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THE SENSE-ORGANS OF NEREIS VIRENS, SARS.¹

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With Plates I to III.

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¹ Work from the Zoölogical Laboratory of the University of Michigan, Jacob Reighard, director.

I. INTRODUCTION.

The following work¹ was begun in the Zoölogical Laboratory of the University of Michigan in 1894 under the direction of Prof. Jacob Reighard and has since been carried on there except during the summer of 1896. At this time, the application of the intra-vitam methylene blue stain to the material in hand was worked out in the Marine Biological Laboratory at Woods Hole under the direction of Prof. A. D. Morrill of Hamilton College.

With the exception of the four eyes, none of the sense-organs of *Nereis virens* have previously been described, though paired cephalic sense-organs of unknown function and isolated epidermal sensory cells have been described in other species of this genus and the latter have been briefly mentioned for *N. virens* itself. The following account contains a detailed description of two kinds of sense-organs—*diffuse sense-organs* and *spiral organs*—which are found scattered over the body in the epidermis of this worm, and also a brief description of two pairs of organs which are found in the prostomium. The diffuse sense-organs are simple epidermal organs which are directly comparable with the epidermal tactile organs of the Oligochæta. Isolated sensory cells, which are similar to the cells of the organs described in this paper and may prove to be identical with them, have been described for other species of *Nereis*; the diffuse sense-organs themselves have never been described for *Nereis* but have recently been described for two other genera of the Polychæta—*Axiothea* and *Clymene*. The spiral organs are complicated organs whose structure differs considerably from that of any organ previously described. They are, however, so nearly like the epidermal ocular organs of various invertebrates, that they may be considered to have for their function the perception of light. The two pairs of cephalic organs are of problematical function and have been already found in other Polychæta.

¹ A brief abstract appeared in *Science*, Vol. V, p. 427 (1897).

A peculiar form of epidermal cell has been incidentally noted. This cell apparently serves as an anchoring cell for the peripheral ends of muscles.

II. METHODS.

My material was obtained along the southeastern coast of New England; it was used in part at once and in part after shipment to Ann Arbor. It was found that the worms which were simply left in the open jar of sand and sea weed in which they had been shipped kept better than those which were placed in artificial sea water. The sand and sea-weed were kept loosely packed and the water lost by evaporation was replaced by distilled water.

Alcohol used as a killing fluid rendered the cuticula so resistant as to interfere with sectioning, but Müller's fluid without the use of anaesthetics gave very good results. When this fluid was used, the cuticula did not become resistant, the tissues stained readily afterward, and the epidermal structures were very well preserved. Paraffin sections were cut $10\ \mu$ thick and mounted by Pringle's variation of the hot water method as given by Lee. I find if my slide is chemically clean, the sections perfectly straightened, and then allowed to dry fully 24 hours before further manipulation, there is not the slightest need of any fixative with this process. The slides may be carried through a complicated process afterward without losing a section. Kleinenberg's hæmatoxylin gave the best results for general work and for a study of the spiral organs. The Biondi-Ehrlich three color mixture, lithum carmine followed by Lyons blue, and Licht grün followed by orange G were useful for differentiating glandular tissues.

For special nerve stains, both the silver nitrate and the methylene blue were tried; the silver nitrate proved so difficult and the methylene blue so easy that finally the latter was used exclusively. The method used was in general that given by Bethe ('95). It was found absolutely necessary that the circulation of the worm should be vigorous at the time of injection; in this case the blood-vessels would be filled with the blue and the nerve tissues well stained; but if the circulation were feeble at the time of injection, the blood-vessels would be found to be filled with clotted blood and but little if any of the nerve-tissue would be stained.

My best results were obtained as follows: Vigorous worms were injected with $1\frac{1}{2}\%$ Ehrlich's methylene blue in normal salt solution. The injection was made into the body cavity of the worm, care being taken not to inject enough in any one place to cause much swelling. The

blue could be seen to pass from the metamere injected through several adjacent metameres. When the body wall began to be distended, an injection was made in another region and this was repeated until the entire body cavity seemed to contain the blue. At first the attempt was made to force in as much fluid as possible at one injection, but this injured the tissues so that it seriously interfered with the circulation. Then injecting a smaller amount and repeating the injection after a short interval was tried—a method also used by Meyer ('96); this always gave very satisfactory results. Usually each worm was injected three times at intervals of about 40 min., using each time great care not to injure the animal more than was absolutely necessary. After the first injection, much more of the stain could be forced in at a time without danger of rupturing the body wall.

Following a suggestion given me by Dr. G. C. Huber, the animals were put away in the dark after each injection. It was found that, if two worms of equal size and apparent vigor were injected with equal amounts of the same methylene blue solution, the one kept in the dark gave surprisingly richer results than the one kept in the light. Instead of leaving the injected worm directly exposed to the air, it was found better to keep it in its normal medium—the sea-water. About four hours after the first injection—a shorter time on very warm days—the worms were taken out and, without being opened, exposed to the light and air. At first the color of the body would be nearly normal, but in about fifteen minutes it would become a rich blue. I am, however, inclined to believe that this exposure causes merely a bluing of the general tissues and that the nerve elements are already stained when the animal is removed from the dark and the sea-water. Several times a worm was removed from the dark and while it was still in the sea-water, a parapodial cirrus was cut off. No matter how quickly this was placed under the microscope, the nerve-cells of the sense-organs were already blue. Sometimes a worm would be so laid that only the parapodia of one side would be directly exposed to the air, yet the nerve tissues of the parapodia from the opposite side would be as richly stained as those from the exposed side. Then, again, several times the brain was richly stained in worms that had not been opened in this region. These facts seem to indicate that direct exposure of the nerve tissues themselves to the air is not always necessary.

My own observations have led me to the conclusion that the main factors in obtaining a rich stain in *Nereis* are: 1. vigorous, healthy worms; 2. the injection of a large quantity of strong stain in such a manner as to avoid interfering with the circulation; and 3. the keeping

of the animals under as nearly as possible normal conditions for a time long enough to allow the stain to be carried all over the body by the blood-vessels.

The same worm can be used for study for from three to five hours after removal from the dark, probably even longer. When a part of the body was mounted in sea-water and covered with a cover-glass, the stain quickly faded from all parts except the nerve-elements, which kept the stain from one half to three quarters of an hour.

Parts of the worm which were to be preserved were dropped into Bethe's fixing fluid (invertebrate formula) which had been previously cooled. The tissues were kept on ice in this fluid for from 4 to 6 hours—or even over night if convenient. They were then washed in a large quantity of distilled water for from 10 to 12 hours, and passed quickly, but by gradual steps, through the various grades of alcohol. The specimens were not only kept on ice, but each grade of alcohol was cooled before using. It was not only found that the warm alcohol removes the stain, as stated by Bethe, but also that warm water does the same. Several times tissues which a microscopical examination showed to be richly stained up to the time of warming for the paraffin bath, were at once ruined by this process and permanent mounts of such tissues showed that they had not been thoroughly dehydrated.

Pure xylol proved to be the best clearing fluid; the transfer from the absolute alcohol to the xylol was made gradually and the xylol kept on ice until all trace of the alcohol was removed. The tissues were warmed gradually to the melting point of the paraffin used and kept for two or three hours in the paraffin which was changed once or twice before embedding. When embedded in paraffin, even if the paraffin is allowed to cool before all the xylol is removed, the tissues retain the stain well. Material which had been kept in a block of soft paraffin for six months before cutting was in excellent condition and was uninjured by re-embedding.

The sections were cut from from 20 to 45 μ thick, and fixed to the slide by means of albumen fixative—the warm water method proving unsatisfactory in this case since it seemed to injure the stain. Mayer's alcoholic cochineal, which stains in 10 min., proved to be the best secondary stain. While in the grades of alcohol and in the stain itself the sections were kept cold; they were cleared in xylol and mounted in xylol balsam. Sections thus prepared show no sign of losing their blue after an interval of three years. The only epidermal structures not well preserved in these preparations are the spiral organs. Lewis ('98) states that the cuticula in *Axiotea* and *Clymene* is badly pre-

served in methylene blue preparations; in *Nereis* I have always found it very well preserved and its structure, especially after the use of the secondary stain, clearly defined.

