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Unerwienie i narządy zmysłowe skrzydeł *Ornithomyia biloba* Dufour *(Diptera, Hippoboscidae)*

The innervation and sense organs in the wing of *Ornithomyia biloba* Dufour *(Diptera, Hippoboscidae)*

napisała

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Introduction

In March, I found several larvae in the nest of a swallow (*Hirundo rustica* L.). At the end of April and in May they hatched out in the form the adult fly, *Ornithomyia biloba* Dufour, belonging to the group *Pupipara*. Since among several species of small flies of which the sense organs and innervation of the wings have previously been investigated (*Tipula* L., *Hoplodonta* Rond., *Silvius* Meig., *Drosophila* Fall., *Oxypterum* Leach), there also occurs the non-flying form *Oxypterum* Leach, (*Cratherrina* Olfers) with markedly reduced wings, also belonging to the *Pupipara* group, it seemed of interest to study the innervation and sense organs in the wings of the *Ornithomyia* Latr. form, which is also parasitic, but has normal wings adapted to flight.

Material and Methods

As the adult forms emerged from the larva I stainded them by injecting them *in vivo* with a 1 per cent aqueous solution of methylene blue, and when the nervous elements in the wings had taken a sufficiently dark stain, I fixed them with a 10 per cent solution of ammonium molybdate.

After some hours the fixed wing was washed in water, and then dehydrated with absolute alcohol, changed three times at ten-minute intervals. The dehydrated wing was put on a slide and, after applying a drop of Canada balsam, protected with a cover slide.

The chitinous sense organs in the wing and their innervation

The following sense organs appear on the wing of *Ornithomyia* Latr.

1) sensory hairs (*sensillae trichoideae*)
2) sensory bristles (*sensillae chaeticae*)
3) campaniform sensillae.

In addition, there are two chordotonal organs at the base of the wing.

1. The sensory hairs

Three kinds of sensory hairs may be differentiated, according to size: large (475-800μ), medium (242-380μ), and small (52-165μ). All the sensory hairs have a characteristic shape. They are arched, and set obliquely on the edge of the wing, i. e. at an acute angle, in fairly deep but narrow ectodermal pits, over the small vein forming the border of the anterior edge of the wing. They are located from the basilar section of the wing as far as the place where the vein R_{4+5} meets the edge of the wing. They gradually diminish in size as they proceed from the base to the end of the wing. The largest hairs are dark, while the medium-sized and small ones are pale yellow or amber-coloured. Not all the hairs on the edge of the wing are innervated by the peripheral axons of the sensory nerve cells. About half the total number of hairs, with the exception of the large ones, exhibit no communication with the nervous system. Most of the uninnervated hairs are found on those parts of the wing more distal from the base. All the large sensory hairs, however, are innervated. In the basilar section of the costal vein, innervated by the costal nerve, two rows of hairs appear: the dorsal row, i. e. hairs set on the dorsal aspect of the costal vein and the costal row, set on the border between the dorsal and ventral aspects of the wing. Two kinds of hairs enter into

b) 17-30 medium-sized hairs situated among the large hairs. The dorsal row ends in the region where the subcostal vein penetrates the margin of the wing, and in the further course of the costal vein there appears only a costal row composed of small hairs set on the border of the wing, initially few but increasing in number after the site where the anterior radial nerve enters the costal vein. This row extends on the border of the wing as far as the termination of the anterior radial nerve. Further on, neither hairs nor sense organs appear on the anterior margin of the wing. Each sensory hair is innervated by a single nerwe cell.

2. The sensory bristles

The bristles are differentiated from the hairs by their smaller dimensions and the absence of arching, being quite straight. They are set in shallow but fairly ample ectodermal pits and stand almost at right angles to the surface of the chitin on the wing, and not obliquely like the hairs. In addition, they are always innervated by a group of four nerve cells, and not by single cells, as are the hairs. They are situated only among the hairs on the anterior margin of the wing, extending from the transversal radial vein (*h*) to the end of the course of the nerve in the wing. In the anterior edge of the wing there are usually nine, seldom ten or eleven. They vary in length from 46 to 61 μ; they gradually diminish in size as they proceed from the base to the end of the wing.

