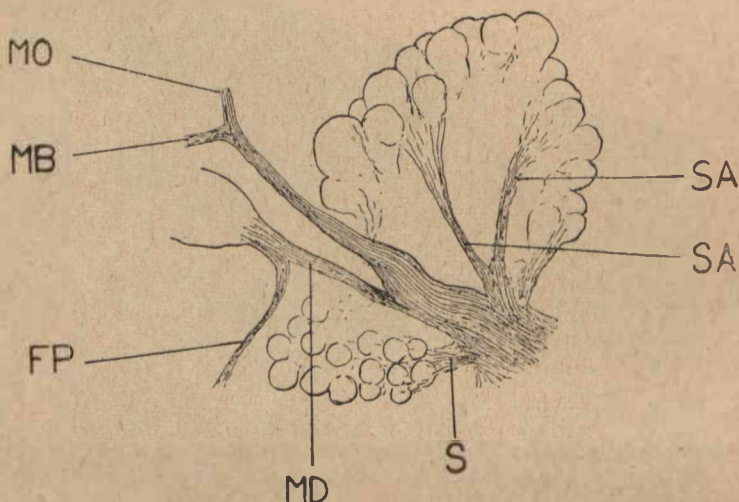


Fig. 5. *Vespa germanica*: The roots — the motor and sensory fibers, bundles of the antennal nerve in the olfactory lobe and its environments (hemi-scheme).

which arise from the ocellar tracts. The ocelli in these insects are not overmuch large; the nerve tracts connecting them are less clear than in *Hymenoptera*. Very likely, however, the connections between the ocellar tracts and antennae appear in other insects, too, besides *Hymenoptera*. This to be stated needs farther investigations.

I have found, that like in cockroach there are motor fibers, conveying impulses from compound eyes also in *Coleoptera* and *Lepidoptera*. I could not find the motor fibers in *Diptera* (*Eristalis tenax*) probably the small dimensions of the antenna account for it. The motor fibers are also small and therefore difficult to be traced out. In *Hymenoptera*, however, those fibers are there, I suppose, though I could not find them.

Besides the large nerve (MS) consisting of motor and sensory fibers, which come out from the brain together, there is in *Periplaneta* as in *Hymenoptera* the small nerve (FP) appearing in its nearest environments. The origin of the latter is probably the same, as the branch of the motor nerve in *Hymenoptera*, which runs to the first antennal segment. The small nerve in *Periplaneta* (FP) runs also to the first antennal segment.

I have found the beginnings of the antenno-motor nerves in the suboesophageal ganglion in all insects I have investigated. In my paper

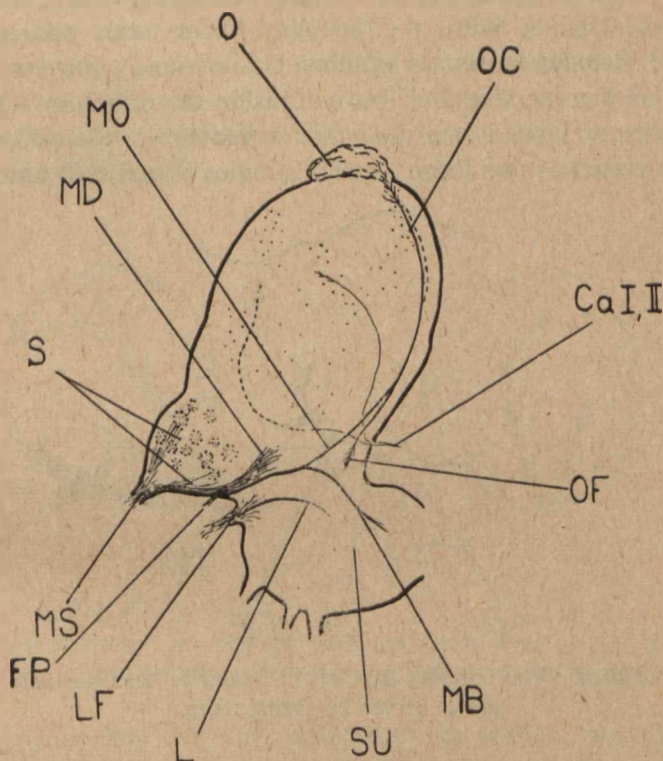


Fig. 6. *Apis mellifica*: The scheme illustrating the distribution of the nerves coming out from the brain, and of their roots. The nerve (Ca I) is marked as on the figure 2.

(1936) „Über Gehirnbau der Käfer“ I have described a hitherto unknown connection of the antenna with the suboesophageal ganglion. As it turns up now, the connection is made by the antenno-motor nerves. The origin of these nerves in insects up till now has not been known. Almost all investigators suppose that antenno-motor nerves arise in the deutocerebrum only. But merely a part of the antenno-motor fibers can take its origin in the deutocerebrum.

Fahländer, a very conscientious investigator on the related group of *Myriapoda*, corroborate my results that the antennal-motor fibers in insects may arise from the circumoesophageal connectives. In insects the antennal-motor fibers run farther to the suboesophageal ganglion.

The antenno-sensory nerves begin in the brain, in the glomeruli of the olfactory lobe (*Lobus olfactorius*) as several investigators have already explained. According to Ionescu their initial parts in the bee consist of two roots-bundles. Their location, however, demands a more exact explanation. The bundle, called by Ionescu the upper one, goes inside the olfactory lobe (fig. 8, SA); the second, lower one, proceeds mainly outside (SB). Besides those two bundles, I have found a third one, a smaller one (fig. 9, SA₁) going like the first one inside the olfactory lobe.

The olfactory lobes in the wasp are larger and a little different than in the bee. The wasp has two large interior bundles (fig. 5, SA) and also fibers,

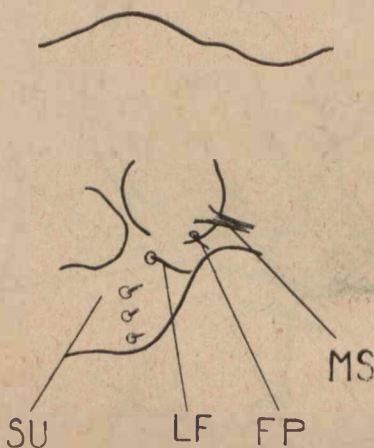


Fig. 7. *Apis mellifica*: The anterior part of the brain, as seen partially from below, shows nerves beginning there.

proceeding from the ventral or lateral parts to their common exit. In the olfactory lobes in *Periplaneta*, among many fibers going to the exit two main concentrations (bundles) are distinctly apparent: the first, interior one, and the second, located a little more close to the lower surface (fig. 10, SA, SB). At the exit all these fibers, in *Periplaneta* as well as in other insects, cross one another, if not completely then partially, at least.

The ocelli in the greatest part of the investigated by me insects are so close to the brain that, strictly speaking, there are only bundles (tracts) running inside the brain. The ocellar tracts run close to the surface of the brain in *Hymenoptera* — (fig. 6, OC), partly they cross one another; some branches are brought in touch with the commissure (inferior optic

commisures) connecting both compound eyes. The ocellar tracts terminate by forking into slight, feather like branches (fig. 6 and 11, OF). It is doubtful, whether they reach the suboesophageal ganglion, as Kenyon has supposed. The ocellar tract in *Hymenoptera* gives off the branches (MO), going to the antenna. I have previously mentioned about these branches as the bundle of the antennal motor nerve. Very likely, that the ocellar tracts give off some fibers, connecting also other parts of the brain. The ocellar tracts in the bee, as Cajal has shown it, and undoubtedly in other insects too, are not the direct protractions of the retinal axon but fibers arising from other cells. The ocellar nerve in *Periplaneta* (fig. 1 and 2, OC) runs almost horizontally beneath the calices to the pons cerebri. Beyond the pons (B) it turns downwards, and in its further course it is difficult to be traced out. The ocelli in *Trixalis nasuta*, although larger than in *Periplaneta*, their tracts being more apparent, too, but

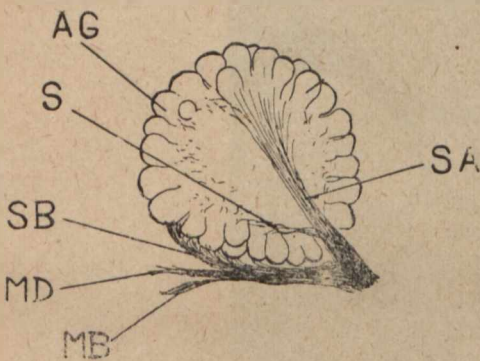


Fig. 8

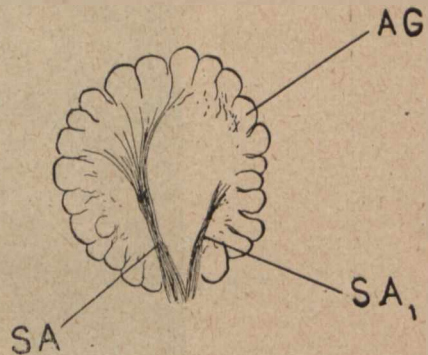


Fig. 9

Fig. 8. *Apis mellifica*: the olfactory lobe sectioned more or less lengthwise.

Fig. 9. *Apis mellifica*: the olfactory lobe sectioned frontally.

beyond the pons, they are also difficult to be traced out. The ocellar tracts in other insects have been examined by Hansström and Pflugfelder, Pflugfelder has described the ocellar tracts in *Hemiptera*. In their general outlines they are the same as in *Hymenoptera*. The above named author does not mention only the branch, running to the antenna. Moreover, according to Pflugfelder, this tract runs between the pons and the central body, (according to Hansström quotation); in all the insects, I have examined, not in the mere *Hymenoptera*, it runs beyond the pons (fig. 2, OC); only a few fibers enter between the pons and the central body. It seems that these nerves in *Hemiptera*, too, run mainly behind the pons, for the remnant ocellar tract I have traced out in *Noto-necta glauca* does not differ from that, found in all other insects.