The removal of the cuticula of *Nereis virens*, owing partly to its greater thickness and partly to the fact that it is more firmly attached to interior structures, is much more difficult than in *Lumbricus*. The alcoholic method used with the latter form (Langdon '95) was a total failure when tried on *Nereis*. Macerating in Müller's fluid for three months gave better results, but my best results were obtained with a 10% salt solution, suggested to me by Miss Margaret Lewis (see Lewis, '98). I found it best to prepare the cuticula as follows: The worms were killed in the 10% salt solution and left for a few days in a small quantity of this fluid. They were then washed thoroughly in plenty of distilled water to remove all trace of the salt, and placed in 35% alcohol to render the cuticula firmer. Each worm was then slit its entire length close to the parapodia of one side, all the parapodia of the other side were cut off, and the body wall cut through along the anterior margin of the buccal cavity. The greater part of the interior tissues were removed with fine forceps and the inside of the cuticula brushed clean. It was found difficult to get all the tissues out of the cephalic cirri. All could be removed from the palps and tentacles and some from the cirri by turning the structures inside out with a pipette, brushing the inner surface, and then turning them back again by the action of the pipette on the opposite surface. When it was desired to mount the cuticula of a given parapodium, the latter, while still attached to the body cuticula, was turned wrong side out, cleaned, turned back again, and then cut off and mounted separately. After being thoroughly rinsed in clean 35% alcohol, the cuticula was cut into convenient lengths, floated onto a slide, pressed down with a brush, and then allowed to dry. The cuticula of the caudal region macerates so quickly that it is best to cut off this region and mount its cuticula after it has been in the salt solution a shorter time than that allowed for the rest of the body.

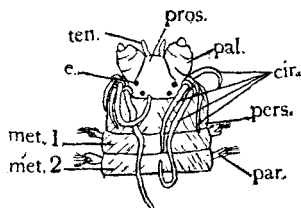
For making a chart to show the distribution of the sense-organs by means of the cuticula, a Zeiss projection microscope fitted with an arc-light was used; it was found that the image of the cuticula was more distinct when the room was not darkened. The distribution of the organs in the various sensory appendages was also studied by means of surface views of living appendages taken from worms that had been injected with the methylene blue. In such appendages the

cuticular location of each sense-organ is shown by a clear white spot in the surrounding blue stained tissue.

Owing to their minuteness, the external openings of the spiral organs could not be distinguished in the removed cuticula. The distribution of these organs in the head and first metamere was studied by means of a wax model of this region. In making this model it was necessary, owing to lack of material, to make use of a series of sections only $10\ \mu$ thick and prepared for another purpose so that there were no reference planes; but there are so many grooves and ridges on the surface of the anterior end of *Nereis* that it was easy, by their aid, to fit the sections together accurately. As each organ appears in at least two sections, only every other section was drawn and the position of each organ was marked in its margin. After the sections were cut out and as they were being fitted together, common pins were stuck into the model so that their heads marked the position of the outer ends of the spiral organs on the surface of the model.

III. EXTERNAL APPEARANCE OF NEREIS VIRENS.

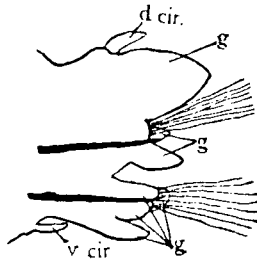
The following brief description is inserted for the convenience of the reader. The body of *Nereis virens* is in general cylindrical, and beside the head itself consists of about 120 metameres. The head consists of a prostomium joined to the dorsal border of the anterior margin of a wide peristome which is supposed to consist of two fused metameres (see Text-figure 1). The prostomium bears the four eyes



Text-figure 1. Outline of the dorsal surface of the cephalic end of *Nereis virens*. *cir.*, cephalic cirrus; *e.*, eye; *met.*, metamere; *pal.*, palp; *par.*, parapodium; *per.*, peristome; *pros.*, prostomium; *ten.*, tentacle.

on its dorsal surface, a pair of palps on its lateral border, and a pair of tentacles on its anterior border. Each tentacle is a small appendage which tapers to a point. Each palp consists of two parts—a thick basal part and a smaller rounded tip which can be almost wholly retracted into the basal part; the body cavity extends into the basal part but not into the tip. Just caudad of the base of each palp, the peristome bears

two pairs, set very close together, of long slender appendages—the cephalic cirri. One cirrus of each pair is over twice as long as the other one. Each cirrus is inserted on a short basal part similar to but smaller than the basal part of a palp, and is kept constantly moving in all directions. The surface of the peristome and of a few of the anterior metameres is marked by numerous grooves which pass obliquely from their anterior to their posterior borders. Each metamere back of the peristome bears on each lateral surface a parapodium—a lobed outgrowth of the body wall (see Text-figure 2). A typical parapodium consists of about seven comparatively flat, pointed lobes which func-



Text-figure 2. Outline of a typical parapodium of *Nereis virens*. *d. cir.*, dorsal cirrus; *g.*, gill lobe; *v. cir.*, ventral cirrus.

tion as gills and of two slender pointed appendages—the dorsal and ventral parapodial cirri—which are purely tactile. The anterior parapodia are very small; passing caudally they increase in size until near the caudal end of the worm. At this extremity, the metameres become very small; the parapodia also decrease in size but are much larger in comparison with the size of the metameres than are the parapodia of the cephalic end of the worm. The anal metamere bears a pair of long slender appendages similar to the cephalic cirri and known as the anal cirri. These cirri are directed backwards.

IV. THE DIFFUSE SENSE ORGANS.

The diffuse sense-organs are found not only in the epidermis over the entire body but also in each of the cephalic and anal appendages and in each lobe of every parapodium. Each organ consists of a small elongated group of bipolar nerve-cells whose central ends taper into nerve fibers which pass into the central nervous system, and whose peripheral ends also taper into processes which pass through modified areas in the cuticula

above each organ and project above the external surface as a group of sensory hairs. These sense-organs are directly comparable with the epidermal sense-organ of *Lumbricus* (Hesse '95 and Langdon '95) and of *Axiothea* and *Clymene* (Lewis '98). The sense-organs found in different regions of the body vary in the position of their cells, in the final termination of their peripheral processes, and in the character of the cuticular openings by means of which these processes reach the exterior. The organs of these various regions will, therefore, be described separately. Since those found in the epidermis of the body itself may be conveniently taken as a type, they will be first considered.

A. Structure.

a. *Diffuse sense-organs of the body epidermis*.—Each diffuse sense-organ of the body epidermis, as seen in the prostomium, peristome and first metamere, consists of from 5 to 8, rarely as many as 16, bipolar nerve-cells. These cells are arranged in a slender spindle-shaped group varying from 4 to 10 μ in width and from 16 to 20 μ in length (Plate II, Figs. 30-32) and *all of the cells in each group are situated entirely within the epidermis itself*. Each of these bipolar nerve-cells may be conveniently analyzed into three parts—the body of the cell, an enlarged part in which the nucleus lies, the central process or axis cylinder, a slender fiber-like part which arises from the central end of the cell-body, and the peripheral process, an equally slender part which arises from the peripheral end of the cell-body. The tip of this peripheral process is differentiated into a sensory hair which is raised above the external surface of the worm (Plate I, Fig. 9; Plate II, Fig. 34).