3. The campaniform sensillae

The campaniform sensillae are distributed on the wings in two ways: 1) in the basilar part of the wing they appear in clusters as the campaniform sensilae groups at the base of the collective vein $Sc+R$, on the dorsal aspect (from the upper surface of the wing) as the radial groups, and also from below the vein as the subcostal groups, 2) in the further course of the costal and radial (R_{4+5}) veins they appear as campaniform sensillae situated singly (fig. 3 and 5). The sensillae forming the groups in the base of the collective vein $R+Sc$ (i. e. *Sc.* I, *Sc.* II, *R* I, *R* II) are distinctly smaller than those lying singly on the

veins. They reach a size of 10 μ in diameter, while the single campaniform sensillae measure as much as 13 μ in diameter. All these sensillae are innervated by sensory nerve cells distinctly larger than those innervating the hairs and bristles.

The grouped campaniform sensillae form five groups, viz., in the base of the collective vein *Sc* + *R* at its anterior edge, three groups of campaniform sensillae appear on the inferior aspect of the wing, and so correspond to the subcostal groups in other small flies. There are the proximal or first group, the central or second group, and the distal or third group. The sensory nerve cells innervating these groups belong to the subcostal nerve. The first group lies in the region where the costal nerve branches from the subcostal nerve. The other two groups lie a short distance beyond the first. The first subcostal group is formed of about seven sensillae, the second of three to four, and the third of eight.

Posteriorly to the first and second subcostal groups, but in the base of the same collective vein *Sc* + *R*, on the superior aspect of the wing, there lie two groups of campaniform sensillae corresponding to the radial groups of other small flies. These are the proximal or first and the distal or second radial groups. The first radial group is composed of 25-30 sensillae about 10 μ in diameter, while the distal group, lying immediately beyond the proximal, contains 5-7 sensillae. Both these groups lie within the subvenous field and terminate just before the fork of the collective vein *Sc* + *R*.

All campaniform sensillae appearing in groups are innervated by sensory nerve cells, distinctly larger than those innervating the hairs and bristles, and belonging in the subcostal sensillae to the subcostal nerve, but in the radial groups to the radial nerve.

The single campaniform sensillae appear on the veins only on the superior aspect of the wing, viz., the first is located on the humeral vein (*humerus*), the next on the vein R_{4+5}, not far from the junction of this vein with the vein M_{1+2}. The third campaniform sensilla is located on the transversal vein joining *v. radialis*$_{4+5}$ with *v. medialis*$_{1+2}$, and the other single sensillae to the number of 5 or 6 lie on the apical section of the

vein R_{4+5}. In addition, 2 or 3 single sensillae appear on the costal vein before its junction with *v. radialis*$_{4+5}$. There are no sensillae campaniformes at all on the other veins, not even single ones.

4. The chordotonal organs

As well as the sensory hairs, bristles, and campaniform sensillae, there are two chordotonal sensory organs. One of these, the ante-alar chordotonal organ, lies in the tegula, while the other, the radial chordotonal organ, is located in the subvenous field. The ante-alar organ is composed of six nervo-chordotonal cells, of which the terminal rod fibrils are directed towards the apical edge of the tegula, while the centripetal axons of these cells form a short chordotonal nerve situated in the tegula. This nerve, joining the nerve branch, forms through the centripetal axons of the cells innervating the hairs lying on the surface of the tegula a longer chordotonal branch separating off from the common costo-subcostal nerve. At the place where this branch ramifies from the costo-subcostal nerve, still another fairly long nerve branch is distinguished in the tegula. This branch gives off a certain number of cells to the hairs situated on the tegula. This is therefore the *nervus tegularis* (fig. 3).

The second chordotonal organ is the radial, lying at the base of the collective subcosto-radial vein, $Sc+R$. It is connected with the radial nerve by a short chordotonal nerve of its own, which is separated from the radial nerve on the posterior aspect of the wing at the level of the first group of radial campaniform sensillae. This organ is composed of 7 or 8 chordotonal cells lying immediately beyond the radial nerve and having peripheral rod axons directed towards the front of the wing, and so in the direction of the radial nerve. No other chordotonal organs in the wing of *Ornithomyia biloba* Dufour were observed.

