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COMPARATIVE INVESTIGATIONS ON THE CILIARY GANGLION OF FRESH-WATER FISHES

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The occurance of ciliary ganglia in fishes is, according to the data of literature (Haller-Hallerstein, 1934; Hirt, 1935; Kolmer-Lauber, 1936; Krause, 1922), much debated. Some have not found it at all (Allborn, Cords, Ónodi), others publish it as a "real" ganglion (Tretjakoff, Herrick, Pankratz, Schneider), often in the form of a double ganglion (Schwalbe, Norris and Hughes). Some have observed it in the form of dissipated neurons, in the course of the oculomotor nerve or in the *ramus ophthalmicus* of trigeminal nerve. In case of our fresh-water fishes, where I have endeavoured to decide the question on the basis of comparative investigations, I found the following situation.

Anatomical situation of the ciliary ganglion

It is made difficult to recognize the ciliary ganglion of fishes by the fact that in these animals the cerebral nerve and the ganglia belonging to them, as well the upper part of the sympathetic nervous system and their connection with the organ of vision have a peculiar position. Therefore the sections, performed as in case of higher vertebrates, bringing the eyes to the surface together with the eye muscle cone from the very bottom of the orbital cavity and trying to find therein the ciliary ganglion, proved to be fully unsuccessful. The *ganglion ciliare* of fishes can be looked for only by dissecting thoroughly the anterior parts of the brain and maintaining the cerebral connections.

For finding it, we have to begin the dissection at the complex group of trigeminal and facial ganglia at the basal limit of the fore- and middle brains. In case of the carp we can observe particularly well two nerves that are leaving the upper ganglial group and running on the superficial surface of the eye muscle cone. The thinner is the superior ophthalmic branch of more cranial course and the thicker and more caudal the *ramus ophthalmicus profundus* (Fig. 1).

The *nervus oculomotorius* enters the orbital cavity through the opening lying proximal behind the *r. ophthalmicus* profundus. After a course of 1—2 mm it is divided and disappears in the eye muscle cone. If we examine carefully the place where the *n. oculomotorius* and the *r. ophthalmicus profundus* are the next, we shall see macroscopically an obvious thickening and several very thin branches. In the thickening can be observed double ganglia with a stereo-microscope. The upper larger ganglion takes place in the course of the *r. ophthalmicus profundus*. The lower minor one is lying on the *n. oculomotorius* with its thicker end but it is attached inseparably to the upper ganglion with its connective tissue sheath and the nerve trunks running beside it. It is shown clearly by the histological examinations that there are two ganglia in question that are fully different from each other as to their structure and function. The upper one is the *ggl. opthalmicum profundum*, of cerebro-spinal character. Their myelinated fibres are running beside the smaller ganglion without establishing any contact with it (Fig. 1b). The smaller ganglion can be named — on the basis of its structure and nerve connections — correctly a ciliary ganglion. The 5—6 very thin nerve trunks that leave the ganglion make the ganglion star-like. These thin nerve-trunks, that can be considered as *nn. ciliares breves*, are getting to the *sclera* in the sheath of the *n. opticus* or in its neighbourhood. They are continuing their way to the ciliary muscle for the greatest part in the *sclera* and only for the smaller part in the *chorioidea*. From the ganglia of *n. trigeminus* several thin nerves are attaching the trunks entering the *sclera*. These are the long ciliary nerves *(nn. ciliares longi)* preserving their independence in the whole course.

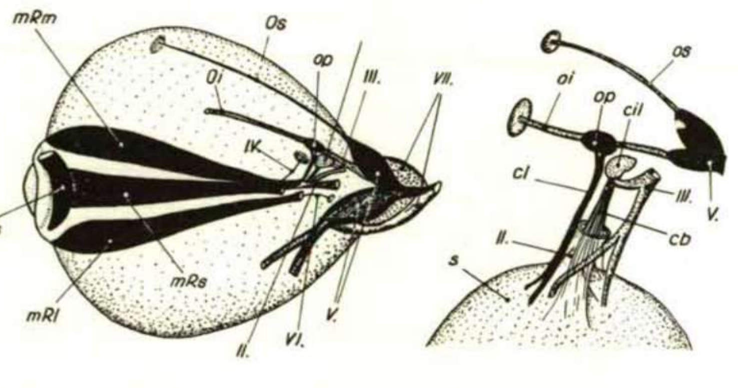

Fig. 1. *Cyprinus carpio:* The site of the ciliary ganglion and its relation to the cerebral nerve courses. II — VII. cerebral nerves and their ganglia, os — *ramus ophthalmicus superior*, oi — *ramus ophthalmicus inferior*, op — *ganglion opthalmicum profundum*, cil — *ganglion ciliare*, mR-MO — eye-muscles, cb — *nervi ciliares breves*, cl — *nervi ciliares longi*, sk — *sclera*.