The body of an individual cell is about 4 μ wide and from 4 to 10 μ long, scarcely larger than its nucleus. The shorter cell-bodies round off abruptly at each end; the longer ones taper at one or both ends. From the central end of each cell, one and only one process arises. I have never found any division of this process nor any branches arising from it, but the cases in which I have been able to trace a central process until it

reaches a nerve are so few that I would not, perhaps, be justified in deciding that such a process never branches. Each central process is slightly sinuous in its course; it takes such stains as Kleinenberg's hæmatoxylin but lightly, appears finely granular, and is of uniform diameter. With the methylene blue method it becomes delicately beaded or coarsely varicose. In fact, it presents all the characteristic appearances of a nerve-fiber. All the central processes, or axis cylinders, which come from the same group of nerve-cells—i. e., from a single sense-organ—pass together in a slender bundle between the central ends of the epidermal cells to the base of the epidermis.

In the base of the epidermis, as is easily seen in sections, are many nerve bundles which can be traced directly into the central nervous system. Even when a cell in one of the diffuse sense-organs is stained intensely blue, it usually happens, in my preparations, that the central process itself is stained for only a short distance centrally from its cell. Moreover, the entire bundle of nerve-fibers from one sense-organ is not only very slender, but always passes to the base of the epidermis in a more or less undulating course so that it is often cut obliquely. These facts render it usually impossible to trace either a single peripheral process or the entire bundle itself into one of the epidermal nerves. In two cases, however, the bundle of central nerve-fibers from an organ turned obliquely in the plane of the section and entered a cross section of an epidermal nerve (Plate II, Fig. 30). Moreover a central process itself in each of these bundles was stained blue for a longer distance than usual and could, therefore, be traced continuously. These two cases may be taken as evidence, it seems to me, that the central processes from all the diffuse sense-organs enter the nerves lying in the base of the epidermis. As will be seen later, this conclusion is abundantly supported by a study of the diffuse sense-organs of the various tactile appendages. In these it is clearly seen that all the central processes pass directly into nerves which in turn pass directly into the central nervous system.

The peripheral end of each cell gives rise also to but a single process. The latter passes, in company with the other

peripheral processes of the cells of the same organ, to the base of the cuticula covering the organ in question. Each peripheral process presents exactly the appearance of a central one. Therefore, as far as morphological appearances go, it is necessary to consider each peripheral process as well as each central one a true nerve-fiber; as will be seen later, a functional interpretation tends to confirm this opinion. When the peripheral processes from an organ reach the cuticula, they enter, still in a bundle, the differentiated area which always exists in the cuticula immediately over each sense-organ.

The cuticula over the body of *Nereis virens* is composed of a thin outer and a very thick inner layer (Plate II, Figs. 30 and 34). The outer layer is only $2\ \mu$ thick and, as seen in sections, is clearly marked by straight striations perpendicular to its outer surface. These striations mark the lines of separation between the individual fibers of which this layer is composed. The inner layer is $18\ \mu$ thick and is faintly marked by undulating striations parallel to the outer surface. In such stains as Kleinenberg's hæmatoxylin and Biondi-Ehrlich, the outer layer takes a much deeper stain than the inner so that the plane separating the two can be clearly seen. Bayer ('98) has found in the Rhynchobdellidæ that the cuticula is composed of layers of different ages, that the striations in the cuticula which run parallel to its outer surface represent the planes of separation between these layers, and that the outermost layer is frequently shed. I know of no observations on the shedding of the cuticula in the lower Annelids but the wear to which the cuticula is subjected by external forces, the strain to which it is subjected by the growth and movement of the worm itself, and also the fact that the outermost layer is so easily detached from the rest of the cuticula in both *Nereis* and *Lumbricus* render it probable, it seems to me, that in the lower Annelids the outer layer of the cuticula is either occasionally shed or gradually worn away. Then the undulating striations in the thick inner layer of the cuticula of *Nereis* would represent planes separating the successive layers. The breaking up of the outermost layer into fibers may be due to the weakening of this layer with age.

The above mentioned differentiated area in the cuticula over each sense-organ consists of two cavities—a larger ovoid cavity in the inner layer of the cuticula and a shallow cavity in the outer layer—separated by a thin layer which is perforated by several fine canals (Plate II, Fig. 34; Plate I, Fig. 9). Each of these ovoid cavities is 16 or $17\ \mu$ deep. A cross section of it taken at any part of its height always presents a circular outline. A longitudinal section shows that the smaller end of the cavity is next to the epidermis and is about $4\ \mu$ in

diameter; the diameter increases gradually until, at the peripheral end of the cavity, it becomes about $8\ \mu$. This ovoid cavity does not extend entirely through the inner layer of the cuticula, but is bounded peripherally by a thin layer of the latter—a layer which forms the perforated membrane previously mentioned. The membrane is about $2\ \mu$ thick, is slightly concave on both sides, and is pierced by from 5 to 16 minute canals. Over it is the cavity in the outer thinner layer of the cuticula. This cavity is really an opening which apparently extends entirely through the outer layer of the cuticula. This opening, together with the slight concavity in the outer side of the perforated membrane itself, forms on the outer surface of the cuticula over each sense-organ a saucer shaped depression slightly more than $2\ \mu$ in depth and about 6 or $8\ \mu$ in diameter (Plate I, Fig. 11).

The entire bundle of peripheral processes from a single sense-organ enters the ovoid cavity of its own differentiated area and passes through this cavity to the perforated membrane. Here the peripheral processes terminate in sensory hairs which pass through the canals in this membrane into the outer cuticular cavity and in the latter form a brush-like group which projects stiffly above the external surface of the body. Usually each peripheral process bears a single sensory hair which passes directly through one of the canals in the perforated membrane to the exterior. In a number of cases, however, I could distinctly see that before passing to the exterior a peripheral process branched into at least two or three processes (Plate II, Fig. 37), thus bearing several sensory hairs, each of which passed through a canal of its own. Owing to the difficulty of obtaining a side view of a cluster of sensory hairs in the removed epidermis, I found it impossible to study those of the general epidermis in the living condition. In material killed by alcohol or Müller's fluid and stained by the usual stains, not only are the cuticular canals but dimly seen, but the sensory hairs are usually withdrawn so that their tips lie either within the canals of the perforated membrane or even beneath the latter in the ovoid cavity itself. I am, therefore, unable to state how far

above the surface these sensory hairs normally project, but, from what I have seen, I am inclined to think it is not very far (Plate I, Fig. 9).

The fact that the perforated membrane is found only in the outer part of the thick inner cuticula and the only cells going to it are the bipolar nerve cells would at first seem to indicate that it is formed once for all. If, however, the outer surface of the cuticula of *Nereis* is either shed or worn away, there must be some provision for the regeneration of the perforated membrane. It may be that the epidermal supporting cells, acting through the thick cuticula, control the formation of a new perforated membrane, or it may be that the nerve cells themselves possess the power of forming cuticula. The latter explanation seems to me the more probable one. Then the extreme thinness of the perforated membrane as compared with the thickness of the general cuticula could be accounted for by supposing that the nerve cells, being highly specialized for another purpose, had retained the power of secretion in but a slight degree. The above supposition must, of course stand or fall by a study of the embryological development and of normal regeneration. Any difficulty in meeting the problems involved cannot, however, be taken as a proof that in *Nereis* or any other worm, the cuticula is an unchangeable formation because in the *Rhynchobdellidæ*, which are known to shed the outer layer of the cuticula, there are epidermal sense-organs above each of which is a perforated membrane.

In the methylene blue preparations, the processes in the cuticular cavities are often variously distorted (Plate II, Figs. 30, 34 and 37). Sometimes a fiber is abnormally thick and ends just under the perforated membrane in a small knob from which one, two, or three finer processes—the sensory hairs—pass through the canals of this membrane. The sensory hair may be normal while somewhere in the course of the peripheral process through the inner cuticular cavity there may be one or more varicosities of various sizes, or the peripheral process may appear normal while the sensory hair itself is swollen into a ball which lies above the cuticula. When these varicosities exist in the peripheral processes themselves, the withdrawal of the sensory hairs, as will be seen later, is due to their formation. In other cases it is due to a decided bending of that part of a peripheral process lying in the cuticular cavity, caused, perhaps, by the protoplasm of the fiber expanding or contracting more on one side than on the other.