The nerve ramifications in the wing

The alar nerve ramifies on entering the wing, even before its penetration, into two long parallel trunks, which run side by side for a certain distance. The anterior trunk represents the

costo-subcostal nerve, while the second trunk is formed by the common radial nerve. The costo-subcostal nerve separates off before the wing into a small branch, which penetrates the tegula and there ramifies into a branch, the tegular nerve, giving off single fibrils with cells innervating the hairs of the tegula, and a short chordotonal nerve terminating in the ante-alar chordotonal organ. The main trunk of this nerve in its further course enters the anterior margin of the wing, where it splits into two branches in the region of the common subvenous field. The first of these, i. e. the anterior branch entering the costal nerve. This nerve continues in the costal vein, innervates a great number of sensory hairs and runs as far as the humeral vein (*humerus*), where it terminates without joining or coming into contact with the nerve running in the latter. The second branch of the costo-subcostal nerve, however, near the place where the costal nerve ramifies, gives off a short bundle of fibrils with cells innervating the first (proximal) group of subcostal sensillae (*sensillae campaniformes subcostales proximales*). This is therefore the subcostal nerve, which in its further course innervates the second small group of campaniform sensillae (*medialis*), and afterwards entering the collective subcostal-radial vein ($Sc+R$) then innervates the third or distal group of campaniform sensillae. In its further course the nerve bends anteriorly, passes through the humeral vein (*humerus*) in the region of which it innervates one campaniform sensilla, after which in continuation it enters the vein lying on the anterior margin of the wing and innervates the sensory hairs and bristles, running almost to the place where the subcostal vein (*sc*) joins the vein of the anterior margin of the wing. Here the ending of this nerve again neither joins nor comes into contact with the neighbouring nerve.

The common radial nerve runs in the base of the wing just beyond and parallel to the subcostal nerve. After entering the base of the wing, it gives off posteriorly a short chordotonal nerve ending in a radial chordotonal organ. Just beside this chordotonal organ, it innervates the proximal radial group of campaniform sensillae and a little further on, just at the base of the collective subcosto-radial vein ($Sc+R$) it innervates the second or distal radial group, afterwards entering the common

subcosto-radial vein ($Sc+R$) and continuing in this. After having reached the place where the common radial vein (R) forks into two branches, it enters the first of these, i. e. into R_1, and then together with the latter, passes into the vein of the anterior alar margin. This is the anterior radial nerve. When it enters the anterior margin, it gives off a short recurrent nerve (fig. 5). In the whole of the costal vein, it innervates numerous sensory hairs and a few sensory bristles, extending as far as the place on the anterior margin of the wing where it comes into contact with the radial vein (R_{4+5}). In its terminal section it innervates some campaniform sensillae as well as the sensory hairs and bristles.

The second branch of the common radial nerve enters the common radial vein (R_{2-5}), and after having passed through this enters the vein R_{4+5}, without giving off any branches or the latter of nerve elements. This is the posterior radial nerve. sensory nerve cells to the vein R_{2+3}, and so completely depriving The nerve running in the vein and omitting the transversal radiomedial vein ($r+m$), gives off a small branch with a cell innervating the campaniform sensillae of this vein, and the main trunk of the nerve continues as far as the place where the radial vein (R_{4+5}) joins the vein of the margin of the wing. Near its termination, this nerves gives off a few cells to the campaniform sensillae lying at the apex of the wing, and terminates without coming into contact with or joining the anterior radial nerve.

The other veins have neither nervous elements nor chitinous sense organs.

A characteristic feature of the innervation of the wing of *Ornithomyia* Latr. is the scanty number of nerve branches, limited to the anterior part of the wing. Some veins such as the subcostal or radial (R_{2+3}) do not exhibit either nervous or sensory organs. The sense organs are distributed chiefly in the base of the wing and on its anterior edge.