The compound eyes of insects are totally connected with the optic lobes. The nerve tracts and their mutual arrangement inside the optic lobes are known quite well. On the other hand, the connections between these lobes and the brain are known only as far as the main tracts are concerned, therefore they should be studied more. I am not able to describe now in detail the course of all these tracts; for that reason i do not place them under a separate chapter, but I merely describe one of them, which is especially important, although it was unknown heretofore. This tract (fig. 12, OB), connects directly the lamina ganglionaris (LA) with the suboesophageal gauglion; it does not give off any branches and is very difficult to be traced out. It traverses the posterior ventral part

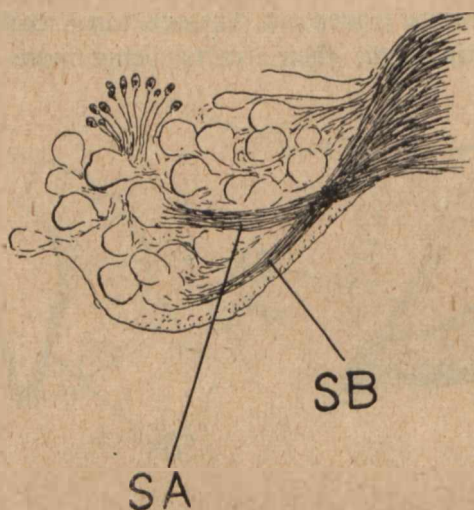


Fig. 10. *Periplaneta americana*: the section of the olfactory lobe with the sensory fibers shown.

of the brain. I have found it in the bee, in *Lucanus cervus*, and in *Diptera*, too. Bretschneider has noticed the connection between the medulla externa and the suboesophageal ganglion in *Lepidoptera*. There is no doubt, that this connection is analogous; I doubt, however, whether these fibers really arise wholly from medulla externa (E). May be there is a certain bundle joining the fibers going from the lamina ganglionaris. The connection between the lamina ganglionaris and the suboesophageal ganglion appears undoubtedly in all *Pterygota* that have properly developed compound eyes. Very likely, such a direct connection of the optic organ with the suboesophageal ganglion, omitting the brain and the superior centers, is one of the reasons, that cause a zigzag flight of insects in con-

sequence of the reflectorial changes in its direction before the superior centers begin to work.

The labrofrontal nerves have been examined in various insects. Not in all insects, however, they are given off from the brain, separately. As I have already mentioned (1936) these nerves in *Lucanus cervus* and in *Orictes nasicornis* go out together with the antennal nerves. The roots of the labral and frontal nerves are in many insects very close each other: the origin of each of them, is not therefore, clearly explained.

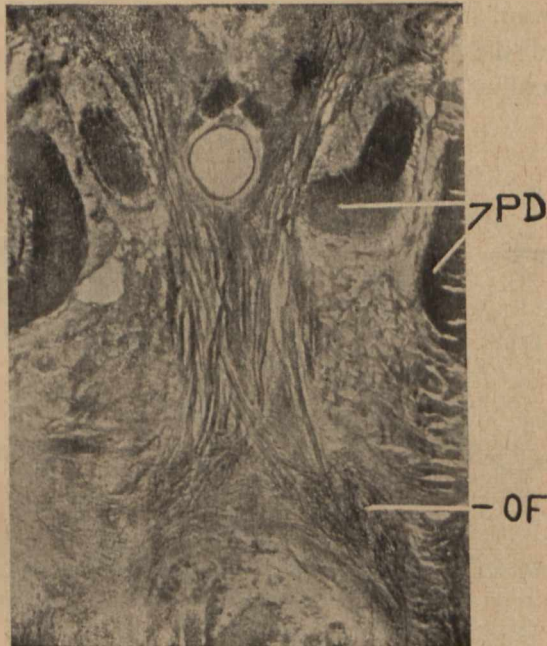


Fig. 11. *Apis mellifica*: impregnated after Cajal. Posterior parts of the brain with apparent ocellar tracts and their terminals

My researches prove, that the labral nerve arises from the suboesophageal ganglion, while the frontal nerve arises from the tritocerebrum. The tritocerebrum in *Hymenoptera* is almost completely reduced. The nerves come out, therefore, from the brain, almost immediately beneath the olfactory lobe (fig. 6, LF and 13. L, F). The tritocerebrum in the cockroach, on the other hand, is developed very well, those nerves make their exit, therefore, much more distant from the olfactory lobe (fig. 2, LF). According to Hansström the labrofrontal nerves in *Petrobius* (*Apterygota*) arise in the tritocerebrum. My researches show, that the tritocerebrum can give rise to the frontal nerve only. I cannot state, however, whether

the branches of this nerve reach further than the tritocerebrum does, or whether to the labral nerve do not join some fibers given off from the tritocerebrum: in any case, the main root arises from different ganglia, as I have already mentioned. A similar condition of the labral and frontal nerve roots is known in *Odonata*. Baldus has proved that the first arises in the suboesophageal ganglion, the second — in the tritocerebrum. Considering the above mentioned data, we can suppose that the origin of these nerves in insects, at least in *Pterygota*, is the same.

Aside from the frontal, odd *), sympathetic nerve, the brain in insects gives off the even, sympathetic nerves. The researches of Hanström and Pflugfelder show that the representatives of the greatest part of the insect families have two pairs of such nerves: the nerve of corpora

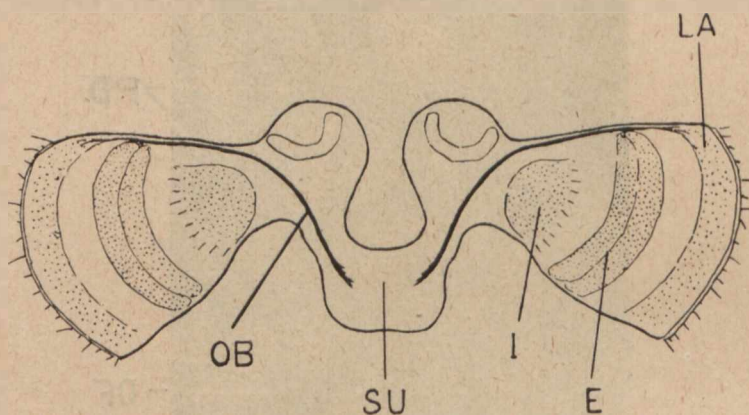


Fig. 12. *Apis mellifica*: schematical drawing of the posterior and ventral parts of the brain sectioned to make evident the connection between the optic lobe and the suboesophageal ganglion.

cardiaca I and the nerves of corpora cardiaca II. These nerves run to the corpora cardiaca and to the corpora allata connected or accreted with these latter. The maternal cells of the mentioned nerves are located in the brain interiorly — (*pars intercerebralis*).

The nerve of the corpora cardiaca I, rather its roots, traverse the ventral side of the brain and cross one another (fig. 2 and 6, CA I). The roots of the nerve of the corpora cardiaca II (CA II) run in the dorsal part and do not cross one another. I have found these nerves in all insects I have investigated. Their connection with the maternal cells was much easier to be traced out on the nerve of the corpora cardiaca II than on

*) This nerve takes its beginning as a pair of nerves, which later on confluence into one nerve.

the nerve of the corpora cardiaca I. These nerves almost in all *Coleoptera*, *Notonecta glauca*, and in the cockroach come out from the brain in the form of two separate pairs of nerves (fig. 2 and 4, Ca I, Ca II). In *Hymenoptera*, on the other hand, they are always united into one pair only (fig. 6, 14, and 15, Ca I, II). This is in the bee and probably in *Hymenoptera* the sole pair of nerves that come out from posterior of the brain.

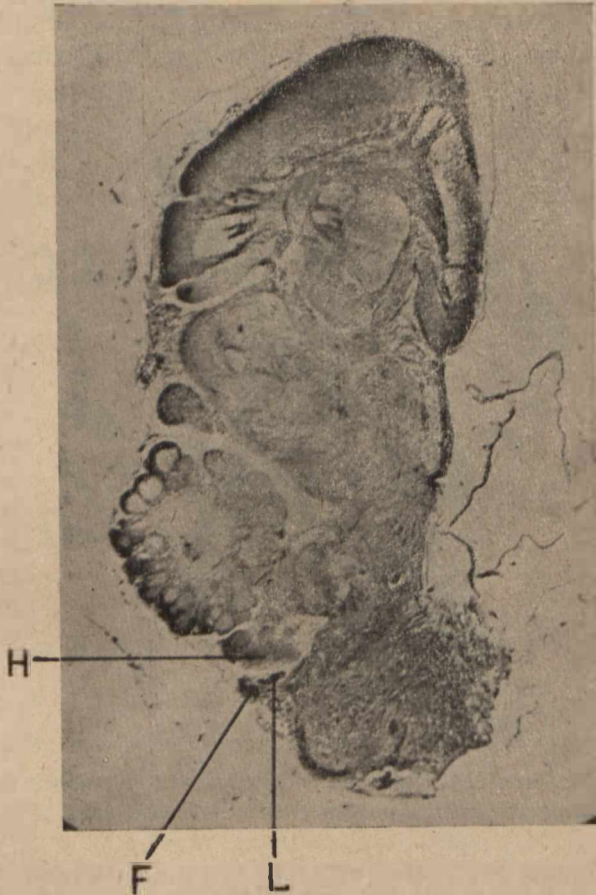


Fig. 13. *Vespa germanica*: impregnated after Cajal. Approximate lengthwise section of the brain.