At looking for the ciliary ganglion of the fishes and investigating their nerve-connections, we have to pay a special attention to the cranial part of the sympathetic nervous system. As it is obvious from the literary data, enumeratd above, some authors are considering the ganglion to belong to this system, resp. to obtain roots from here, too. The cranial sympathetic system of fishes is highly peculiar. The most

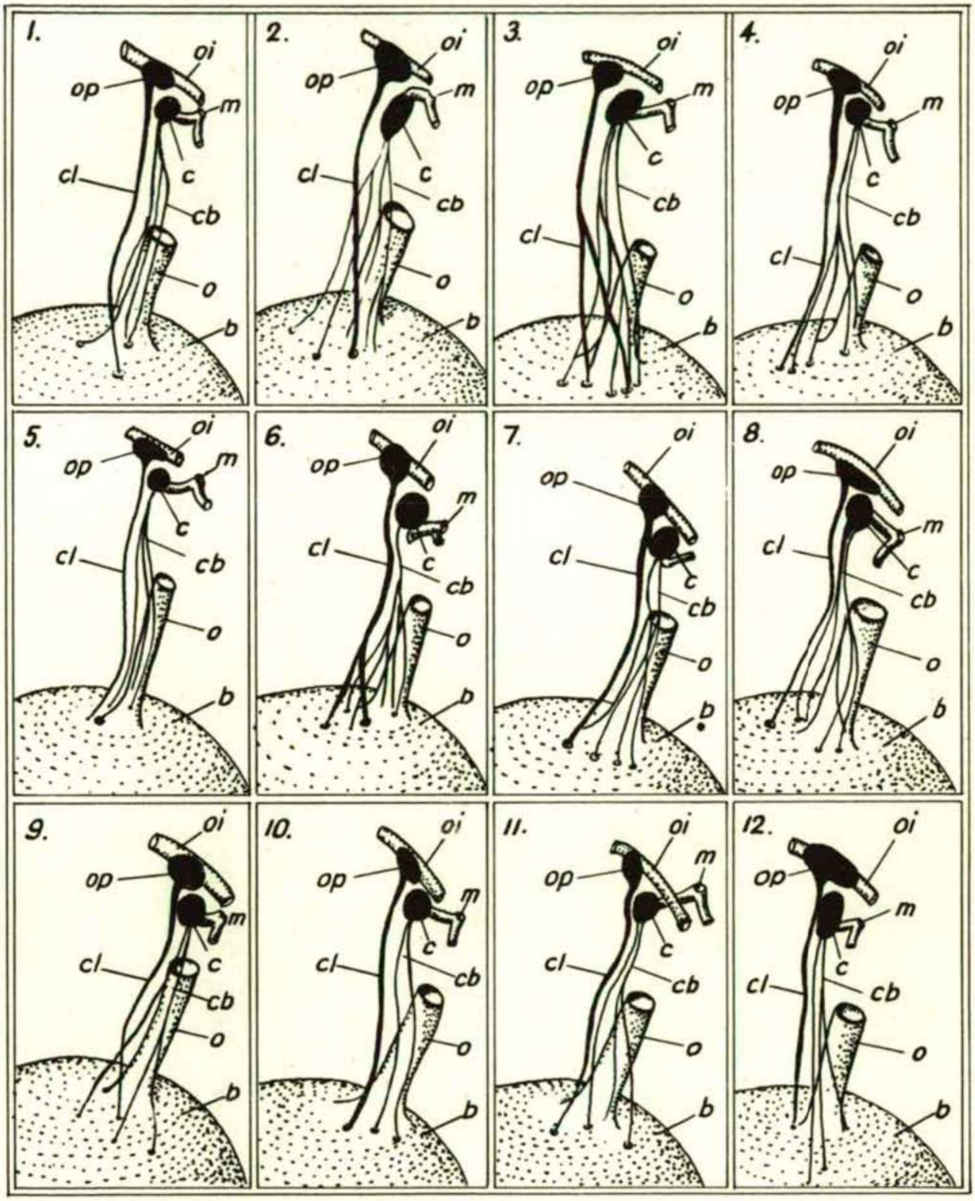

Plate I
The nerve connections of the ciliary ganglion of fishes: b — *bulbus*, c — *ganglion ciliare*, o — *nervus opticus*, m — *nervus oculomotorius*, cb — *nervus ciliaris longus*, oi — *ramus ophthalmicus inferior*, op — *ganglion ophthalmicum* profundum.

1. *Acipenser ruthenus*, 2. *Salmo trutta*, 3. *Esox lucius*, 4. *Carassius carassius*, 5. *Barbus barbus*, 6. *Rutilius rutilus*, 7. *Abramis brama*, 8. *Tinca tinca*, 9. *Cyprinus carpio*, 10. *Misgurnus fossilis*, 11. *Silurus glanis*, 12. *Perca fluviatilis*.

obvious and interesting difference from those of the higher vertebrates is that here the cephalic part of the sympathetic trunk is running on the base of the skull near to the cranial nerves highly possible the connection between the two systems.

In carp heads of large size, in which I have dissected out also the ciliary ganglion, I had the opportunity to investigate also the cranial sympathetic system. The cranial system can be observed beside the *arteria basialis* that is running on the brain-base and its connection with the ciliary ganglion was found as follows.

The uppermost three sympathetic ganglia are lying quite close to one another, they almost seem to be fused; the fourth one is located a little farther, and the fifth one much deeper on the base of the cranium, about so high that it corresponds to the height of the *ggl. cervicale supremum* of the reptiles and birds but higher than the uppermost cervical ganglion at the most part of mammala and at man. From the cranial sympathetic ganglia of fishes several nerves are running to sheaths of the adjacent cerebral nerves. It could be established with the microscopic investigations that not only nerve fibres but also sympathetic nerve cell groups can be found in the course of these nerves. From the uppermost cranial sympathetic ganglion, the most fine branches run in the wall of the ophthalmic artery. The plexus formed in the vessel-wall is very rich in fibres and nerve cells can be observed in it too. Some of the