In the methylene blue preparations that have been restained by the cochineal, there are often seen in each organ a

few cells and peripheral processes which were untouched by the blue but are now stained a deep pink by the cochineal (Plate II, Fig. 32). In these cases it can not only be seen that the bodies of these cells, like those stained by the blue, lie entirely within the epidermis; but that, in the body epidermis, *all the bodies of the cells of a sense-organ generally lie above the middle height of the epidermis*. I have seen but very few of these sense-organs whose cell-bodies reached almost to the base of the epidermis. The cells stained by the blue sometimes lie in the center, sometimes in one or both margins of an organ; the cells stained pink are not only exactly like the others but clearly send peripheral processes into the cuticular cavity over each sense-organ: it would therefore appear that *each diffuse sense-organ is composed of but one kind of cell and that cell is clearly a bipolar nerve-cell*. The epidermal cells around an organ show no signs of being modified into covering cells.

In forty organs especially examined for this point in sections of the peristome, only three showed but a single blue cell. Such cases might at first sight be taken as proof of the existence of isolated sensory cells, but in each of these three cases around the single blue cell there were found, by the use of the secondary stain, other cells which presented the same characteristic appearances as the blue cell. Moreover, whenever the cuticular cavity belonging to the organ in question appeared in the same section, there were found in this cavity not only the blue stained process of the blue cell, but also other peripheral processes untouched by the blue. These processes were entirely free from pigment, which is always found in the peripheral ends of the supporting cells of the epidermis—therefore they cannot belong to the common cells of the epidermis. In hundreds of diffuse sense-organs examined for various purposes, I have always found more than one cell. I therefore consider that I am justified in deciding that in the body epidermis of *Nereis virens* *there are no isolated sensory cells, the bipolar nerve cells there present are all grouped into definite sense-organs*.

b. *Diffuse sense-organs of the appendages.* In the thickened bases of the palps, of the cephalic cirri, and of the parapodia, the diffuse sense-organs are exactly like those found in the body-wall and the cell-bodies of these organs always lie in the epidermis itself.

In the slender distal portions of the cephalic and anal cirri, in the tips of the palps and in the tentacles and parapodial cirri, the diffuse sense-organs differ from those of the body itself mainly in the following points: the inner cuticular cavity, owing to the greater thinness of the inner cuticular layer in these appendages, is almost lacking, and the outer cavity is replaced by an elevation; the bodies of the cells of the sense-organs lie farther beneath the cuticula and those belonging to several sense-organs are often massed together so that a given group usually contains cells belonging to two or more organs.

Each of the appendages mentioned in the last paragraph is covered by a cuticula consisting of the same two layers found in the body cuticula, but in this region the inner layer is only 2 or 3 μ thick and the outer layer only 1 or 2 μ . Under the cuticula is a layer which is lacking in gland cells and is thus composed of but one kind of cell—the epidermal supporting cell. The bodies of these cells are 16 μ in length; they have their greatest width next to the cuticula and taper gradually to a pointed base which in every case is prolonged into one or more basal processes. These processes pass into the interior of the appendage and there, together with the processes from a few stellate cells which lie in this region, are loosely interwoven into fibrous tissue which fills the greater part of the appendages. In the longitudinal axis of each appendage, from its base almost to its apex, passes an axial nerve.

Retzius ('92a and '92b) has considered that in such appendages, the bodies of the epidermal cells form the epidermis itself, that the space between these bodies and the axial nerve—that is, the space filled by the basal processes of the epidermal cells—is beneath the epidermis; and that, therefore, the sensory cells which lie in this region have sunken beneath the epidermis. Pruvot and Racovitza ('95) and Racovitza ('96) have stated that in the Polychæta the "stylodes," i. e., the distal portions of the various sensory appendages—are purely epidermal outgrowths. In my work on *Nereis* I have myself been led to the same conclusion. In *Nereis* these appendages never contain an extension of the body cavity. In them are found only structures which are found in the epidermis of the body. In the latter, the bodies of the supporting cells of the epidermis are the same in form and almost the same in size as those of the appendages, but one never thinks of locating the base of the epidermis of the body at the base of the bodies of these cells. In this epidermis, the slender basal processes of the epidermal supporting cells are almost as long as the basal processes of similar cells in the appendages and extend centrally for a long dis-

tance before forming a basement membrane. This basement membrane lies between the epidermis itself and the layer of circular muscles just beneath it. In the distal parts of the cephalic, anal, and parapodal cirri, and in the tentacles there are no muscles whatever; those found in the retractile tips of the palps do not form a circular muscle layer, but are the ends of muscles which enter these appendages exactly as similar muscles enter the epidermis of the body itself. *These appendages must be, therefore, purely epidermal outgrowths—strictly homologous with the epidermis itself—and the base of the epidermis of any one of these structures can only be found at the base of the structure itself.* The axial nerves of each appendage would then be but one of the nerves which lie in the base of the epidermis and receives the central processes of several sense-organs.

It will be observed that the gills and the thickened bases of the palps and of the anal and cephalic cirri are not included in this discussion. All of these structures contain an extension of the body cavity and the base of the epidermis of each is, at least in places, limited by a basement membrane which lies in the structure itself and not at its base. These structures are, therefore, evaginations of the entire body wall and cannot be considered as differentiations of the epidermis alone.

It follows from the above that everything contained within the cuticula of the distal portion of the cephalic and anal cirri, in the retractile tips of the palps, and in the tentacles and parapodial cirri is in the epidermis; therefore *all the sensory cells in these appendages, no matter how far they lie beneath the cuticula, are really situated in the epidermis itself*, beneath the bodies of the epidermal cells, it is true, but among their basal processes.

In the cephalic cirri, the bodies of the cells of the diffuse sense-organs lie anywhere between the bodies of the epidermal cells and the axial nerve of the cirrus, but usually somewhat nearer the former. In these appendages I have seen nothing which can be interpreted as a sensory system of isolated nerve-cells—*all of the sensory-cells lie in definite groups* (Plate I, Fig. 1, Plate II, Fig. 33). The cells of any one group do not, however, always belong to a *single* sense-organ as is the case in the epidermis of the body. Sometimes all the peripheral processes from one group of sense-cells pass to a single modified area in the cuticula and in such a case this group constitutes a single sense-organ. Often the bundle of peripheral processes from a single group of sense-cells, before reaching the bodies of the epidermal cells, divides into two or three smaller bundles each of which passes to a separate area in the cuticula (Plate I, Fig.

2, and Plate II, Fig. 38). Such a group may be considered as made up of as many organs as there are cuticular areas to which its peripheral processes pass. In this case it may at first seem difficult to distinguish a grouping of cells into definite organs. But one may suppose that originally the sense-organs lay nearer the cuticula—as is the case in the body wall, that in the base of the epidermis the central fibers from several organs passed into a small nerve, and that several of these smaller nerves joined to form a larger one. If now the bodies of the cells of these organs sink centrally from their original position, their course would naturally be along the course of their central processes and they would come to lie somewhere in the original course of these processes. In those cases in which the central processes from two or more organs soon joined to form a common nerve, the bodies of the cells of these organs would come to lie side by side at this point of junction or even along the former course of this common nerve itself; and the original course of the outer portion of the central processes from these organs would be shown by the final position of the inner portions of their peripheral processes. *In the cephalic cirri, therefore, I consider that one of the modified areas through which a group of sensory hairs pass to the exterior, the small bundle of peripheral processes going to this area and bearing these sensory hairs, and the cells giving origin to these peripheral processes, whether associated with cells belonging to other organs or not, constitute a sense-organ.* Such an organ would be directly comparable with the diffuse sense-organs found over the general body of *Nereis*.