The cardiac nerves in the queen-bee are much thicker than in the worker. This phenomenon is probably connected with the dimensions of the innervated glands. Hanström, for instance, states that corpora allata in the queen-bee are eight times larger than in the worker. In drones I did not find, however, any difference in the thickness of the cardiac nerves, comparing them with the worker's, although Hanström wri-

tes, that the corpora allata are larger in the worker than in the drones. The roots of these nerves are sometimes even such more apparent in the drones than in the worker. Besides in studying a greater number of individuals, representing the various casts of bees, one comes across some fluctuations in the thickness of their cardiac nerves. Very likely it depends upon the differences in the glandular dimensions within the same cast. The glandular dimensions can vary according to the age: Holmgren, for instance, states (according to Hanström quotation) that in old queen-termites the corpora allata as well as the corpora cardiaca increase in

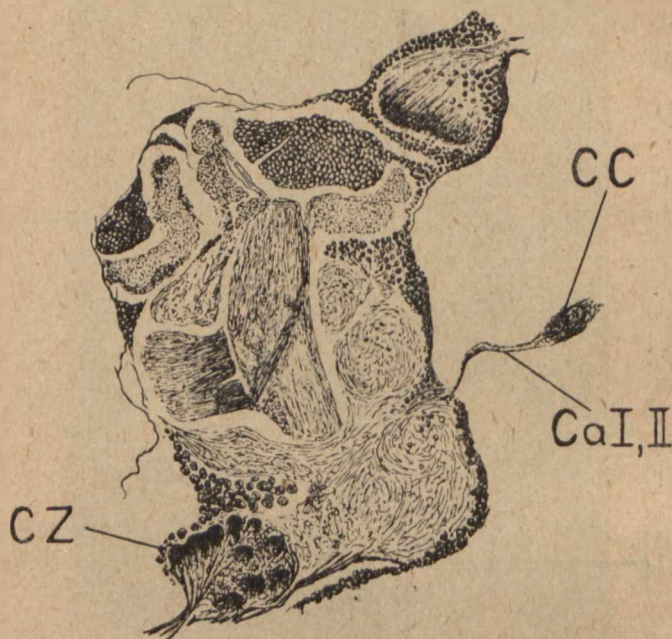


Fig. 14. *Apis mellifica*: The drone. The brain sectioned almost obliquely in the point wherefrom the cardiac nerves, connected in one, arise.

size and even change their structure. Detinova noticed recently that the corpora allata in the gnat increase in size just during the imago life.

Among several authors, as for instance Wigglesworth, Pflugfelder and Hanström, who examined the glands of insects, the latter has lately devoted many papers to researches on the activity and structure of the corpora allata and corpora cardiaca. These glands, according to Hanström, exert a considerable influence upon the genital glands: their activity is to a certain degree analogous with the activity of the hypophysis in vertebrates. The hypophysis is innervated by the supraoptic nucleus. The cardiac nerves arise in pars inter-

cerebralis where are their maternal celled. Hanström noticed in the course of his interesting researches (1943) a second similarity with the vertebrates, namely: in the same way as the cells in the hypothalamus secrete some substances acting as glands so also do the maternal cells of the cardiac nerves.

Besides the above described nerves coming out from the brain, I have not found any other nerves and it seems very doubtful, whether they can exist at all. The tritocerebral nerve and its even roots both described by Ionescu in the bee, have not been found by me in any case, neither in bee, nor in any other *Hymenoptera*. Janet mentions the appearance of the odd tritocerebral nerve in the ant (*Lassius niger*). It seems to me that the place, where the nerve should come out, according to Janet's description, belongs rather to the suboesophageal ganglion.



Fig. 15

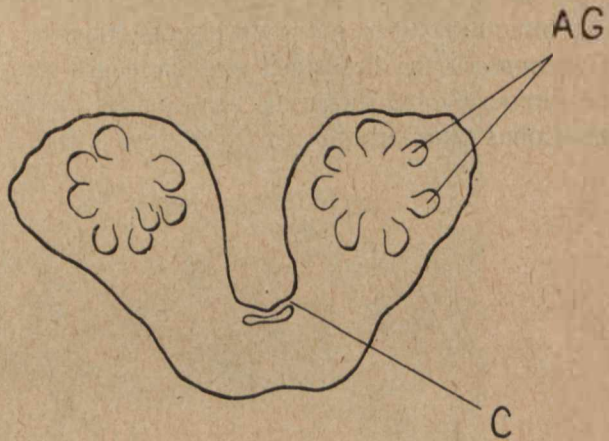


Fig. 16

Fig. 15. *Apis mellifica*: The drawing of one half of the brain showing nerves arising from its posterior parts. (The cardiac nerves).

Fig. 16. *Apis mellifica*: The outlines of the lower part of the brain and suboesophageal ganglion sectioned transversally.

In my testing materials, not many as there were, samples of ants, I could not find the nerve. Kenyon described the salivary gland nerves in the bee; they are said to arise from the lateral parts of the tritocerebrum. Ionescu describes these nerves too. In spite of the thorough researches I did not find them in the bee. I did not find them either in the related *Hymenoptera*. Very likely, what the above named authors have defined as the salivary nerves are really the cardiac nerves. Their course and connections in *Hymenoptera* have been traced out lately. As regards the figure 12 placed in the Ionescu's paper there is no doubt, that we deal

with the cardiac nerves, not with the salivary nerve, as the author has suggested.

Writing about the nerves, coming out from the brain, I do not take into account the tritocerebral commissures, for they really do not come out from the brain, but merely connect some parts of it. Hanström gives forth a very distinct description of these commissures in *Petrobius*. At any rate in insects I have investigated especially *Hymenoptera*, (fig. 16, C) they have these commissures much less developed than *Muchilidae* (*Apterygota*) — a family, to which *Petrobius* belongs.

The Olfactory Lobe.

A characteristic feature of the olfactory lobes in *Hymenoptera* is the absence of antennal glomeruli in the central region of the lobes; these glomeruli are there arranged more peripherally (fig. 5, 8, 9 AG and 17). The olfactory lobes in other insects may be similar, of course, but in *Hymenoptera* the described state appears as a rule. The dimensions of the glomeruli are different, as Ionescu has noticed in case of the bee. Lobus olfactorius forms in its lower part a small lobulus (fig. 17 H).

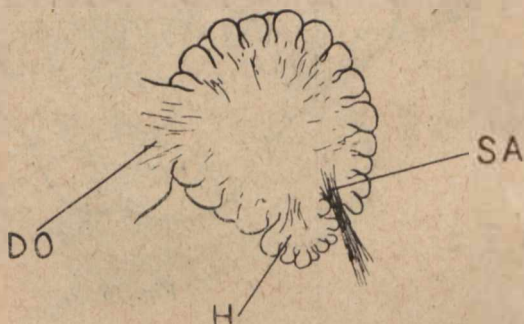


Fig. 17. *Apis mellifica*: The olfactory lobe sectioned approximately in a lengthwise way. The section is made in a little different place than on the fig. 8.

In *Vespa* this lobulus is much larger than in the bee (fig. 13 H). The lobuli contain relatively greater amount of glomeruli of smaller dimensions. In *Vespa*, particularly in *Vespa crabro*, the whole of the upper part of the olfactory lobe, forms small lobuli, rather foldings.

The olfactory lobes in *Periplaneta* are more or less oval. In one place the particular glomeruli protrude towards the dorsal lobe; (fig. 18, AP): they often confluence together. The olfactory lobes are almost entirely filled with the glomeruli of various dimensions, just as in *Hymenoptera*. The anterior parts contain a greater quantity of the small glomeruli than the posterior ones. The glomeruli are arranged here more chaotically

than in *Hymeroptera* where for the most part, their narrow tips are turned towards the middle. The olfactory lobes in *Trixalis nasuta* (fig. 19 and 20, LO) differ from those in *Periplaneta*. The antennal glomeruli of the *Periplaneta* are perhaps more like the glomeruli of other insects, even less closely related to it than with those, we find in *Trixalis nasuta*. The antennal glomeruli in *Trixalis nasuta* (AG) are small, considerably smaller, than in *Periplaneta*; they are also more closely arranged. They

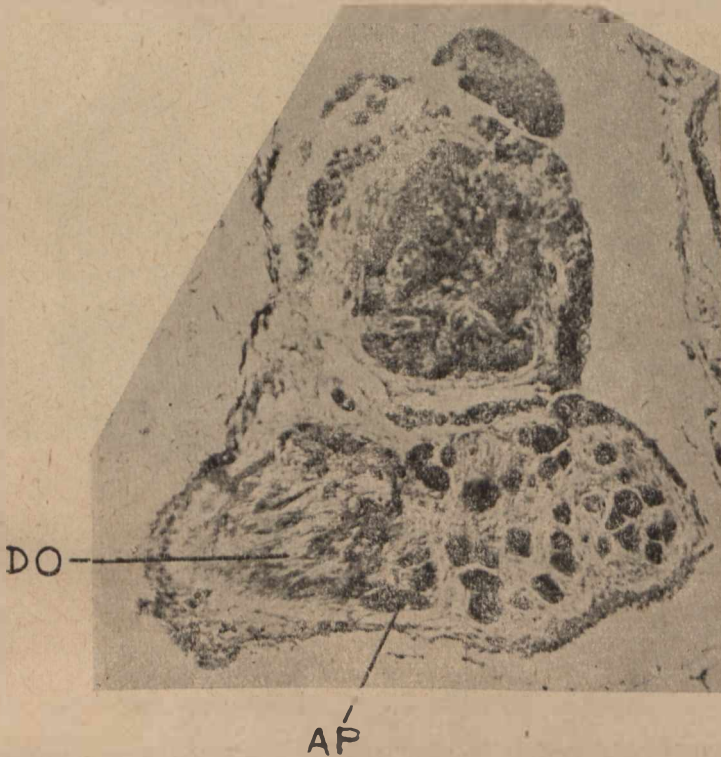


Fig. 18. *Periplaneta americana*: Stained with iron-hematoxylin. The deutocerebrum and a part of the protocerebrum sectioned approximately lengthwise, a little closer to one margin.

do not fill the median parts of the olfactory lobes so closely as one can see in *Periplaneta*. Hanström describes a similar structure in the case of *Acrididae*, to which *Trixalis nasuta* belongs also. Very likely on the different structure of the glomeruli depends the ability to react to some special smells or of feeling them in some particular way or of perceiving perhaps some other stimuli. On this point *Acrididae* differ from *Periplaneta* and from the insects, whose glomeruli are the same as in the

species belonging to the genus *Periplaneta*. The olfactory lobes and the glomeruli they contain demand farther researches in many insects.