fine thin sympathetic branches are advancing towards the eye, others are running on the immediate surface of the optic nerves. In our opinion, some of these fibres can join the rich plexus system developing at the meeting point of the *nn. ciliares breves* et *longi;* it could, at any rate, not be established either macroscopically or on the basis of the microscopic structure, that the cranial sympathetic system has a direct connection with the ciliary ganglion.

Comparative anatomical data

We have dissected the ciliary ganglia of fish species of different ways of life and belonging to various families. According to the investigations, there is some difference in site and shape of ganglia, as well in the number and course of the postganglionic fibres (Plate I,1—12). The most obvious differences are, however, to be seen in the size of ganglia.

THE SITE OF GANGLION changes because of its relation to the *ggl. ophthalmicum profundum.* While in case of the carp *(Cyprinus carpio)* the two ganglia nearly fused, there are species where the two ganglia are farther from each other (Plate I,2,3,6,11,12). Owing to this change of site, mostly the shape of ganglion changes, as well.

THE SHAPE OF GANGLION is generally longish and oval (Plate I2,3,12) which reminds us generally of the ciliary ganglia of birds; sometimes, however, it is fully round (Plate I,5,8,10). Tri-, resp. quadrangular forms don't belong to the rarities, either (Plate I,1,4,7,9,11).

THE POSTGANGLIONIC NERVES are everywhere very thin and their number is very high. Immediately after leaving the ganglion the plexus formation of postganglionic fibres begins. From the postganglionic nerves there are running a great lot of fibres through the sheath of the optic nerve to the superficial connective tissue layer of the *sclera* and towards the *cornea*. Apart from entering by the sheath of the optic nerve, some nerves enter the eyeball through the *sclera* to the *chorioidea* as well. These branches are less numerous and somewhat thicker in size. In the number of the postganglionic nerves there are obvious differences. At the mudfish *(Misgurnus fossilis)* we see only two nerves, at the tench *(Tinca tinca)* three ones. At these species, the number of side branches is low, too (Plate I,4,11). At the others, the number of the postganglionic nerves is 6—12; because of the side branches, however, in the sheath of the optic nerve and at entering the *sclera*, as many as 14—22 can be counted.