In these cephalic cirri, a group of sensory cells varies in length from 25 to 80 μ , in width from 12 to 16 μ , and contains from 7 to 16 cells. The cells composing a single group lie at different depths beneath the cuticula (Plate I, Fig. 1). Occasionally the body of one cell is separated from the others, but usually the body of one fits between the tapering ends of others. There is a greater difference in the form of these cells than is found in the cells of the diffuse sense-organs of the body epidermis, seemingly because in the latter region the cells are more pressed upon by adjoining tissue. In the general epider-

mis, each organ is not only surrounded by the bodies of the epidermal cells, but among these are many gland cells which when distended by their secretion, crowd the structures around them. Thus the cells of the sense-organs in this region must be crowded into a small space. In the cirri, the region in which the sensory cells lie—i. e., the region between the bodies of the epidermal cells and the axial nerve—is filled merely by fibrous connective tissue. The sensory cells in this region, therefore, are less crowded and are generally more elongated—varying from 4 to 12 μ in length and from 1 to 4 μ in width.

Each group of cells has its long axis oblique to the longitudinal axis of the cirrus and the peripheral processes—i. e., the peripheral nerve-fibers—from a given group pass together for a short distance in a course which is oblique to the bodies of the epidermal cells. If the group of cells belongs to a single organ, all the peripheral processes take the same course between these cell bodies. If the group belongs to two or more organs, the bundle of peripheral processes soon separates into two or more smaller bundles which diverge from each other; each smaller bundle then takes its separate course oblique to the bodies of the epidermal cells.

As a given bundle of peripheral processes passes between the bodies of the epidermal cells, it generally becomes slightly less in diameter and bends so that its course is almost at right angles to the cuticula. Quite often, however, the bundle of fibers continues its oblique course until almost to the cuticula, then turns and passes at right angles to it. The peripheral ends of the epidermal cells are thickly covered with brown pigment which does not quite reach the cuticula. In sections the position of the bundle of peripheral processes among the epidermal cells is clearly indicated by the absence of pigment among these processes, so that, wherever such a bundle approaches the cuticula, the band of brown pigment is interrupted by a clear area. It is these clear areas which first catch the eye and enable one to locate the peripheral ends of the sense-organs.

As a bundle of peripheral processes approaches the cuticula, the individual processes separate from one another (Plate

I, Figs. 1 and 2) and the greater number of them branch once or twice (Plate I, Fig. 4 and Plate II, Fig. 35); thus the space occupied by such a bundle just beneath the cuticula is greater in diameter than that at the base of the bodies of the epidermal cells. The entire space is usually somewhat funnel shaped, and the peripheral processes do not always completely fill it. In the latter case, it is clearly seen that the surrounding epidermal cells form an actual stiff-walled cavity. As this was observed in living as well as in prepared material, this cavity is clearly a normal structure (Plate I, Figs. 2, 3, 5A, 13A, 13B and 16).

In the cuticula of a cirrus, over each of these ultimate ends of the peripheral bundles, is a characteristic area which resembles more that over the sense-organs of *Lumbricus* (see Cerfontaine, '90 and Langdon, '95) than that over the sense-organs of the body epidermis of *Nereis*. As seen in surface views such areas do not show the delicate striations of the rest of the cuticula. Near the center of each of these areas are from 5 to 20 minute irregularly grouped pores through which the sensory hairs pass to the exterior (Plate I, Fig. 6). In longitudinal sections of the epidermis, it is seen that the outer layer of the cuticula is apparently lacking over this area—the perforated membrane through which the sensory hairs pass, in the cephalic cirri as well as in the body-wall, appears to be formed entirely from the inner cuticular layer (Plate I, Figs. 5A and 16). In the cirri, however, the absence of the external layer of the cuticula does not produce an external depression such as is found over a diffuse sense-organ in the body epidermis. The outer surface of the perforated membrane in the cephalic cirri is generally more or less convex so that the surface of the cuticula over one of these areas is either plane or actually elevated, rarely concave. The perforated membrane of a sense-organ in the cephalic cirri is only $1\ \mu$ thick and the inner cuticular cavity beneath it is but $2\ \mu$ deep.

In the minute canals which pierce this perforated membrane, lie the ultimate tips of the peripheral processes, each bearing a stiff sensory hair which normally, as may be seen in living cirri, projects some distance above the cuticula (Plate I,

Fig. 3 and Plate II, Fig. 36). The living nerve-cells have a rather coarsely granular central protoplasm surrounded by a clear outer neuroplasm. The same parts may be seen in both central and peripheral processes, each of which has a granular axial strand and a clear outer neuroplasm. The sensory hair itself contains no trace of the granular axial part but appears to be composed entirely of somewhat rigid neuroplasm; or it may be that the extreme peripheral end of each sensory cell, like that of each of the epidermal supporting cells, is actually cuticularized. That the sensory hair is not attached to the general cuticula but is a prolongation of the peripheral process itself is shown by the fact that, whenever a contraction of a peripheral process takes place, the sensory hair is always drawn partly or wholly beneath the cuticula (Plate I, Fig. 4). In the methylene blue preparations, the peripheral processes are often varicose; a large swelling may form at a point where one peripheral process branches (Plate II, Fig. 35) or the sensory hair itself may be swollen into a ball which lies on the external surface of the cuticula (Plate I, Fig. 4). This may even happen to all the sensory hairs in one group and then the entire group appears above the cuticula as a crowded group of spherical bodies (Plate I, Fig. 20). It must be born in mind, however, that these varicosities and swellings are all artefacts.

The central processes from the cells of the diffuse sense-organs present exactly the same appearance as the peripheral ones. The central fibers from one group of cells pass, either alone or after joining those from other groups, to the longitudinal axis of the cirrus and enter the axial nerve (Plate I, Fig. 1). The center of this nerve contains the central processes or nerve fibers from organs lying in the tip of the cirrus; passing toward the base, each organ adds its fibers to the outer surface of the nerve in its neighborhood, and the outermost fibers of the nerve at its base thus come from the organs lying in the base of the cirrus. Generally the fibers enter the axial nerve on the side on which their cells lie, but occasionally they cross the axial nerve and enter it on the opposite side.

The diffuse sense-organs of the anal cirri as seen in hæmatoxylin preparations are exactly like those of the cephalic cirri. Owing to the fact that the caudal end is broken off by the contortions of the worm when injected it is difficult to obtain methylene blue preparations of this region.

In the tentacles and the retractile tips of the palps the sensory cells are also grouped into definite sense-organs which are practically like those of the cephalic cirri. Because of the smaller size, however, of the tentacles and palps, their sense-organs have less room and the sensory cells are, therefore, crowded toward the median axis of each appendage, thus giving rise to what appears to be a crowded mass of isolated cells. It can be seen, however, that each modified cuticular area is supplied by peripheral processes from several sensory cells, thus plainly showing the grouping of these cells into definite organs (Plate I, Figs. 14 and 15.)

In sections of the *palp*, it is a little more difficult to locate a bundle of peripheral processes in its cavity among the bodies of the epidermal cells because the latter, instead of stiffly outlining this cavity as in the cephalic cirri, press closely against the bundle of processes (Plate I, Fig. 15). The modified cuticular area over a sense-organ in this region, as seen in sections, differs from that of the cephalic cirri in but one point—the inner cuticular layer is thinner in the palps thus rendering the concavity beneath the perforated membrane more shallow than in the cirri. A surface view of this cuticular area presents several differences. The pores through which the sensory hairs pass are smaller and more numerous—varying from 8 to 21 in number—and they form an almost circular group.

Each of these groups is in some preparations of the removed cuticula surrounded by a number of larger pores which resemble gland pores (Plate I, Fig. 8). Sections through the palps, however, show that not only are there no glands whatever in the tips of the palps but that there are no canals in the cuticula aside from those through which the sensory hairs pass—i. e., those which lead to the central group of minute pores seen in a surface view. A discussion of these larger pores will be left until the anchoring cells found in the epidermis are described.