Moreover, I have found some differences in *Periplaneta* in the structure of the olfactory lobe, which are related to sex. And so: In the males the larger glomeruli or the glomeruli concentrations (fig. 21, CZ) are located quite close to the antennal exit. As a result of my farther researches I have found similar differences in the bee and the wasp (fig. 22, CZ). The larger glomeruli or their concentrations are located, for the most part at least, in the upper and lateral parts of the olfactory lobes. The

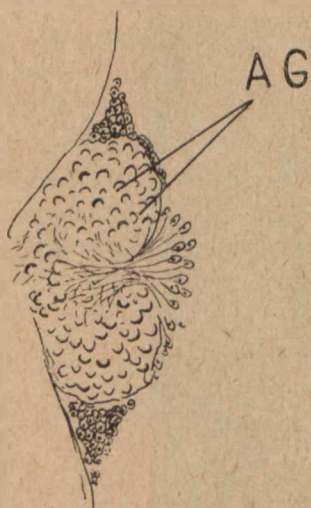


Fig. 19

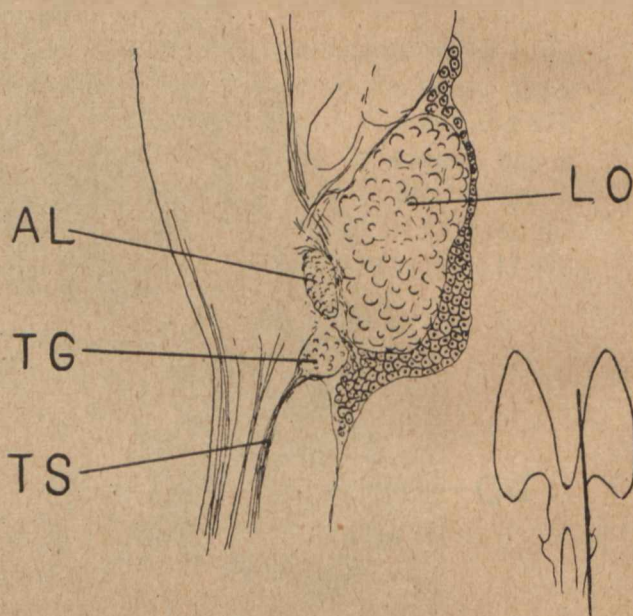


Fig. 20

Fig. 19. *Trixalis nasuta*: The olfactory lobe sectioned almost lengthwise.

Fig. 20. *Trixalis nasuta*: The olfactory lobe and the tritocerebrum sectioned lengthwise.

concentrations (CZ) look sometimes like very large glomeruli splitting into many small ones. The interior bundles of the sensory fibers running to these concentrations is larger in the drone than in the worker. The sexual differences in the olfactory lobes were hitherto noticed in *Lepidoptera* only. Bretschneider has described them in the species *Bombyx mori* and in *Lasiocampa quercus*; the sexual dimorphism is especially striking in this latter species. The antenna in male individuals are much larger than in female ones; they are provided with greater number of the sensory apparatus, too. (Sinneshaaren-Bretschneider). As the result of my present researches I suppose that the glomeruli in the

male individuals, formed otherwise than in females are the centers of the special sense of smelling of some special kind. This particular sense serves to recognize and find out the opposite sex. It is known, that many insect females give off a special smell to attract the male. About the phenomenon of attracting males by the females in insects wrote lately i. Prüffer *).

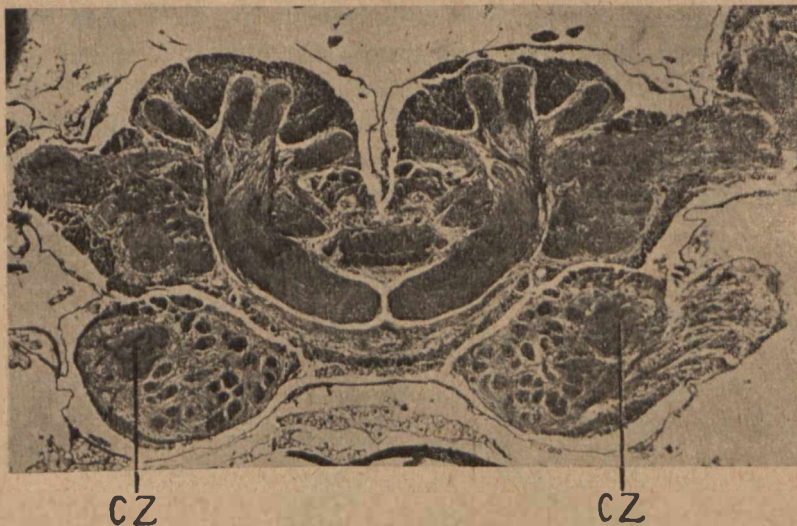


Fig. 21. *Periplaneta americana*: Male individual. Stained with iron-hematoxylin. The brain sectioned frontally.

The connections of the Olfactory Lobes.

In *Hymenoptera* the connections of the olfactory lobes are exactly described only in the bee. We owe much to works by Kenyon and Ionescu. The results of my researches on *Hymenoptera* do not completely agree with the results of the above named authors.

The inner olfactory globular tract in *Vespa* *) (fig. 23, T1) has two large branches: one of them (V1) is located close to the exit where the tract leaves the olfactory lobe; the other is located a little above it (V2).

*) Quelques-unes recherches sur l'odeur sexuelle chez les femelles de *Lymantria dispar* L. Travaux de l'Institut de Zoologie de l'Universite de Wilno, N 28, 1935.

*) *Tractus olfactorio-globularis* in insects — according to Hanström. Inner Antenno-cerebral tract in the bee — according to Kenyon. *Funiculus antennalis superior* in the bee — according to Ionescu.

As regards the first one I could not trace out where it runs to, probably it may enter the central body, in part at least. The second one most likely corresponds to the optico-antennal branch described by Ionescu in the bee. I did not find there, however, the direct connections with the optic lobe, as Ionescu observed it. I did not find them neither in the bee nor in the related *Hymenoptera*. May be only a few fibers enter the medulla interna, but even this is doubtful. The main bundle of fibers of the olfactoro-globular tract terminates by entering the calices from their posterior margin, they enter not merely the inner calyx, but the outer one, too.

Beside the two main branches of the discussed tract in *Vespa* there appear, apparently, some others, too. For instance, I have observed some particular fibers proceeding to the inferior optic commissure (*tractus opti-*

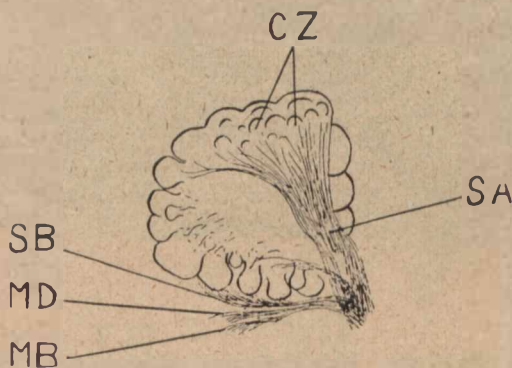


Fig. 22. *Apis mellifica*: The drone. The olfactory lobe sectioned almost lengthwise.

cus). At any rate, those other fibers, aside from the main tract, are not frequent and are considerably smaller. The exterior olfactoro-globular tract *) (TE) arises in the olfactory lobe in the nearest environments of the inner tract. Although both tracts run close one to another they do not made of fibers, which joined from parts, situated near the lobus olfacto-one; its final part is also easier to be traced out. Close to the inferior optic commissure, which goes horizontally, the exterior tract gives off a few branches. I cannot, however state, whether those ramifications are not made of fibers, which joined from parts, situated near the lobus olfactorius, but not from the lobus olfactorius itself. On the fig. 23 marked TR, one of them ramification is shown to be running downwards. The exterior tract, together with the bundles proceeding from the compound eyes make

*) The analogous tract in the bee: the outer antenno-cerebral tract according to Kenyon, and *funiculus antennalis inferior* according to Ionescu.

their entrance in the calyx. The endings, just as in the inner tract, reach the next, neighbouring calyx.

I have inserted this description of the connections between olfactory lobes with the protocerebrum in *Vespa germanica*. The connections differ only slightly from those in the bee or in other related *Hymenoptera*. For instance, the first branch (V1) of the inner tract in *Xylocopa violacea* is smaller than in the bee. I doubt, however, whether there is any major difference at all in the described tracts in *Hymenoptera*. I must mention, however, that I could not examine those tracts too closely neither in *Ichneumonidae* nor in the ant, for the material, I have had, has been insufficient for that purpose.

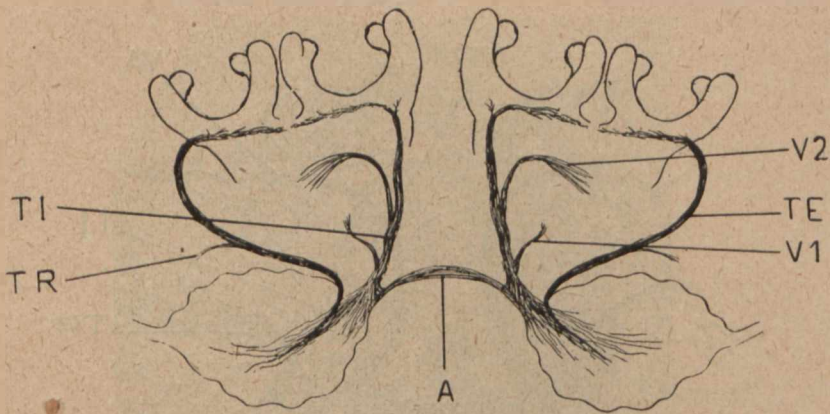


Fig. 23. *Vespa germanica*: The scheme illustrating the distribution of the olfactory tracts within the brain.