Comparison with the alar innervation in other small flies

In comparison with other small flies, of which the nerves and sense organs of the wings are already known, *Ornithomyia* Latr. is not very different as regards the course of the nerve

branches in the wing. The greatest differences appear between the flies in question and *Silvius vituli* F. In *Silvius* Meig. the distribution of the nerves in the wings is similar, except for the nerve branch running in the radial vein (R_{1+5}) and terminating in the region of the fork of the veins R_4 and R_5, without reaching the margin of the wing. In *Hoplodonta* Rond. there is no such division of this vein, and the nerve runs in it up to its contact with the anterior alar margin. In addition, in *Silvius* Meig. there are two ante-alar chordotonal organs in the tegula, and 6 groups of campaniform sensillae on the subcostal and radial veins. Again, typical bristles have not been found in *Silvius* Meig. or in *Hoplodonta* Rond. but at most a sort of intermediate form between hairs and bristles. The genus *Drosophila* Fall. has no sensory bristles whatsoever, the course of the nerves in the wing is completely similar, while six groups campaniform sensillae appear on the subcostal and radial veins (*Sc* and *R*). In *Oxypterum* Leach. belonging to the same group as *Ornithomyia* Latr., i. e. *Pupipara*, although the wings are markedly reduced, there are yet nervous elements and sensory organs corresponding in every aspect as regards their distribution to the genus *Hoplodonta* Rond. which has normal wings adapted to flight.

In *Tipula paludosa* Meig., as in *Ornithomyia* Latr. there appear three groups of radial campaniform sensillae. There are, however, three chordotonal organs, one on the tegula and the two others on the alar lamella. One of these belongs to the radial-axillary nerve, the others to the axillary nerve. In the course of the ramifications of the nerves, there appears in *Tipula* L. a tegulo-costal nerve, entering the costal vein from the tegula and joining the recurrent branch of the subcostal nerve (*ramus recurrens nervi subcostalis*). The margin of the wing is completely innervated by the subcostal nerve, while in *Ornithomyia* Latr. only one-third is innervated by this nerve, and the remaining two-thirds by the anterior radial nerve.

Elisabeth E r h a r d t has described certain details of the sensory organs of the wings of *Eristalis floreus* L., *Tabanus bovinus* L., and *Tipula gigantea* Schrk. She submits that in these flies numerous campaniform sensillae appear on the wing, and are disposed differently in various families. She does not, however, say any-

thing about the innervation of the wing. The innervation of *Drosophila* Fall. and its larva has been investigated by Hertweck [3].

Final observations

In general, the innervation of the wing of *Ornithomyia* Latr. resembles that of *Oxypterum* Leach, although the former is a normal fly, i. e. well adapted to flight, with long, broad wings normal in shape, while *Oxypterum* Leach has markedly reduced and narrow wings, with the apices so tapering that it is totally unable to fly. In *Ornithomyia* Latr. the appearance of sensory organs on the wings is also interesting. Other flies, e. g. *Drosophila* Fall., lack these, which gives evidence of the earlier differentiation of these pupiparal flies from the groups in which the sensory bristles have been preserved, while in other higher flies the bristles have disappeared secondary.

STRESZCZENIE

Na skrzydle muchówki *Ornithomyia biloba* Dufour mieszczą się następujące narządy zmysłowe:

1. Włoski zmysłowe wielkie, średnie i małe, unerwione przez pojedyncze komórki nerwowe.

2. Szczecinki zmysłowe unerwione przez grupę czterech komórek zmysłowych.

3. Kopułki zmysłowe unerwione przez komórki nerwowo-zmysłowe występujące pojedynczo, lub grupami (w nasadzie żyłki *Sc-R*: trzy subkostalne po spodniej stronie skrzydła i dwie radialne po wierzchniej stronie skrzydła).

4. Dwa narządy chordotonalne: jeden w płytce przedskrzydłowej unerwiony przez nerw brzeżno-podbrzeżny, drugi w polu podżyłkowym unerwiony przez nerw promieniowy.

Nerw skrzydłowy wchodzi do skrzydła rozgałęziony na:

1. Nerw brzeżno-podbrzeżny, rozgałęzia się na brzeżny, biegnący w żyłce *C*, i podbrzeżny, biegnący w żyłce *Sc-R*, *h*, *C*.