In the tentacles, the cells of the diffuse sense-organs lie in some cases among the basal parts of the bodies of the epidermal cells. Many of the sense-cells, however, especially in the distal half of the tentacles, lie in the median axis of the latter. It thus happens that the central fibers from these organs do not form a distinct nerve until the base of the tentacle is reached. In sections of the tentacles it is even more difficult than in the palps to locate the position of the epidermal cavity containing each bundle of peripheral processes. It will be noted that in the cephalic cirri (Plate I, Fig. 5A) the peripheral ends of a few epidermal cells are found attached to the cuticula just within the margin of the inner cuticular cavity. In the tentacles this is carried so far that very slender peripheral ends of epidermal cells almost fill both the epidermal and cuticular cavities and are attached to the cuticula up to and even among the peripheral processes of the sense-cells (Plate I, Fig. 14). As these cell ends are pigmented, their presence under the perforated membrane obliterates the clear area that rendered it easy to distinguish the position of the epidermal cavity in the cephalic cirri.

Around each cuticular area, as seen in the removed cuticula, is found the same arrangement of groups of larger pores that is found in the palps (Plate I, Fig. 8).

In the gill-lobes, the diffuse sense-organs are scattered and each contains but a few cells whose bodies always lie in the epidermis. The modified cuticular area over each sense-organ is exactly like that found in the cephalic cirri.

In the parapodial cirri, large numbers of bipolar nerve-cells are stained by the methylene blue and at first sight appear to be isolated cells. But a study of the removed cuticula reveals the groups of fine pores in modified cuticular areas which enable one to identify the diffuse sense-organs with certainty.

In sections of the *ventral parapodial cirri*, it is clearly seen that the peripheral processes from a few nerve-cells join each other and pass through a slender epidermal cavity to a single modified area in the cuticula (Plate I, Fig. 5B). The bodies of these cells always lie some distance apart and thus give, in sur-

face views of an entire cirrus, the appearance of isolated cells. In sections of the *dorsal parapodial cirri*, there is sometimes found what appears to be a case of isolated sensory cells (Plate I, Fig. 7). It should be noted, however, that each epidermal cavity appears large for a single peripheral process; that the tip of the latter does not show any sign of branching into several sensory hairs as would be necessary if a single cell supplied one of the perforated membranes which, so far as I have been able to determine, always contains several canals; and that, in one of the epidermal cavities figured, a second peripheral process can be seen, although neither its peripheral end nor its cell-body appears in the section. These sections were so faintly stained that one could not determine whether or not other processes were present in the epidermal cavities. In some sections of a dorsal cirrus stained with Kleninberg's hæmatoxylin, the sensory cells appear plainly grouped into definite organs (Plate I, Fig. 17). In my study of sensory hairs in living dorsal cirri, I have sometimes seen such an appearance as that figured in Plate I, Fig. 23. It will be seen that, near the base of this cirrus, some of the sensory hairs appear to be isolated. But in other dorsal cirri, all of the sensory hairs along the same margin were clearly arranged in groups (Plate I, Fig. 18). It must be either that all of the sensory cells of a dorsal cirrus—except perhaps those supplying the extreme tip—are grouped into definite sense-organs and the apparent cases of isolated cells we owe merely to irregularities in the stain or to the destroying of some of the sense-hairs; or else that cirri from the same metameres in different worms or from different metameres in the same worm vary—some having all of the cells grouped into definite sense-organs and some having the cells at the base isolated. From the evidence in hand I am inclined to the former view. In the tip of both dorsal and ventral cirri, as seen in living material, there always appears to be a few short isolated sensory hairs. I have not yet obtained sections or mounts of the removed cuticula which would enable me to verify this observation. In the tips of the cephalic cirri, which are homologous with the parapodial cirri, it can plainly be seen that the

sense-hairs are in definite groups, thus indicating the presence of definite organs (Plate II, Fig. 36).

In these parapodial cirri, the sensory hairs always project a very long distance above the cuticula (Plate I, Fig. 27). In a dorsal cirrus only $300\ \mu$ wide at its base and having a cuticula only $2\ \mu$ thick, the sensory hairs on its dorsal border, as seen in living material, were $32\ \mu$ long and those on its ventral border from 24 to $28\ \mu$. The length of these hairs decreased toward the tip of a cirrus; at the tip itself they were only from 4 to $6\ \mu$ long.

It will now be seen that, with the exception of the doubtful cases in the tips of the dorsal and ventral parapodial cirri and the doubtful cases occasionally seen in the base of a dorsal cirrus, *the sense-cells found in the appendages of Nereis virens, like those found in the body-wall, are all grouped into definite sense-organs. Moreover, since these tactile appendages are purely epidermal outgrowths, it will also be seen that all of their sense-organs, and therefore all of their bipolar sensory cells are situated in the epidermis itself.*

B. Study of the Living Diffuse Sense-Organ.

The diffuse sense-organs of the cephalic and parapodial cirri of *Nereis virens* are excellent objects for a study of living nerve-tissue. If a cirrus be removed from a living worm, mounted quickly in sea-water under a cover-glass, and examined immediately, with the oil immersion, the living nerve-cells, nerve-fibers, and sensory hairs may be studied before any appreciable change takes place in them.

The living nerve-cells of the diffuse sense-organs are more elongated and smoother in outline than are the same tissues after fixation by reagents. Each cell always tapers more or less gradually into both processes (Plate I, Fig. 12)—the rounded form with abruptly attached processes which is so often seen in sections does not appear in living material. As the tissue dies, there appears a tendency for the entire cells to shorten and widen under the action of surface tension.

Living nerve-fibers, while sometimes varying slightly but always gradually in diameter, are comparatively cylindrical and even in outline; they never show any of the varicosities so pronounced in fixed tissues. These varicosities, whether large or small, are always artefacts and never appear until the tissue is dying. They then form in such tissue whether it has been treated with reagents or not. As the tissues die, the nerve-fibers begin to shorten and widen. Occasionally this takes place through some considerable portion of its length, causing an abnormal thickening of the fiber through this part. Usually a nerve-fiber is affected at numerous isolated but often adjacent parts; this causes the fiber to become finely beaded or coarsely varicose, or even, if the contraction goes far enough, to become broken up into a row of disconnected granules. The last condition is more likely to be found in very delicate fibers. If a pigment granule is present in the neuroplasm of a nerve-fiber, a varicosity is apt to form around it. A slight but normal enlargement of a nerve-fiber is apt, during post-mortem changes, to become a large varicosity.

The living sense-hairs are best studied in the parapodial cirri. It can be seen that each living sensory hair is of uniform diameter throughout and has a bluntly rounded apex free from any enlargements whatever (Plate I, Fig. 27). As particles hit against the living hairs, the impulse given by the blow causes a sidewise movement of the sensory hair which is struck. *I never saw anything that I could interpret as a normal withdrawal of one of these hairs.* Since the nerve-cells bearing these hairs lie in the removed cirrus, it seems probable that the removal of the latter does not cause any immediate disturbance of the normal action of the peripheral processes of these cells. As the tissues die, the sensory hairs are often withdrawn, but *always through the formation of varicosities in the peripheral processes.* Often the tips of the sensory hairs swell into a rounded knob (Plate I, Figs. 4 and 24). Sometimes a hair can be seen to form a knob at its apex and then to be slowly withdrawn until this knob rests upon the cuticula (Plate I, Fig. 26). In living tissue stained by methylene blue it can be seen, in such

a case as that just mentioned, that this withdrawal is caused by a swelling of the peripheral process just beneath the cuticula. The part of the sensory hair withdrawn beneath the cuticula often enters into and helps form this varicosity. Sometimes, but more rarely, the apex of this sensory hair remains normal but the base enlarges (Plate I, Fig. 25). In very many cases the formation of a varicosity or the thickening of a considerable portion of a peripheral process withdraws the sensory hair and then the apex swells into a rounded knob (Plate I, Fig. 7). If ammonium picrate or Bethe's fluid be run under the cover-glass upon these sensory hairs while they are still in the normal condition, the same changes take place in them, but more quickly.