Species	Ciliary ganglion			The greatest diameter of the eyeball	Number of relation	Order of sequence
	length	width	average			
Acipenser ruthenus	0.6	0.3	0.45	10	22	13
Salmo trutta	1.6	0.5	1.05	15	14.2	5
Esox lucius	1.6	0.8	1.2	14	11.6	1
Carassius carassius	0.9	0.5	0.7	13	18.5	10
Barbus barbus	0.8	0.7	0.75	12	16	6
Rutilus rutilus	0.8	0.8	0.8	11	13.7	4
Abramis brama	0.8	0.6	0.7	13	18.5	9
Tinca tinca	0.7	0.7	0.7	14	20	12
Cyprinus carpio	1.1	0.5	0.8	15	18.7	11
Misgurnus fossilis	0.5	0.5	0.5	8	16	7
Nemachilus barbatulus	0.6	0.5	0.55	9	16.3	8
Silurus glanis	0.3	0.3	0.3	7	23.3	14
Amiurus nebulosus	0.3	0.2	0.25	7	28	15
Perca fluviatilis	1.6	0.6	1.1	14	12.7	2
Lucioperca lucioperca	1.4	0.8	1.1	15	13.6	3

The nerve fibres coming from the trigeminal nerve are only attached to the postganglionic fibres of the ciliary ganglion. The trigeminal connection seems to derive mainly from the *gg. ophthalmicum profundum*. The number of the nerve branches leaving this ganglion and connected with the postganglionic plexuses of the ciliary ganglion is usually one, exceptionally two (Plate I,3,10,12). Their side branches appear only in the confused network of the plexus system and are running, as demonstrated, in the nerve trunks of *sclera*, in the same nerve-trunk as the postganglionic nerve fibres.

THE SIZE OF GANGLION is very heterogeneous. Among the differences shown in the ciliary ganglia of various fish species, the differences in size are the most remarkable. This phenomenon is getting the most obvious if we dissect and compare with each other the ciliary ganglia of same sized species (about 25 cm).

As a result of comparsion, we have found so that the sizes of eyes and ganglia are not always in the closest connection with each other, as it is demonstrable by the values contained in the Table below. The data of Table want to express relative sizes. The longitudinal and latitudinal averages of the ganglion are compared with the greatest diameter of the bulb.

Bringing the results obtained in connection with the way of life of the animal species, we are receiving considerable data. The order or sequence of the relative numbers is, namely, referring to the closest connection with the way of life. The smallest relative number, i.e., the comparatively largest ganglion can be found in the pike *(Esox lucius)*. The large and strongly differentiated external and internal eye muscles and skeleton muscles are in connection with the predatory way of life, the fast swimming. The next one is the size of ciliary ganglion of the perch *(Perca fluviatilis)* and the next the pike-perch *(Lucioperca lucioperca)* they are alert even in the mud, watching for the prey and falling quickly on it. The latter is almost identical with the minnow *(Rutilus rutilus)* of a well-known excellent eye-sight.

We have found so that at fish of twilight and night activity not only the eyes but also the ciliary ganglia are of great size, too. This is effecting first of all the trout *(Salmo)* that become alert at twilight and swim for getting food in the evening hours. Their alertness, dexterity and falling on the victim is characteristic of their getting the food. If in their youth they content themselves with getting insects, worms, snails and tadpoles, in their developed age they rival the outspokenly predacious fish in greed. From the species investigated, the ganglion of the barbel *(Barbus barbus)* of night life is the next one. The sizes of ganglia of the alert and agile meadow mudfish *(Misgurnus fossilis)* and those of the stone mudfish *(Nemachilus barbatulus)* swimming the whole night after its prey are of middle value. It is highly interesting that in the species belonging to the family *Cyprinidae* the ciliary ganglion is small. The most of them are actually unambitious animals.