The protocerebral tracts in the olfactory lobes in *Periplaneta* differ considerably from those in *Hymenoptera*. The inner olfactoro-globular tract (fig. 24, TI) has not so many branches as in *Hymenoptera*. Close to the central body it forks into two branches: one goes anteriorly, (VA), the second-posteriorly (VP) beneath the calyx. Not all the fibers of those two branches make their entrance into the calyx; some of them go further. The two branches are the main bands of this tract. Just as in *Hymenoptera* or in the insects described beneath it is possible that small and not numerous branches can appear in the inner olfactoro-globular tract, too. The cockroach has not got the external globulo-olfactorius tract. Instead this tract, there is another tract, appearing to take its origin entirely in the lobus olfactorius (fig. 24, 25 TP). It is, however a tract, consisting mainly of motor fibers running towards the antenna, as I have already previously described. Probably also some other fibers from the olfactory

lobe or its neighbourhood join the tract, because it is broad and it seems unlikely to me, that it is formed only by one of the mentioned above roots.

The connections of the olfactory lobes in *Periplaneta* were lately examined by H a n s t r ö m. The results I have obtained in my researches do not completely agree with the data, published by him. These differences are to be seen by comparing the figure 583 of H a n s t r ö m's (1928) paper with the figure 24 of the present paper.

About the olfactory-globular tracts (Riechstrang) in *Coleoptera* I gave a description in my previous paper (1936). There is only one pair of these tracts, like in *Periplaneta*. In *Lepidoptera* and also in *Diptera* (*Eristalis tenax*) I found the same state. I was not in position to examine the rami-

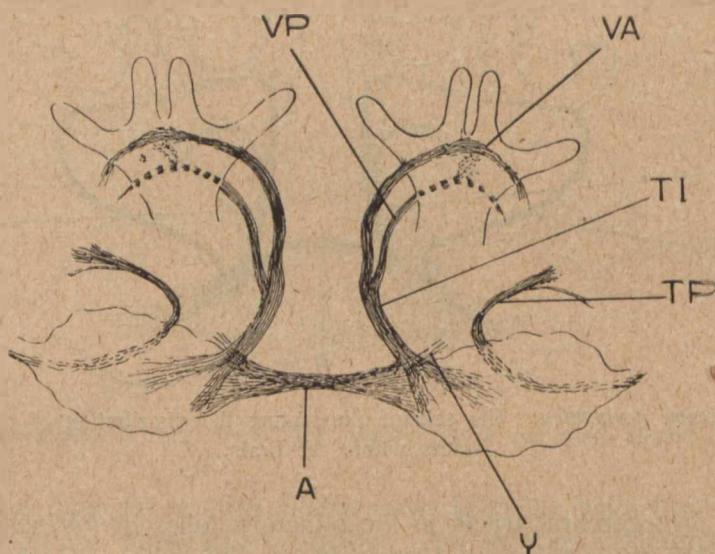


Fig. 24. *Periplaneta americana*: The scheme illustrating the distribution of the olfactory tracts within the brain.

fications of these tracts in *Lepidoptera*. In any case this tracts has not many branches and it is rather more similar to the analogous tract in *Hymenoptera*. In *Eristalis tenax* (fig. 26. T I) this tract has not got such large branches, as in the described above insects. Such a simplification of the tracts may be explained by the fact, that the main sense organon is the organon of vision and not of smelling.

In comparing the above described connections in various insects species, the attention is called by *Hymenoptera*. Their inner tract is branched

much more and, what is most important, there are two pairs of the tracts make their entrance into the calyx. In other insects there is one pair of tracts only, the inner one, connects the olfactory lobe with calices or corresponding forms in other insects.

The double connection depends certainly upon the corpora pedunculata being in *Hymenoptera* developed very well. Their complicated structure I have previously described (1934). The corpora pedunculata in *Periplaneta* are undoubtedly more simple than in *Hymenoptera*.

Writing about the connections of the olfactory lobes with the corpora pedunculata I should mention that in other insect species I did not find such distinct crossings of the fibers of the inner tracts as in *Coleoptera*

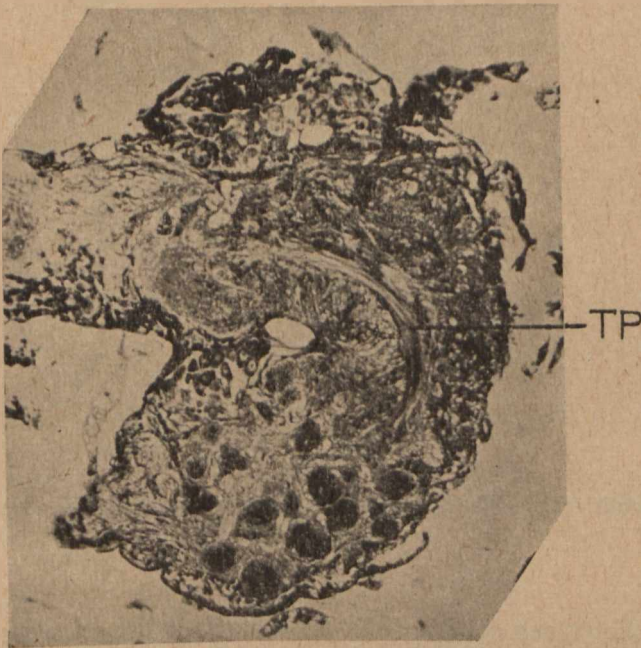


Fig. 25. *Periplaneta americana*: Stained with iron-hematoxylin. The section of the olfactory lobe and a part of the protocerebrum.

(fig. 19 of my paper of 1936). I have seen in *Periplaneta* only distinctly crossing each other bundles of fibers (fig. 24 Y) but I am not certain if those crossing fibers run from opposite olfactory lobes or from some other part of the cerebrum. Those bundles of fibers come out on the external side of the inner tract, it means, on a different side, than is shown in fig. 19. I could not trace out the entire way, passed by these fibres,

but they do not reach the external calyx. Interesting are the suppositions of Hanström, who assumes, that the crossing of olfactory tracts appears in *Petrobius* likewise as in *Oryctes nasicornis* (fig. 19). The problem of crossings of the olfactory tracts needs farther investigations. The antennal commissure (A) which consists of fibers, arising from the opposite olfactory lobes and therefore of fibers, partially crossing one another does not need of course, to be more investigated.

To finish the description of the olfactory tracts in the brain I should like to add, moreover, that I did not find any more tracts connecting the central body with the olfactory lobes. On the other hand, however, I think that such tract should exist. If they do exist, they should consist of mere

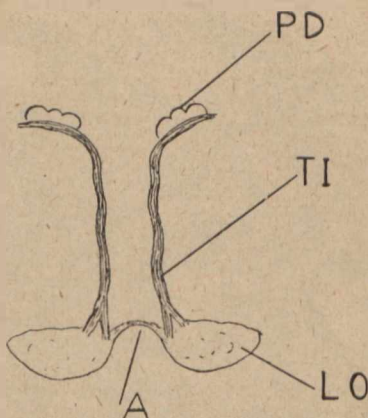


Fig. 26. *Eristalis tenax*: The scheme of the inner olfactory-globular tracts and of their connections.

small branches given off from the main tract or they are separate minute tracts coming out from the olfactory lobe itself.

Aside from the tracts proceeding in the brain from the olfactory lobe, there are also direct connections going to the suboesophageal ganglion. For instance, the connection going to the suboesophageal ganglion in *Periplaneta* (fig. 27, AB) is formed by the tract, proceeding from the above mentioned antennal glomeruli (fig. 18, AP) which protrude towards the dorsal lobe. As far as I know, the connection between the suboesophageal ganglion and the olfactory lobe are in the literature hitherto not mentioned.

The Tritocerebrum.

The tritocerebrum in *Hymenoptera* — as I have already mentioned previously — is almost completely reduced; in the cockroach, on the other hand, it is developed very well. The tritocerebral glomeruli (fig. 3 and 27, TG) are really the concentrations of almost spherical forms that to a certain degree resemble the antennal glomeruli, although they are smaller and more closely arranged in the part of the tritocerebrum which is close to the deutocerebrum; looking further backwards they diminish and form as if a spotty substance (Bretschneider's Punktsub-

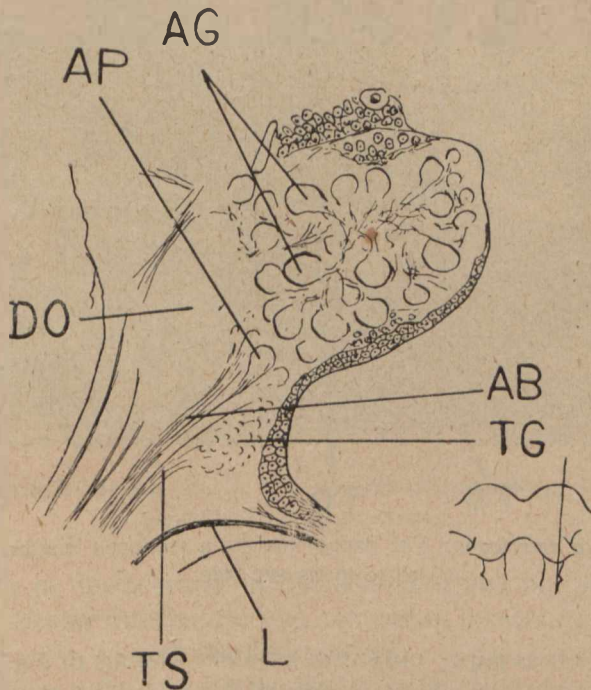


Fig. 27. *Periplaneta americana*: The deutocerebrum and the tritocerebrum sectioned longitudinally.

stanz). I enclose here the description of the connections of the tritocerebral glomeruli, for heretofore it is not known exactly. The tritocerebral glomeruli give off a tract to the olfactory lobes and to the protocerebrum (fig. 28 TO). On the opposite side the broad tract (fig. 27 TS) connects them with the subesophageal ganglion. The tritocerebral glomeruli in *Trixalis nasuta* (fig. 20 TG) are located more close to the olfactory lobes than in *Periplaneta*; the particular glomeruli are here much smaller and they confluence together much more apparently. The sections through

certain directions of the brain in *Trixalis nasuta* are strikingly similar with the drawings of Viaillanes drawn of *Oedipoda coerulescens*. In *Periplaneta*, too, these parts of the brain are quite similar. It is undoubtful that in *Orthopteroidea* and *Blattoidea* there is a more or less similar structure of the tritocerebrum.