2. Nerw promieniowy wspólny rozszczepia się na promieniowy przedni, biegnący w żyłce *Sc-R*, R_1 i *C* oraz tylny, biegnący w żyłce R_{2-5} i R_{4+5}.

Pozostałe żyłki skrzydła nie mają ani elementów nerwowych ani chitynowych narządów zmysłowych.

PIŚMIENNICTWO — LITERATURE

[1] Berlese, A., Gli Insetti, Milano 1909.

[2] Erhardt, E., Zur Kenntnis der Innervierung und der Sinnesorgane der Flügel von Insekten, Zool. Jahrbüch. Abt. f. Anat. u. Ontogenie. Jena. 39, 1916.

[3] Hertweck, H., Anatomie und Variabilität des Nervensystems und der Sinnesorgane von *Drosophila melanogaster* Meig., Zeitschr. f. wiss. Zool., Leipzig. 139, 1931.

[4] Noe, G., Contribuzione alla conoscenza del sensorio degli insetti, Atti della reale Accad. d. Lincei, Roma 1903.

[5] Zaćwilichowski, J., Unerwienie skrzydeł owadów, Rozprawy Wydziału Mat.-Przyrodniczego PAU, Kraków, 70, 1930, p. 1-150.

[6] Zaćwilichowski, J., Über die Innervierung und die Sinnesorgane der Flügel der Lausfliege *Oxypterum* Leach, Bull. de l'Acad. Polon. d. Sc. et d. L. Cl. de Sc. Math. et Nat. Ser. B, Kraków 1934, p. 251-257.

[7] Zaćwilichowski, J., Über die Innervierung und die Sinnesorgane des Flügels der Schnake *Tipula paludosa* Meig., Bull. de l' Acad. Polon. d. Sc. et d. L. Cl. de Sc. Math. et Nat. Ser. B, Kraków, 1934, p. 397-413.

EXPLANATION OF FIGURES

Fig. 1. Distribution of hairs and bristles on the wing of *Ornithomyia biloba* Dufour. *Ww* — large hairs; *Ws* — mediumsized hairs; *Wm* — small hairs; *Szcz* — bristles.

Fig. 2. Course of the anterior subcostal and radial nerves in the costal vein: *Szcz* — bristles; *Wł* — hairs; *gr* — group of four cells innervating a sensory bristle; *kn* — single cell innervating a sensory hairs; *n. Sc* — *nervus subcostalis; n. Ra* — *nervus radialis anterior.*

Fig. 3. Chitinous elements and sensory organs of the base of the wing and tegula: *nt* — *nervus tegularis*; *nch* — *nervus chordotonalis*; *nCSc* — *nervus costo-subcostalis; nR* — *nervus radialis; nal* — *nervus alaris; nC* — *nervus costalis*; *nSc* — *nervus subcostalis*; *teg* — *tegula*; *ch.a.al.* — *organum chordotonale antealare; chr* — *organum chordotonale radiale*; *Sc* I — campaniform sensillae, subcostal group I (proximal); *Sc* II — campaniform sensillae, subcostal group II (medial); *Sc* — III campaniform sensillae, subcostal group III (distal); *R* I — campaniform sensillae, radial group I (proximal); *R* II — campaniform sensillae, radial group II (medial); *R* III — campaniform sensillae, radial group III (distal); *K* — ringle campaniform sensillae; *KN* — cells innervating the hairs; *VC* — *vena costalis.*

Fig. 4. The tip of the wing, on wich may be seen the end of the anterior and posterior radial nerves: *K* — sensillae *campaniformes*; *szcz* — bristles; *Wm* — small hairs; *gr* — group of four cells innervating a bristle; *nRa* — *nervus radialis anterior; nRp* — *nervus radialis posterior.*

Fig. 5. Course of the nerves and veins in the wing: *nal* — nervus alaris; *nCSc* — *nervus costo-subcostalis*; *nR* — *nervus radialis*; *nC* — *nervus costalis*; *nSc* — *nervus subcostalis; nRa* — *nervus radialis anterior*; *nRp* — *nervus radialis posterior*; *VC* — *vena costalis; VSc* — *vena subcostalis*; *VR* — *vena radialis; VM* — *vena medialis; VCuM* — *vena subito-medialis; VAn* — *vena analis*; *Vrm* — *vena radio-medialis*; *Vmcu* — *vena medio-cubitalis*; *h* — *vena humeralis.*