On the basis of comparative investigations we have come to the conclusion that the ciliary ganglion of fishes are hardly changing with the age and body-size. As we dissected the ciliary ganglia out of large-sized carp heads, they were not larger, too, than those got from carps of smaller body-size. In view of size of ganglia, the sturgeons and siluruses are among the last ones. The strugeon *(Acipenser ruthenus)* is looking for its food on soft bottoms, half digged in, rather crawling than swimming. Siluruses *(Silurus glanis)* have a similar way of life. It can be established that where the other organs of sense are well developed, the eye and its nerve components are less developed. Thus, in case of the licking, touching strugeons and siluruses that taste the material of the muddy bottom with well-developed barbs and a trunklike mouth-piece and corresponding to these, supposedly with well-developed mechanical and chemical organs of sense, the size of eyes and that of the ciliary ganglia are particularly small. It is convincingly verified by the comparative data of the Table that the sizes of eyes and ciliary ganglia that belong to them are strongly influenced by the way and possibility of life and feeding.

Microscopic structure of the ciliary ganglion

According to the literary data the microscopic structure of the ciliary ganglia of fishes has not been investigated by anybody, as yet, and almost the same can be said also about the sympathetic and cerebrospinal ganglia. As the result of the anatomical investigation about the "existing" ciliary ganglion in our fresh-water fishes could only be decided with the help of the microscopic structure, we have made a careful examination concerning it. The literary data missing we have made a comparison for recognizing the structure of the ciliary ganglion and establishing its connections. For being able to compare correctly, we have examined also the structure of the cerebrospinal sensory ganglia and that of the sympathetic ganglia. As a result of the investigations we have established that the ciliary, cerebrospinal and sympathetic ganglia of the carp, the species of fishes investigated the most carefully, are structurally differring from one another.

CILIARY GANGLION. The cells of the ciliary ganglion of fish are unipolar. The cell process is thin, appearing but with difficulty even after being impregnated. The size of the cells is 10—15 μ, their staining being similar. The protoplasm of the cells is granular; the size of granules is as compared with those of higher vertebrates, much smaller. In the cell plasm the neurofibrils are very fine (Plate II, 1). The *nucleus* is comparatively large, its chromatin substance is rich. The *nucleolus* is separated from the nuclear substance only rarely. The cells are located densely near to one another; the fibre substance of the ganglia consists of thin fibres; a very thin myelin is only on the fibres of the nerve entering the ganglion. Round the cells granular glial cell nuclei take place. Their number is not high, round a cell 6—8. In the connective tissue around the ganglion and among the cells, near to the cellbody or on the cell-body itself there appear terminal heads, terminal clubs in high number (Plate III,1,2). These end-formations are considered to be preganglionic fibre terminations. Their size is 0.2—2 μ, mostly also the nerve fibre connection can be observed well.

CEREBROSPINAL GANGLION. The structure of the ciliary ganglion is absolutely different from the cerebrospinal sensory ganglia in which uni- and mainly bi-polar cell types are dominant (Plate III, 3). The T-shaped bifurcation of the cells that is particularly characteristic in the higher vertebrates here is very rare. The two processes originate generally from the two opposite poles. The size of cells is large, as a rule, between 35—50 μ, being almost double of the size of the ciliary ganglion cells. A characteristic property of the cells is the great difference appearing in their staining. Apart from dark impregnated cells, there are frequent also neurons stained light yellow. The number of dark-stained cells is always higher. These cells as well their processes and the thick myelinated fibres running in the ganglion are verifying doubtless tehir belonging to the cerebrospinal system.

SYMPATHETIC GANGLIA. The ciliary ganglion of fishes are not similar structurally to the ganglia of the ganglia of the cranial sympathetic system, either. Having investigated the five pairs of cranial ganglia of the carp, we established that the most important feature of their histologic structure is the difference in the sizes of the cells. Beside the large cells of the diameter of 25—30 μ, groups of thoroughly small cells of 8—10 μ take place (Plate III,4). The body of the larger and smaller nerve cells is similarly round, with a granular plasma pattern. The cell process appears but rarely. Thus, a great part of cells can probably be classified into the unipolar type. After prolongated impregnation the large cells have two, resp. even three processes. The cells of smaller or larger size appear alike in an identical colour (Plate II, 2). There aren't among them any cells stained very dark. Also in the nerve trunks between the ganglia, there are some nerve-cells classified into the small cells as to their size. The nerve fibres have Schwann-sheaths. The Schwann's *nuclei* in the cranial ganglia of the carp are particularly long, 15 μ. In the nerve-trunks we do not see any fibres stained stronger, resp. of thick sensory character. Round the cells glial cell *nuclei* are located. Around the larger cells, these *nuclei* are larger and longish. As in the vegetative ganglia generally, a great number of synapses appear also here, i.e., preganglionic fibre-ends. These terminations appear generally on the large cells or in the immediate vicinity of them. The termination in the form of a dark stained end-head or end-bulb is always stained black, in that way being well separated from the glial cell *nuclei*. These synapses can be found in great number in the cranial sympathetic ganglia.