Fig. 28. *Periplaneta americana*: The part of the brain sectioned lengthwise a little more close to its one side.

In his extensive paper published in 1940 Hanström encloses the drawing (217) of Sanchez; it shows the axons of the globular cells in *Periplaneta orientalis*. The numerous offshoots are there not on the mere endings of the axon only, but almost on its entire length. My researches corroborate this phenomenon entirely. I have found similar offshoots in the species investigated by Sanchez; my recent researches allow me to suppose that they exist in the bee, too *). Very likely these small offshoots stay in some connection with the insect intelligence. The

*) On the basis of my recent studies I have stated that the axons proceeding from the outer and inner calyx do not run in a parallel line one to another, as I thought before, but they partially cross one another and pass from one root to the other—just as Ionescu supposed.

smaller these offshoots are the greater number of them can be contained within one axon and the greater is the number of the contacts. As one can judge by the outer structure of the cauliculus and beams (balken) i. e. roots of corpora pedunculata, not all insects are provided with such small offshoots, but very many insects, nevertheless, have them. It is undoubtful that the insect intelligence depends, first of all, upon the size of the corpora pedunculata; such a conclusion has been clearly brought forth by Hanström. As an exemple I enclose also the schematic drawing of the frontal section through the brain of the workers in the bee and in the ant (*Formica rufa*). Both sections are brought to equal dimensions (fig. 29). It shows apparently that the calices are larger in the ant than in the bee, and thus fill the brain more compactly. It behoves to suppose, therefore, that the ant is more intelligent than the bee. It must, however, depend also on their more or less complicated structure. The corpora pedunculata, or rather their calices, reach the

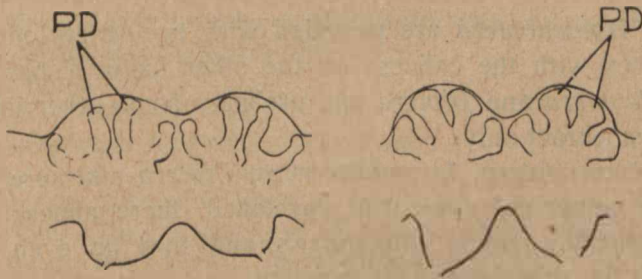


Fig. 29. The brain in the bee and in the ant (*Formica rufa*) sectioned frontally and brought to equal dimensions.

highest degree of development in *Hymenoptera* and one must agree that evidences of greater intelligence one can see in insects, belonging to *Hymenoptera* than in insects of other groups. As one can assume basing upon the location of the brain in the investigated *Hymenoptera* the corpora pedunculata are located in its dorso-anterior part. It is to a certain degree analogous with the location of the forebrain of vertebrates that is quite similarly located dorso-anteriorly. The development of the forebrain, is commonly said to be closely connected with animal intelligence.

Conclusions.

1. The brain in *Hymenoptera* and in *Periplaneta* is differentiated according to the sex. These differences appear in the glomeruli, which are in some places of the olfactory lobes and which are formed a little otherwise in the case of males than in the case of females. According

to Bretschneider's description the similarly formed glomeruli appear also in the male individuals of certain butterfly species: *Lasiocampa quercus* and *Bombyx mori*. It behoves to suppose, therefore, that the males in all these insects are provided with the centers of a special sense of smelling to recognize and find out the females.

2. The brain in *Periplaneta* gives off a pair of nerves hitherto unknown. I call them „*nervi medii*“, for they arise from the parts of the brain, which are close to the median brain.

3. The olfactory tracts arising from the olfactory lobes as well as their location within the brain in *Vespa germanica* and *Periplaneta* are shown on the figures 23 and 24.

4. The motor fibers of the antennal nerves in all insect species arise in the suboesophageal ganglion, and in some species they can take origin not only from nerves, conveying stimuli from compound eyes but also from the ocelli. In the dorsal lobe, motor nerves can take their origin only partially.

5. The *Hymenoptera* are provided with two tracts connecting the olfactory lobes with the calices; on the other hand, *Periplaneta*, *Lepidoptera*, *Coleoptera* and *Diptera* and probably some other insect species have one such a tract only.

6. In *Hymenoptera*, *Lucanus cervus*, *Diptera* and surely in all the insects with compound eyes well developed, there appear direct connections joining the lamina ganglionaris, and, may be, even the medulla externa, with the suboesophageal ganglion.

7. The olfactory lobe in *Periplaneta*, and undoubtedly in other insect species too, is directly connected not only with the brain, but with the suboesophageal ganglion, too.

8. In the bee, at least in the queen and workers, the olfactory lobe is provided with three fiber bundles and not two, as was supposed till now (Ionescu).

9. The ventral part of the olfactory lobe in the bee, like in the wasp, forms a lobulus. It is much larger in the wasp, than in the bee.

10. I did not find the tritocerebral nerve in the bee, nor in *Vespa*, nor in the related *Hymenoptera* at all. I did not find, too, the salivary nerve (Speicheldrusennerv-according to Ionescu) neither in the bee nor in *Vespa*. Very likely, what the authors described (Kenyon and Ionescu) as the salivary nerve will turn up to be the cardiac nerves in the light of recent researches.

EXPLANATION OF ABBREVIATIONS.

- A — antennal commissure.
- AB — connection between the olfactory lobes and the suboesophageal ganglion.
- AG — antennal glomeruli.
- AL — forms probably analogous with the protruding glomeruli (AP) in *Periplaneta*.
- AP — glomeruli protruding towards the dorsal lobe.
- B — pons cerebalis.
- C — anterior tritocerebral commissure.
- Ca I. — The first nerve of the corpora cardiaca.
- Ca II. — second nerve of the corpora cardiaca.
- Ca I, II. — both nerves of the corpora cardiaca joined.
- CC — cardiac corpus (*corpus cardiacum*).
- CZ — concentrations of glomeruli within the male olfactory lobe.
- DO — dorsal lobe (*lobus dorsalis*).
- E — medulla externa.
- F — frontal nerve (*nervus frontalis*).
- FP — branch given off from the motor antennal nerves to the first segment of the antenna.
- H — ventral lobulus in the olfactory lobe.
- I — medulla interna.
- L — labral nerve (*nervus labralis*).
- LA — lamina ganglionaris (aussere Fibrillarmasse).
- LF — labrofrontal nerve (*nervus labrofrontalis*).
- LO — olfactory lobe (*lobus olfactorius*).
- MB — antenno-motor fibers arising from the suboesophageal ganglion.
- MD — antenno motor fibers coming from the dorsal lobe.
- MO — antenno-motor fibers arising from the ocellar tracts.
- MS — antennal motor sensory nerve.
- NM — median nerve (*nervus medius*).
- NT — tegumentary nerve (*nervus tegumentaris*).
- O — ocelli.
- OB — tract connecting the lamina ganglionaris with the suboesophageal ganglion.
- OC — ocellar nerve.
- OF — final part of the ocellar tract.
- PD — corpora pedunculata.
- S — sensory fibers.
- SA — inner bundle of the sensory fibers.
- SA₁ — inner bundle (smaller) of the sensory fibers.
- SB — ventral bundle of the sensory fibers.
- SU — suboesophageal ganglion.
- TE — exterior olfactoro-globular tract.
- TG — tritocerebral glomeruli.
- TI — inner olfactoro-globular tract.
- TO — tract connecting the tritocerebral glomeruli with the olfactory lobe and with the protocerebrum.
- TP — antennal motor fiber bundles running from the protocerebrum and which come in contact with the tracts coming from the compound eyes.

- TR — ramification of the exterior olfactory tracts.
 TS — connection between the tritocerebral glomeruli and the suboesophageal ganglion.
 VA — anterior branch.
 VP — posterior branch.
 V1 — first branch.
 V2 — second branch.
 Y — fibers crossing one another given off probably from the opposite olfactory lobes.

All microphotographs made by Dr. A. Demianowicz

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STRESZCZENIE

Materiały histologiczne do badań nad mózgiem owadów gromadziłem przed wojną. Znaczna część tych materiałów uległa zniszczeniu. Obecnie posiadam wystarczający materiał dla dokładniejszych badań tylko nad nielicznymi gatunkami, jak: *Periplaneta orientalis*, *P. americana*, *Apis mellifica* i *Vespa germanica*. Preparaty z mózgu innych owadów służyły mi głównie jako materiał porównawczy.

Nerwy odchodzące od mózgu.

Mózg *Periplaneta americana* został szczegółowiej zbadany przez Bretschneider'a. Na swych preparatach *Periplaneta orientalis* a także *P. americana*, znalazłem jeszcze jedną parę nerwów dotąd nie notowaną, wychodzącą prawie na granicy *deutocerebrum* (ryc. 1, 2 NM). Nerwy te wychodzą z przedniej strony mózgu ze środkowych jego części, dlatego też nazywam je „*nervi medii*”. Korzonki ich biegną aż od *tritocerebrum*, gdzie zaczynają się w pobliżu kłębków (*glomeruli*) tritocerebralnych (ryc. 2, 3 — NM). Dokąd biegną same nerwy, nie mogłem wysledzić. Rozmiary tych nerwów zapewne ulegają wahaniom i przypuszczalnie są większe u samicy niż u samców.