TABLE I

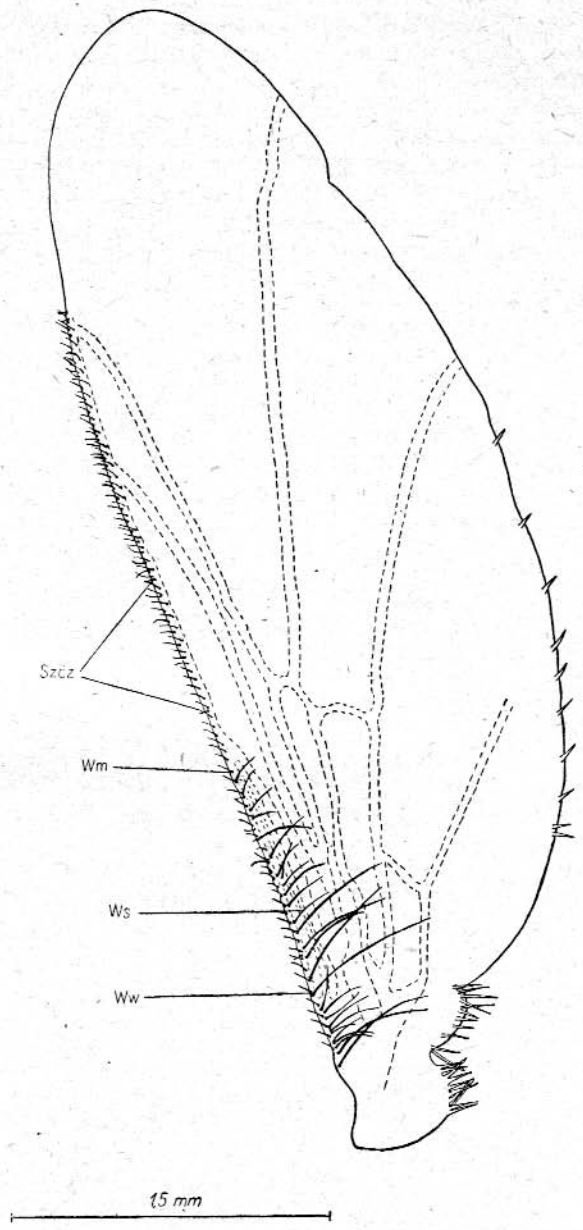

Fig. 1

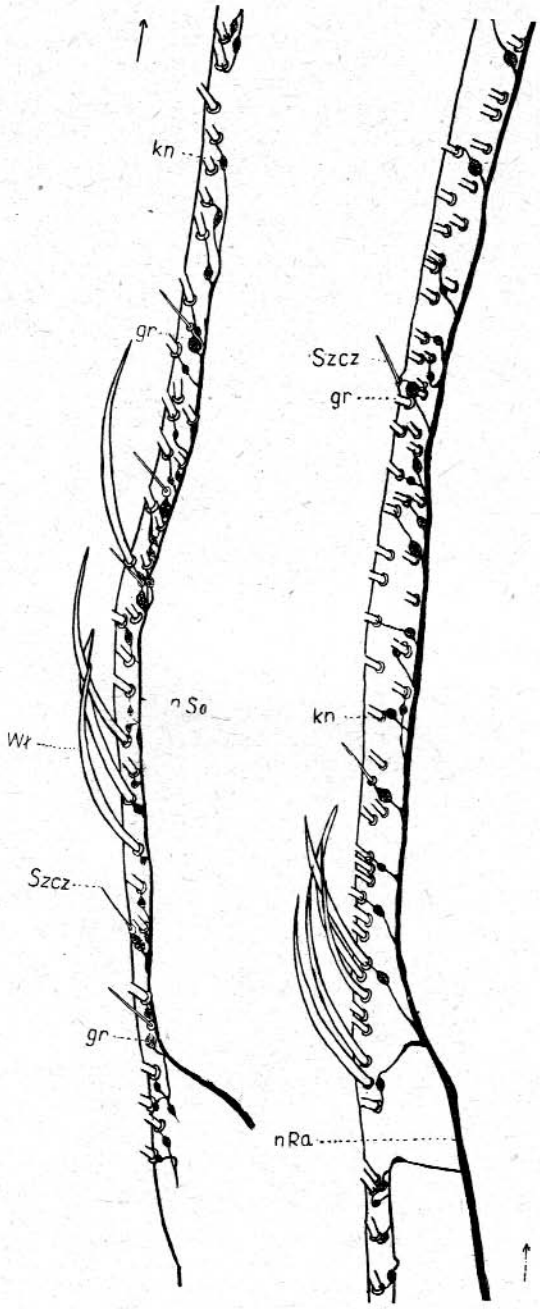

Fig. 2

TABLE III