It is referred to by the comparative structural differences that the structure of the ciliary ganglion of fishes is peculiar. It does not show any similarity to the cerebrospinal or the sympathetic ganglia. The cause of the differences can be looked for as evolutionary deviations, in the origin from the mesencephalon and, as a result of that, in their exclusively close connection with the oculomotoric nerve.

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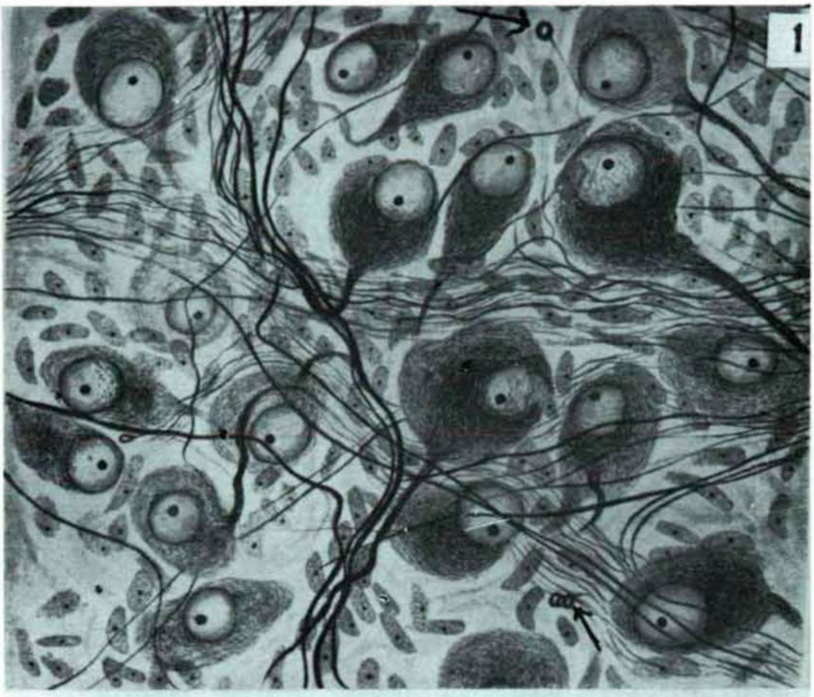