Nerwy antenalne owadów, szczególnie u błonkówek, są więcej złożone niż to można przypuszczać z dotychczasowych opisów. U *Vespa* biegną ku antenie, z różnych stron mózgu, przede wszystkim dwa główne pęczki — szlaki nerwowe motoryczne (ryc. 5). Jeden z nich (MD) wychodzi z tak zwanej części motorycznej w *lobus dorsalis* w *deutocerebrum*; od niego odchodzi gałązka (FP) ku pierwszemu członowi anteny. Bardzo możliwe, że do niej dołącza się wiązka czuciowych włókien antenalnych. Drugi większy pęczek składa się właściwie z dwu pęczków. Część włókien (MB) biegnie od zwoju podprzetykowego, a inna część (MO) od dróg łączących *ocella*. Oba te pęczki zbliżają się do siebie na poziomie *deutocerebrum* i biegną dalej razem ku antenie. Oprócz tych dwóch głównych szlaków nerwowych — motorycznych wchodzi do anteny jeszcze inne, mniejsze. Między wyżej opisanymi nerwami osy i pszczoły zasadniczych różnic nie znalazłem. Załączam schemat ilustrujący m. i. przebieg analogicznych szlaków u pszczoły (ryc. 6). I o n e s c u, natomiast, ograniczał pochodzenie włókien motorycznych u pszczoły wyłącznie do *deuto-*

cerebrum. Załączam również rysunek (ryc. 7) uwidoczniający, według moich badań, nerwy odchodzące od mózgu z przedniej jego strony. Czuciowe i motoryczne nerwy antenalne (MS) odchodzą razem. Nerwu tritocerebralnego, który podawał Ionescu, nie znalazłem.

U *Periplaneta* biegną ku antenie niemniej niż dwa główne pęczki włókien motorycznych (ryc. 2). Podobnie jak u błonkówek jeden z nich (MD) wychodzi z *lobus dorsalis*, drugi zaś (MB) bierze początek w zwoju podprzetykowym. W skład pierwszego z nich wchodzi również włókna, wychodzące z *protocerebrum* (ryc. 24 TP). Biegną one nieco w innej płaszczyźnie, niż pęczki włókien na ryc. 2. Włókna te podawał już Bretschneider. W *protocerebrum* stykają się one z drogami biegnącymi od złożonych oczu i pośredniczą w przenoszeniu podniet wzrokowych, podobnie jak to się dzieje u błonkówek w opisanych przeze mnie szlakach, idących do oczek niezłożonych. Zwój podprzetykowy u *Periplaneta* (na rysunkach nie uwidoczniiony) jest znacznie więcej oddalony od zwoju nadprzetykowego (mózgu) niż u błonkówek; z tego powodu łatwiej wysledzić szlaki włókien biegnących od zwoju podprzetykowego, gdyż są one widoczne na większej przestrzeni. Nie znalazłem u *Periplaneta* włókien biegnących od dróg łączących oczka (*ocella*). Motoryczne włókna niosące podniety ku antenie od złożonych oczu, podobnie jak u karalucha, znalazłem również u chrząszczy i motyli. Z pewnością występują one i u błonkówek, aczkolwiek nie mogłem ich wykryć.

Oprócz dużego nerwu (MS), u *Periplaneta*, gdzie włókna motoryczne wychodzą razem z czuciowymi, podobnie jak i u błonkówek, znajduje się w bezpośrednim jego sąsiedztwie mały nerw (FP). Pochodzenie tego nerwu jest z pewnością takie same, jak i rozgałęzienia motorycznego nerwu błonkówek, idącego ku pierwszemu członowi anteny. Nerw ten również u *Periplaneta* biegnie ku pierwszemu członowi anteny.

Początek antenalnych nerwów motorycznych w zwoju podprzetykowym wykryłem u wszystkich innych, badanych przeze mnie, owadów.

Fakt, że nerwy motoryczne u owadów częściowo pochodzą ze zwoju podprzetykowego mogą potwierdzać bardzo dokładne badania Fahländer'a nad pokrewną gromadą wijów.

Czuciowe nerwy antenalne, jak to już wyjaśnił szereg badaczy, biorą początek w kłębkach płatów węchowych (*lobi olfactorii*). Według Ionescu u pszczoły zaczynają się one dwoma korzonkami — pęczkami włókien. Jednakże położenie tych korzonków wymaga dokładniejszego wyjaśnienia. Ten, który Ionescu nazywa górnym, przebiega wewnątrz płatu węchowego (ryc. 8 SA), drugi zaś dolny znajduje się głównie nazewnątrz (SB). Oprócz tych korzonków znalazłem jeszcze trzeci,

nniejszy (ryc. 9 SA₁), występujący podobnie jak i pierwszy wewnątrz płatów węchowych. Osy, u których płaty węchowe są większe i nieco innego kształtu niż u pszczoły, posiadają dwa duże wewnętrzne pęczki (ryc. 5 SA), a także włókna biegnące z dolnej części i nieco z boku płatu węchowego ku wspólnemu wyjściu. W płatach węchowych *Periplaneta* wśród szeregu włókien, biegnących ku wyjściu, widoczne są dwa główne skupienia: jedno wewnętrzne, drugie bliżej powierzchni (ryc. 10 SA, SB).

U błonkówek, drogi łączące oczka niezłożone z różnymi częściami mózgu biegną przy samej jego powierzchni (ryc. 6 OC), częściowo krzyżując się. Niektóre rozgałęzienia wchodzą w kontakt z włóknami łączącymi złożone oczy. Od dróg tych u błonkówek odchodzi też gałąź (MO) ku antenie, o której już wspomniałem, pisząc o korzonkach motorycznych nerwów. W tylnej, dolnej części mózgu drogi biegnące od wspomnianych oczek kończą się i rozpadają na drobne gałązki w kształcie piórek (ryc. 6, 11 OF).

U *Periplaneta* drogi od niezłożonych oczek (ryc. 1, 2 OC) biegną prawie poziomo pod kielichami ku mostkowi. Za mostkiem (B) zwracają się ku dołowi i w dalszym swym biegu trudne są do wyśledzenia.

Złożone oczy owadów są całkiem związane z płatami ocznymi (*lobi optici*). Szlaki nerwowe i ich wzajemne ustosunkowanie wewnątrz płatów ocznych jest dość dobrze zbadane, natomiast połączenie płatów z mózgiem wymaga jeszcze szczegółowszych badań. U *Hymenoptera*, *Lucanus cervus*, a także u *Diptera* wykryłem szlak nerwowy, łączący bezpośrednio zwój podprzelykowy z *lamina ganglionaris* (ryc. 12 OB).

Nerwy labrofrontalne były badane u różnych owadów. Nie u wszystkich owadów nerwy te odchodzą samodzielnie, mogą być one połączone razem z nerwami antenalnymi. U błonkówek, nerwy te wychodzą z mózgu prawie bezpośrednio pod płatem węchowym (ryc. 6 L.F, 13 L. F); u karalucha zaś posiadającego dobrze rozwinięte *tritocerebrum*, wyjście ich jest znacznie oddalone od płatu węchowego (ryc. 2 L. F). Według moich obserwacji nerw frontalny bierze u wszystkich owadów początek w *tritocerebrum*, labralny zaś w zwoju podprzelykowym.

Oprócz frontального, nieparzystego, współczulnego nerwu, zaczynającego się parzystymi korzonkami, mogą odchodzić od mózgu jeszcze współczulne parzyste nerwy, opisywane już przez kilku badaczy. Nerwy te biegną ku gruczołowym twórcom *corpora cardiaca* i złączonym z nimi *corpora allata*. Komórki macierzyste wspomnianych nerwów, znajdują się w śródmózdzu (*pars intercerebralis*). Są to właściwie dwie pary parzystych nerwów: nerwy *cor. car. I* i nerwy *cor. car. II*. Nerwy *corpora cardiaca I*, a raczej ich korzonki (ryc. 2, 6 CA I), przebiegają po dolnej stronie mózgu i krzyżują się, korzonki zaś nerwu *corpora cardiaca II*

(CA II), — w górnej jego części i nie krzyżują się. Nerwy te znajdowałem u wszystkich badanych owadów. U karalucha odchodzą one jako dwie oddzielne pary (ryc. 2, 4 CA I, CA II); natomiast u błonkówek są one połączone zawsze w jedną parę (ryc. 6, 14, 15 CA I, II). Pszczoła matka posiada nerwy kardiakalne znacznie grubsze, niż robotnica; stoi to niewątpliwie w związku z wielkością unerwianych gruczołów.

Badaniom czynności i budowy *corpora cardiaca* i *corpora allata* ostatnio poświęcono wiele prac. H a n s t r ö m znajduje pewną analogię co do czynności przysadki mózgowej (*hypophysis*) u kręgowców i czynności wspomnianych gruczołów u owadów.

Oprócz wyżej opisanych nerwów, odchodzących od mózgu, występowanie innych wydaje mi się bardzo wątpliwe. Nerwu tritocerebralnego nie znalazłem nie tylko u pszczoł, ale i u innych błonkówek. Również nie znalazłem u błonkówek ślinowych nerwów, opisywanych przez K e n y o n a i I o n e s c u.

Płat węchowy.

Dla płatów węchowych błonkówek jest charakterystyczne, że w środku nich pozostaje przestrzeń nie wypełniona przez kłębki antenalne. Kłębki te układają się peryferycznie (ryc. 8, 9 AG). Inne owady mogą mieć pod tym względem podobne płaty węchowe, lecz u błonkówek występuje to z reguły. W dolnej części płatu węchowego pszczoł znajduje się płatowaty wypstę (ryc. 17 H), u *Vespa* wypstę ten jest znacznie większy (ryc. 13 H).