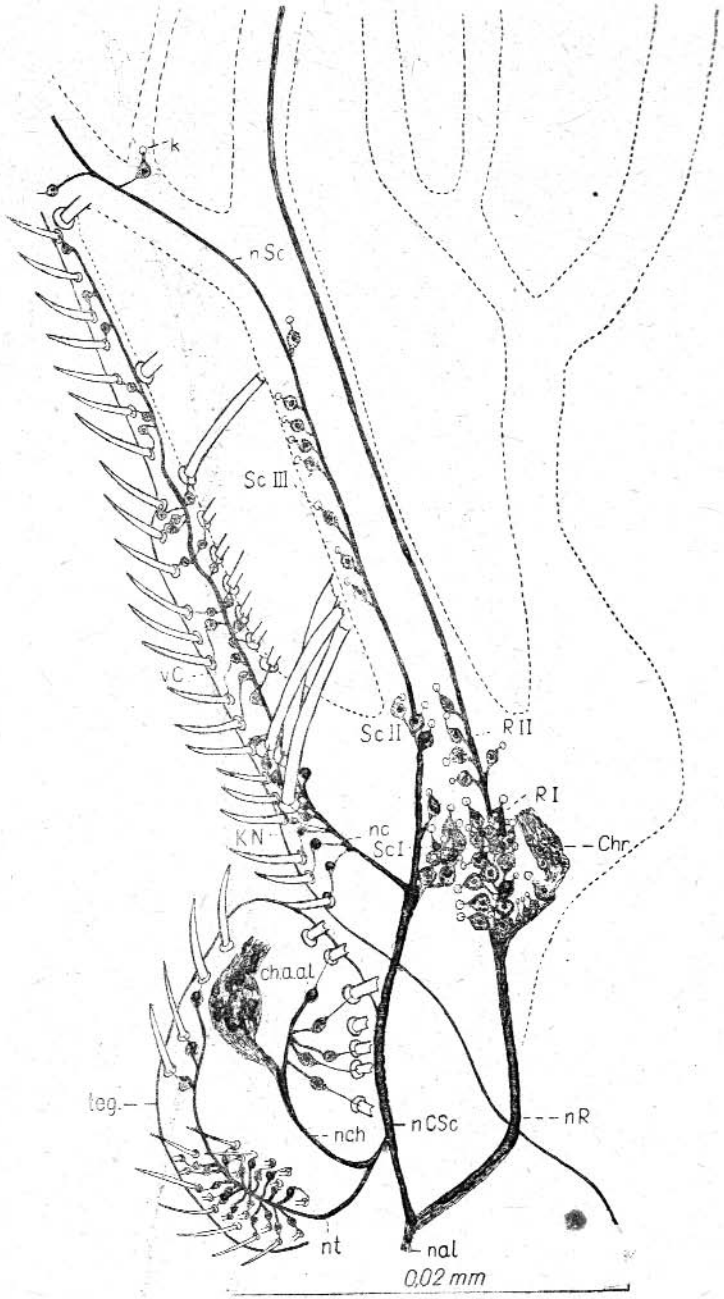

Fig. 3

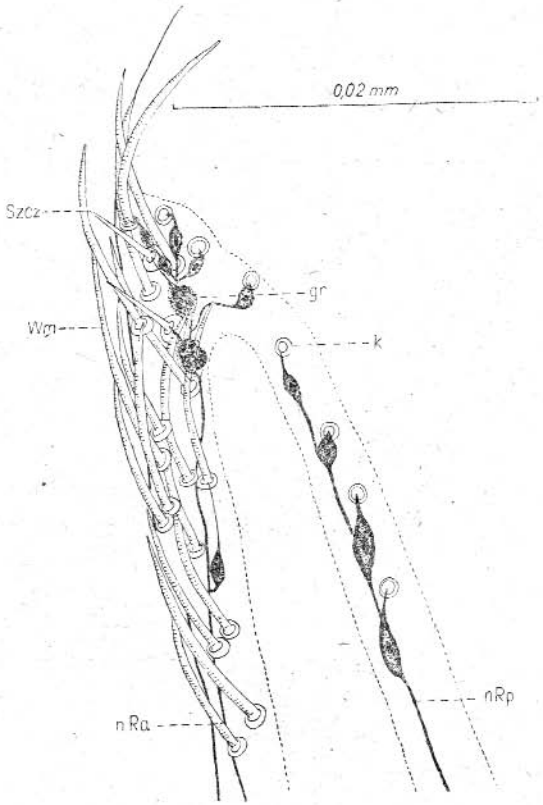

Fig. 4

TABLE V