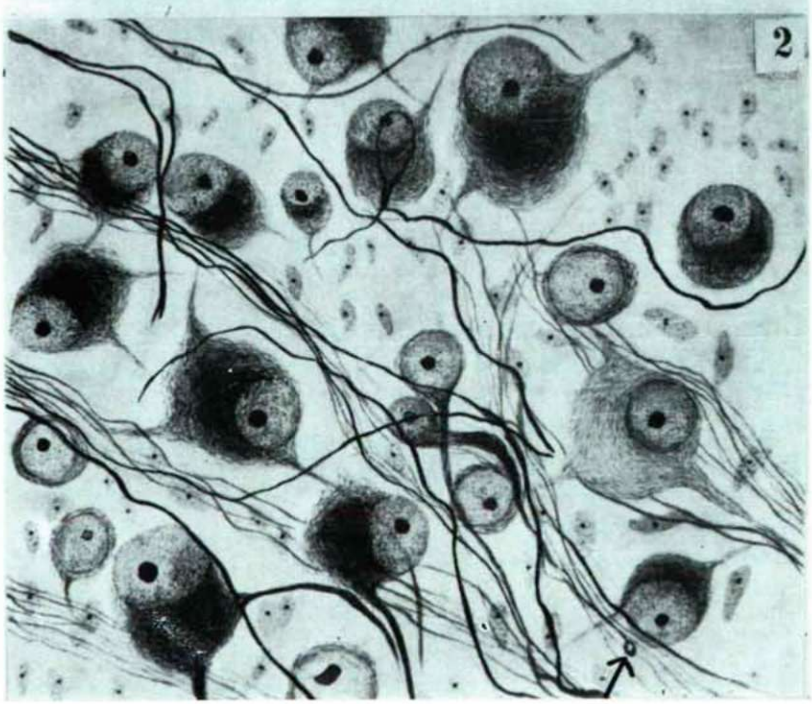

PLATE III

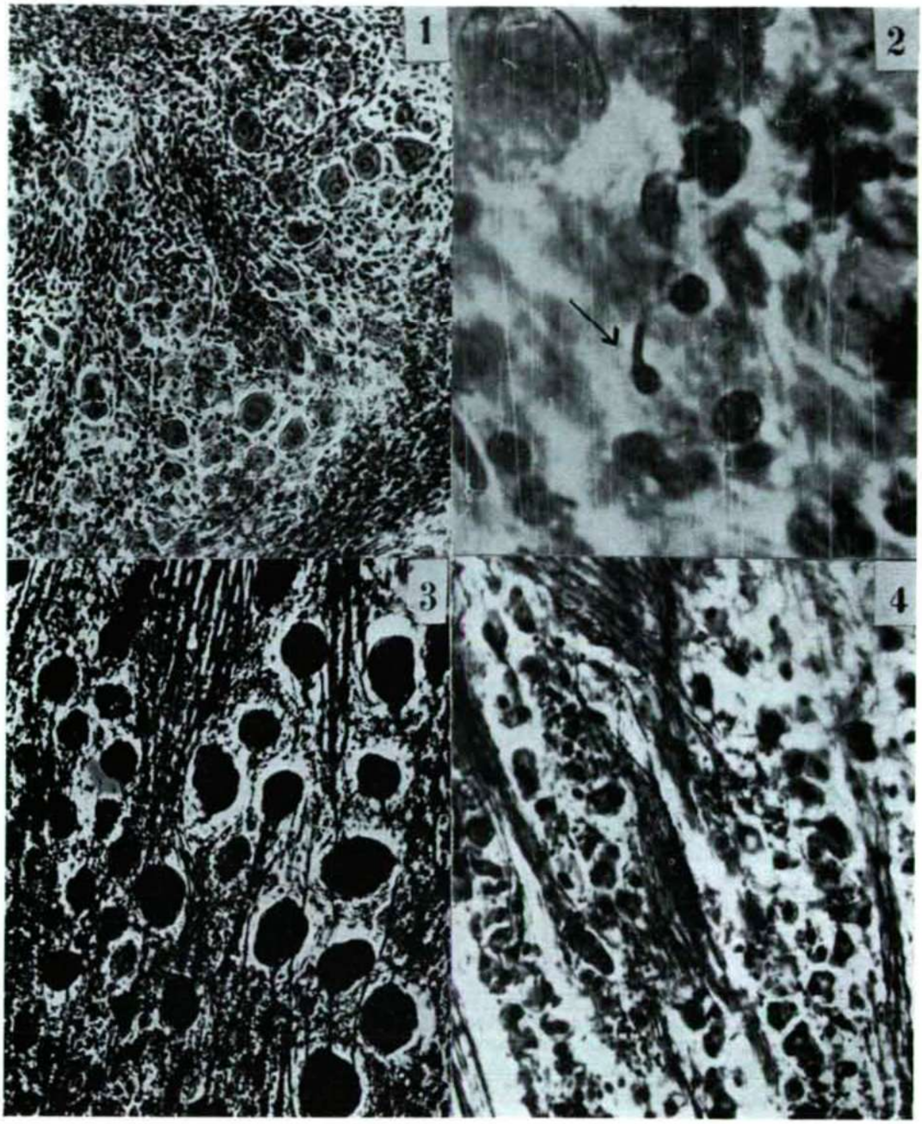

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Plate II

Fig. 1. *Cyprinus carpio*. The structure of the ciliary ganglion. end-ring.Magn. 600 x.

Fig. 2. *Cyprinus carpio:* The structure of the II. Cranial Sympathetic ganglion. end-ring. Magn. 600 x.

Plate III

Fig. 1. *Cyprinus:* The structure of ciliary ganglion.

Fig. 2. *Cyprinus:* End-bulb among the ciliary cells.

Fig. 3. *Cyprinus:* The structure of ganglion opthalmicum profundum.

Fig. 4. *Cyprinus:* The structure of II. Cranial sympathetic ganglion.