Peliplaneta posiada płaty węchowe mniej więcej owalnego kształtu, tylko w pewnym miejscu wybiegają poszczególne kłębki ku *lobus dorsalis* (ryc. 18 AP). Kłębki te często zlewają się z sobą. Płaty węchowe są wypełnione prawie całkowicie kłębkami. Kłębki te są różnych rozmiarów, podobnie jak u błonkówek. Są one jednak bardziej chaotycznie ułożone niż u błonkówek, gdzie przynajmniej większa ich część zwrócona jest wyższym końcem ku środkowi płatu węchowego. U *Trixalis nasuta* płaty węchowe są inne niż u *Peliplaneta* (ryc. 19, 20 LO). Kłębki antenalne gatunków rodzaju *Peliplaneta* są może więcej podobne do analogicznych kłębków u innych owadów, mniej spokrewnionych z *Peliplaneta* niż *T. nasuta*. Kłębki antenalne *T. nasuta* (AG) są małe, znacznie mniejsze niż u *Peliplaneta* i gęściej ułożone: nie wypełniają one w takim stopniu środkowej przestrzeni płatu węchowego, jak to widzimy u *Peliplaneta*. Podobną też budowę kłębków antenalnych jak i całych płatów węchowych opisuje H a n s t r ö m u *Acrididae*, do których należy *T. nasuta*. Bardzo możliwe, że z różną budową łączy się reagowanie na różnej kategorii za-

pachy lub odczuwanie tych samych podniet w jakiś inny sposób. *Acrididae* więc pod tym względem różniły by się od *Periplaneta* a także od owadów mających takie same kłębki jak i okazy należące do rodzaju *Periplaneta*. Płaty węchowe wraz ze znajdującymi się w nich kłębkami wymagają u wielu owadów jeszcze dalszych badań.

Poza tym u *Periplaneta* stwierdziłem różnice w budowie płatów węchowych w związku z płcią. Mianowicie u samców znajdują się bliżej wyjścia anteny większe kłębki, lub skupienia kłębków (ryc. 21 CZ). W wyniku dalszych badań okazało się, że podobne różnice występują u pszczoł (ryc. 22 CZ) a także u os. Większe kłębki, lub ich zagęszczenia występują mniej więcej w przedniej górnej części płatów węchowych. Zagęszczenia te (CZ) wyglądają nieraz jak bardzo duże kłębki, rozpadające się na szereg mniejszych. Różnice płciowe w płatach węchowych dotąd notowane były tylko u *Lepidoptera*, przez Bretschneider'a u gatunku *Bombyx mori*, a także *Lasiocampa quercus*, u którego dymorfizm płciowy jest specjalnie silnie wyrażony. Anteny samców są znacznie większe niż samic i posiadają więcej czuciowych narządów (Sinneshaaren Bretschneider). Na zasadzie obecnych moich wyników należy przypuszczać, że inaczej ukształtowane kłębki u samców niż u samic są ośrodkami specjalnego rodzaju powonienia: powonienia dla rozpoznania lub odnalezienia samic. Jak wiadomo wiele samic owadów wydziela specjalną woń w celu wabienia samców. O zjawiskach wabienia u owadów ostatnio pisał J. Prüffer.

Połączenia płatów węchowych.

U błonkówek dokładniej zostały opisane połączenia płatów węchowych z innymi częściami mózgu tylko u pszczoł. Prace te zawdzięczamy Kenyon'owi i Ionescu. Moje badania niezupełnie jednak zgadzają się z wynikami powyższych autorów.

U *Vespa* węchowo-globularny wewnętrzny szlak (ryc. 23 T1) posiada dwa znaczniejsze rozgałęzienia. Jedno z nich (V1) znajduje się w pobliżu wyjścia szlaku z płatu węchowego, drugie zaś — (V2) nieco wyżej. Co do pierwszego z nich nie mogłem wyśledzić dokąd prowadzi, możliwe, że częściowo wchodzi do ciała centralnego (*corpus centrale*). Drugie — prawdopodobnie odpowiada rozgałęzieniu optyczno - antenalnemu, opisywanemu przez Ionescu. Nie znalazłem tam jednak takich bezpośrednich połączeń z płatem ocznym, jak to podawał Ionescu, nie znalazłem też tych połączeń u żadnej z błonkówek. Oprócz tych większych rozgałęzień zapewne występuje też i inne, lecz są one nie liczne i znacznie mniejsze — cieńsze. Zewnętrzny szlak węchowo-globularny (TE) zaczyna się w płac-

cie węchowym w bezpośrednim sąsiedztwie szlaku wewnętrznego. Szlak ten jest dłuższy od wewnętrznego i w końcowej swej części łatwiejszy do wyśledzenia. Odchodzi od niego rozgałęzienie (TR). Szlak zewnętrzny wchodzi do nasady kielicha razem z drogami biegnącymi od złożonych oczu. Połączenia płatów węchowych u os, pszczoł i pokrewnych im błonków mało się różnią.

U *Periplaneta* połączenia te są inne, niż u błonówek. Wewnętrzny szlak węchowo-globularny (ryc. 24 T1) nie posiada takich rozgałęzień jak u błonówek. W okolicy ciała centralnego rozdziela się on na dwie części, jedna z nich (VA) przebiega z przodu, druga (VP) z tyłu kielichów. Nie wszystkie włókna wchodzi do kielichów, część ich biegnie dalej. Oprócz tych głównych dróg odchodzą zapewne i nieliczne mniejsze podobnie jak u błonówek. Zewnętrznego szlaku węchowo-globularnego *Periplaneta* nie posiada. Zamiast tego szlaku odchodzi szlak pozornie powstający całkowicie w płacie węchowym (ryc. 24, 25 TP). Jest to jednak szlak, składający się przede wszystkim z włókien motorycznych, wchodzących do anteny, o których pisałem wyżej.

O węchowo-globularnych szlakach (Riechstrang) u chrząszczy pisałem uprzednio (1936). Występuje tam tylko jedna para szlaków łączących się z kielichami, podobnie jak u *Periplaneta*; to samo stwierdziłem u *Lepidoptera* a także u *Diptera*.

Przy porównaniu wyżej opisanych połączeń u różnych owadów zwracają uwagę błonówki. Posiadają one więcej rozgałęzione wewnętrzne szlaki, a co ważniejsze, dwie pary szlaków łączących się z kielichami. U innych owadów badanych przez mnie występuje tylko jedna taka para. To podwójne połączenie stoi zapewne w związku z wysoko wykształconymi *corpora pedunculata* u błonówek. O złożonej ich budowie pisałem już uprzednio (1934). Niewątpliwie *cor. ped.* u *Periplaneta* nie są tak skomplikowane jak u błonówek i prostsze co do swej budowy.

Oprócz połączeń płatów węchowych w zwoju nadprzelykowym znajdują się jeszcze także bezpośrednie połączenia ze zwojem podprzelykowym. Takie np. połączenie występuje u *Periplaneta* (ryc. 27 AB).

Tritocerebrum.

U *Periplaneta*, jak wspomniałem, *tritocerebrum* jest dobrze rozwinięte (ryc. 3, 27 TG). W nim się znajduje skupienie t. zw. kłębków (*glomeruli*) tritocerebralnych. Są to owalne lub w przybliżeniu kuliste twory nieco przypominające kłębki antenalne, tylko znacznie mniejsze od tych ostatnich. Skupienia kłębków tritocerebralnych mają z jednej strony połączenia z płatami węchowymi i *protocerebrum* (ryc. 28 TO), z drugiej

zaś strony łączą się one szerokim szlakiem (ryc. 27 TS) ze zwojem podprzelykowym. Nie ulega wątpliwości, że podobne ukształtowanie i połączenia kłębków tritocerebralnych występuje w ogóle u *Orthopteroidea*.

W obszernej swej pracy (1940) H a n s t r ö m załącza rysunek (217) S a n c h e z'a, przedstawiający neuryty (axony) komórek globularnych u *Periplaneta (Blatta) orientalis*. Liczne wyrostki znajdują się nie tylko na końcu neurytu, ale prawie na całej jego przestrzeni. Moje badania całkowicie to potwierdzają. Podobne wyrostki znalazłem również u tego gatunku, i jak mogę wnosić ze swoich ponownych badań, egzystują one u pszczoły. Bardzo możliwe, że te małe wyrostki mają pewien związek ze zmyślnością, „inteligencją“ owadów. Im mniejsze wyrostki, tym więcej się ich może zmieścić na neurycie — tym większa ilość kontaktów, tym różnorodniej kombinują się podniety. Sądząc z zewnętrznej budowy korzonków *corpora pedunculata*, bardzo wiele owadów, choć nie wszystkie, mogą posiadać małe wyrostki. Niewątpliwie inteligencja — możliwość wykonania bardziej złożonych czynności u owadów w ogóle, zależy przede wszystkim od wielkości *corpora pedunculata*, jak to można wnosić z prac H a n s t r ö m'a. Załączam schematyczny rysunek frontalnego przekroju mózgu robotnicy pszczoły i mrówki (*Formica rufa*), sprowadzone do jednakowych rozmiarów (ryc. 29). Jak widać kielichy mrówki są większe niż u pszczoły, należy też przypuszczać, że mrówka przewyższa inteligencją pszczołę. Nie tylko jednak wielkość *corpora pedunculata*, ale i ich więcej skomplikowana budowa ma wpływ na przejawy zmyślności — inteligencji owadów. Najwyższy szczyt rozwoju osiągają *corpora pedunculata*, a właściwie kielichy u błonkówek i, trzeba to przyznać, objawy większej inteligencji — zmyślności spotykamy częściej wśród gatunków błonkówek, niż u innych owadów.

Jak można wnosić z położenia mózgu błonkówek, *corpora pedunculata* zajmują górno-przednią jego część. Zachodzi tu pewne podobieństwo z położeniem przedniego mózgu u kręgowców zajmujących podobne położenie, a z rozwojem tego mózgu kręgowców łączy się pojęcie o większej inteligencji zwierząt.