It seems to me possible, after seeing the normal form in living tissue, watching the actual formation of these artefacts, and afterward observing their appearance in sections, that such artefacts have been in the past described as normal structures. It appears to me especially desirable that those cases in which a peripheral process from a sensory cell is described as ending in a little knob just beneath or in the cuticula, should be re-investigated—if possible by means of living material.

I consider I am amply justified in deciding that *in Nereis virens every varicosity or beading found in the peripheral processes of the bipolar nerve cells or any end-knobs found on their sensory hairs are artefacts produced during post-mortem changes*. Normally these processes, or nerve-fibers, are cylindrical and almost uniform in diameter and the sensory hairs are cylindrical, bluntly pointed rods which always project above the external surface of the body.

Allen ('94) made a study of the varicosities in the nerve fibers of Crustacea and explains their formation as follows: "Both the phenomena of beading and the formation of end-swells appear to be due to a simple physical cause, namely the difference of surface tension between two fluids. A fluid cylinder surrounded by some other fluid of different surface tension is in a state of unstable equilibrium and tends to break up

into spherical drops." Allen evidently considers that the entire nerve-fiber takes part in the formation of these varicosities; both Dogiel ('93) and Huber ('97) have called attention to the fact that in vertebrate nerve-fibers it is the neuroplasm alone which swells under the influence of post-mortem changes and forms varicosities on the more resistant axial strand. In my own work with *Nereis*, I have been able to see that in the nerve-fibers it is usually the neuroplasm alone that forms these varicosities. Since the granular axial strand is lacking in the sensory hairs it must be that here also it is the neuroplasm that swells when death allows surface tension to act.

C. Course of the Central Processes to the Central Nervous System.

As before stated, the central processes of the diffuse sense-organs found in the body epidermis, including those in the base of the cephalic cirri and palps, were but rarely stained for any distance. It has, therefore, been impossible in my methylene blue preparations to trace these central processes directly into the central nervous system. In a few cases these processes could be seen to enter the nerves in the base of the epidermis. In the prostomium these epidermal nerves pass to the brain; in the rest of the body to the ventral nerve-cord in the metamere in which the epidermal nerve in question is situated.

In the various appendages, the central processes were so well stained by the methylene blue that they could be traced directly into special ganglia or into the brain itself.

The nerves from the anterior or internal pair of cirri pass into a small ganglion which is situated on the circum-œsophageal commissure just ventrad to the point at which this commissure divides into its larger dorsal and ventral roots. The nerves from the posterior or external cirri pass to a second ganglion slightly latero-ventrad of the first. From this ganglion a separate nerve passes to the anterior end of the sub-œsophageal

ganglion.¹ The central nerve fibers from the diffuse sense-organs of a cephalic cirrus can be traced directly through the axial nerve of the cirrus in which they lie into the ganglia at its base and seem to have a definite connection with the cells of the latter structure.

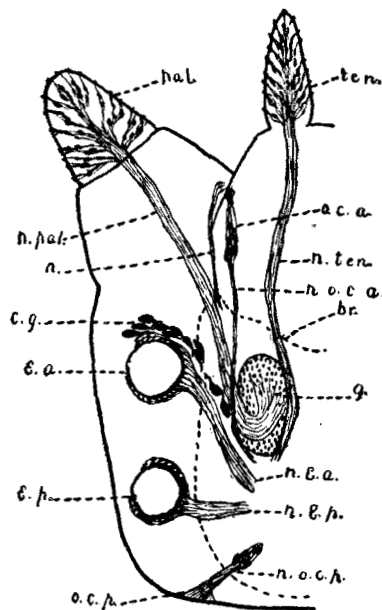
The central processes from the diffuse sense-organs of the tips of the palps pass into the axial nerve of the palp. Each of the two palp-nerves passes to the anterior projection of the brain which lies on its own side. Each then passes directly to the caudal part of the lateral margin of a palp ganglion—a mass of minute ganglion cells situated in the cephalic half of each side of the brain,—and finally mesad and cephalad into this mass of cells. (See Text-figure 3).

Retzius ('95) has figured and described a mass of minute cells—which he calls “vordere Haufen groben Korner,” just in front of each anterior angle of the brain, but entirely outside of it. Racovitza ('96) considers that each of these “Haufen” is composed of two ganglia—“ganglions palpaire et ganglions antennaires,” and that they are in the brain itself. Hamaker ('98) likens the “Haufen” of Retzius to merely the “ganglions antennaires” of Racovitza. He evidently doubts the connection of these bodies with the tentacles and considers them equivalent to the “mushroom bodies” of the insect brain, bodies which are supposed to be the center of control of intelligent action. I have not yet had time to make a thorough study of the brain itself; but from

¹ A point which, so far as I know, has not been previously noted is that this nerve—the “accessory connective” of Turnbull ('88)—is possibly a complete connective—a second circum-oesophageal commissure. From the second cirral ganglion, in which this connective has been described as ending, a nerve which appears to be a continuation of the accessory connective, passes through the first ganglion and, just dorsad of the latter, joins the dorsal border of the circum-oesophageal commissure or primary connective. In the dorsal border of this connective, the nerve in question can be traced for a short distance toward the brain, but finally the sheath separating it from the rest of the connective disappears, although the bundle of fibers seems to retain its original position. Just after this the primary connective gives off its dorsal root *from its dorsal border*. It may be possible that this dorsal root is simply the nerve from the cirral ganglion. In this case the “accessory connective” would be a complete connective passing from the sub-oesophageal ganglion to the brain. In a recent article, Hamaker ('98) notes the nerve connecting the two cirral ganglia, but does not note its further course. He also describes a second, very slender, dorsal root passing from the commissural ganglion into the brain. I am not able to state whether this also appears to be a continuation of the accessory connective.

what I have incidentally observed in some richly stained methylene blue preparations, I judge that Retzius' "vordere Haufen" are merely the palp ganglia mentioned above—ganglia connected only, so far as I can determine, with the retractile tips of the palps. There is no doubt that they are included within the limits of the brain.

The diffuse sense-organs of the tentacles send their central processes into the axial nerve of these appendages and each of these nerves passes to the anterior border of the brain farther dorsad and nearer the median line than does the axial nerve from the corresponding palp. On entering the brain, each passes



Text-figure 3. A diagram of the left half of the prostomium showing the course of the nerves from the tactile appendages and the special sense-organs into the brain.

br., outline of brain; c. g., large ganglion cells which lie beside the anterior eyes and in the adjoining region of the brain; e. a., anterior eye; e. p., posterior eye; g., mass of small ganglion cells to which the palp nerve goes; n., nerve from the supposed sensory area on the base of the palp; n. c. a., nerve from the anterior eye; n. e. p., nerve from the posterior eye; n. o. c. a., nerve from the anterior paired cephalic organ; n. o. c. p., nerve from the posterior paired cephalic organ; n. pal., nerve from the palp; n. ten., nerve from the tentacle; o. c. a., anterior paired cephalic organ; o. c. p., posterior paired cephalic organ; pal., palp; ten., tentacle.

around the median side of the palp ganglion of its own side and appears to enter a mass of large ganglion cells just caudad of the latter.

All the nerves containing the central processes of the diffuse sense-organs found in the various lobes of a parapodium join into a main trunk which passes into the parapodial ganglion situated near the base of each ventral parapodial cirrus. From this ganglion a nerve passes directly to the ventral nerve cord of its own metamere.

D. Ultimate Endings of the Central Processes.

From the foregoing description, it is seen that the central processes or nerve-fibers from the diffuse sense organs situated in the various appendages of the body may either be traced directly into the central nervous system or into peripheral ganglia connected with the central nervous system. The central nerve-fibers from the organs found in the body epidermis without doubt also pass into the central nervous system, but this cannot be so readily demonstrated. The final termination of all these central processes is a question which cannot be definitely decided by means of my present material.