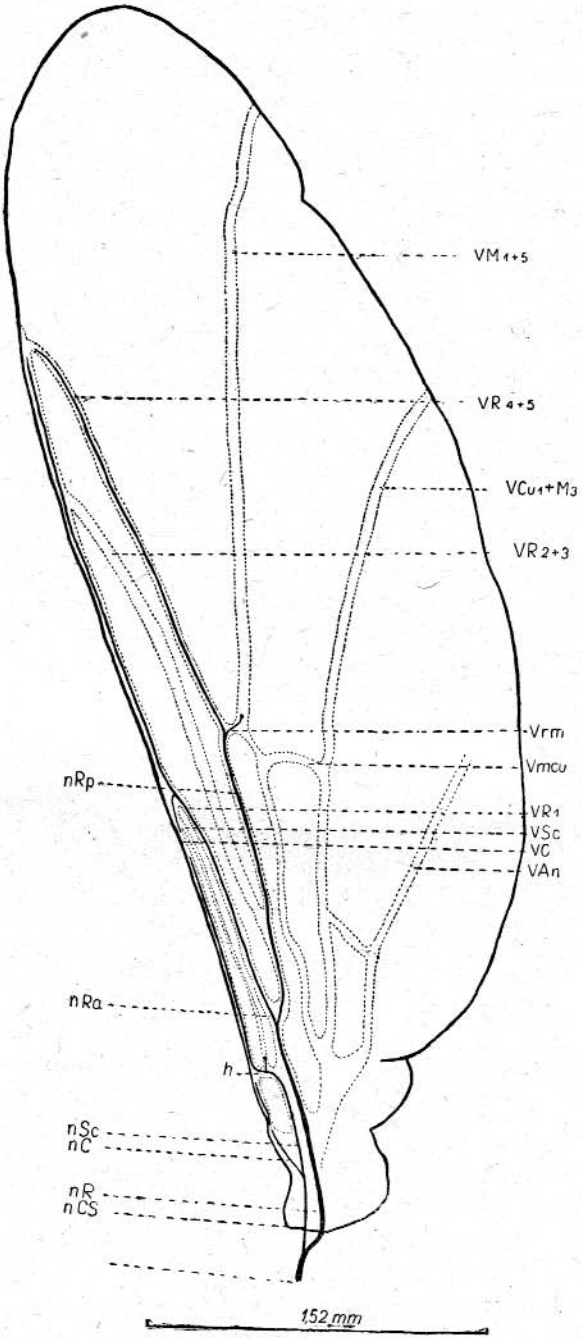
VM 1+5
VR 4+5
VCu1+M3
VR 2+3
Vrm
Vmcu
nRp
VR1
VSc
VC
VAn
nRa
h
nSc
nC
nR
nCS
1,52 mm

Fig. 5