In my methylene blue preparations, large numbers of the ganglion cells in the ventral nerve-cord, in the brain, and in the ganglia at the base of the parapodia and the cephalic cirri are surrounded by *apparent pericellular nerve-baskets*. I use the term *apparent* advisedly for I feel yet undecided whether all or any of these structures are normal. Most of the ganglia in which these baskets are found probably receive other centripetal fibers besides those from the diffuse sense-organs. But in my preparations the central processes of these organs are the only centripetal fibers which are stained. Moreover, two of the ganglia which show these apparent baskets—the two palp ganglia in the anterior part of the brain—receive, so far as I can see, only centripetal fibers from the diffuse sense-organs. Therefore, if proved normal, these pericellular baskets would be without doubt the final terminations of the central processes from the diffuse sense-organs.

These pericellular baskets are apparently formed of deep blue branching and anastomosing fibers which lie within the capsule of the enclosed ganglion cell either just on or above the surface of the latter (Plate II, Fig. 39). The individual fibers are generally beaded or coarsely varicose and closely resemble the nerve-fibers in these same preparations. Sometimes an apparent nerve-fiber can be traced along the axis cylinder of the ganglion cell and directly into one of these pericellular baskets (Plate II, Fig. 40). In all cases in which the wall of the enclosed ganglion cells is wrinkled, the fibers of its basket are situated upon the summit of the folds due to this wrinkling. When the basket is but little more deeply stained than the cell itself, this apparent network is probably the optical section of the wrinkles. In other cases the difference in depth of color between the stains of the walls of the ganglion cell and that of the pericellular basket is too great to be accounted for by a mere fold of the former. If one looked through a pale blue membrane so wrinkled as to show anastomosing ridges separated by intervening depressions, the colored material through which the light would pass to meet the eye would be of greater depth in the ridges than in the depressions between them. This greater depth in material would give a proportionally greater depth in color.

At Professor Reighard's suggestion, I tried an experiment which seems to show that such an explanation as the above will not account for the apparent dark network lying on the surface of a light colored ganglion cell. I placed under the microscope a pale blue ganglion cell which was surrounded by a dark blue network. I then took a thin-walled glass tube and poured into it enough of a light-colored methylene blue solution to give, when one looked into the tube and consequently through the depth of fluid, just the pale blue color of the cell wall. After noting the depth of this solution, I poured in enough more of the solution to give just the deep blue color of the network and compared it with the first mentioned depth. I then measured the thickness of the cell wall itself and that of an apparent fiber of the network. If the apparent fiber were a ridge of the cell

wall, it would seem as if the ratio between its depth and that of the cell wall should be the same as that between the two columns of fluid in my tube. I found that a given fiber of the apparent network was of the same depth as the cell wall itself. If the fiber were the summit of a ridge, the depth of the ridge would then be twice the depth of the cell wall. Therefore, if we overlook for the moment the possibility of refraction, the depth of the stain in the glass tube necessary to produce the same depth of color should be just twice that which gave the color of the wall itself. But the depth of fluid in the glass tube which gave the color of the network was 25 times that which gave the color of the cell wall. The experiment was repeated on other cells with practically the same result. If the greater depth of color in this apparent network were due to refraction, changes in the light and in the focus would render the color brighter; but these changes produce no effect in the depth of color and, therefore, the latter can not be due to refraction. Moreover, it sometimes happens that a dark blue network is found around a cell whose wall is stained pink by the secondary stain. There must be, therefore, some normal or artificial structure along the summit of the folds which of itself, takes a much deeper stain than the cell wall.

An appearance exactly resembling this network is often seen on the varicosities of the nerve-fibers where a pericellular nerve-basket certainly does not normally exist. After my experience in studying living, normal nerve-tissue and in observing the formation of artefacts during post-mortem changes—artefacts that have in the past been considered normal,—I feel that I am not prepared to discuss the question as to whether this basket-like appearance is an artefact in all cases or is a normal structure in the one case and an artefact in the other until I am able to investigate the subject in living material. In my mounted preparations, I can select a ganglion cell which one would say was without doubt surrounded by a terminal nerve-basket. I can select others in which one would instantly decide that the basket was an artificial appearance due to the wrinkling

of the wall. I can also find cells which show all gradations from one of these conditions to the other.

I can, therefore, at present only offer the two following statements:

1. If the appearances described above are pericellular nerve-baskets, some, if not all, of them are the final terminations of the central processes from the diffuse sense-organs. The fibers of these baskets must then strengthen the wall of the ganglion cells with which they are in contact so that these parts, upon the wrinkling of the cell wall become the summits of folds, and the apparent baskets found in other cases—i.e., on varicosities—must be artefacts which further study will enable one to clearly distinguish from the true structure.

2. If the appearance described above is not a pericellular nerve-basket, it is due to the formation of an artificial network in or on the wall of the ganglion cell and this network must differ chemically from the wall so that it takes the blue stains with greater readiness than does the wall itself.

E. Distribution.

A study of the distribution of the diffuse sense-organs by means of the modified cuticular areas as they are seen in a surface view of the removed cuticula and a comparison of the results of this study with the form of the body of *Nereis* reveals several suggestive facts. (See Plate III, Fig. 50.) The anterior end of the body, which is naturally more exposed to contact, is supplied with a very large number of sense-organs. All portions of the surface that lie in grooves and are thus protected by their position are entirely destitute of sense-organs. Those portions that are protected by a position near special tactile appendages are sparingly supplied with sense-organs; for instance the organs are very numerous over the cephalic metameres but become very few on the caudal ones because the caudal end is so narrow that both dorsal and ventral surfaces are protected by the relatively large parapodial cirri. Those portions of the body that have a uniform surface have a uniform distribution of their sense-organs; both the dorsal and ventral surfaces of the

caudal metameres are uniformly level and their sense-organs have, therefore, a uniform distribution; in metameres 6-20 the ventral line is depressed and the sense-organs are, therefore, fewer in the mid-ventral line and more numerous on the raised areas on either side.

The preceeding observations enable one to formulate the following general law of distribution: *The number of sense-organs with which a given portion of the body is supplied is directly proportional to the degree to which this surface is exposed to mechanical stimuli—that is, to the extent of its elevation above surrounding parts.*

The distribution of the diffuse sense-organs in the various parts of the body in accordance with the preceeding law may be summarized as follows:

1. Numerous sense-organs are irregularly scattered over the entire surface of all the special tactile appendages—the cephalic, anal, and parapodial cirri, the retractile tips of the palps, and the tentacles. (See also Plate I, Figs. 19 and 21 and Plate III, Fig. 51.)

2. Over the bases of the parapodia and of the cephalic and anal cirri and over the gill lobes the organs are few in number. The dorsal surfaces of the enlarged bases of the palps are supplied with a very large number of organs; the ventral surfaces contain a very small number.

3. The dorsal surface of the prostomium contains numerous irregularly arranged organs—about 400 in all—of which those on the anterior portion are fewer and smaller. On the ventral surface of the prostomium the organs are smaller and fewer in number.

4. The peristome contains a very large number—about 3600—of sense-organs. These organs are irregularly scattered over the surface in broad irregular bands which pass obliquely cephalo-caudad across the peristome and are limited by the grooves which mark its surface. The sense-organs are more numerous on the dorsal and larger on the ventral surface. They are both larger and more numerous around the anterior than around the posterior part. Around the anterior margin of the

ventral surface is a comparatively wide band entirely destitute of sense-organs.

5. That part of the buccal cavity which corresponds in position to the peristome and which is protruded when the animal is feeding contains a small number of very large sense-organs. Their distribution is practically the same as that in the peristome.

6. In the first metamere the sense-organs are more uniformly distributed than in the peristome. They are somewhat more numerous on the dorsal than on the ventral surface and are less numerous around the parapodia.

7. Passing caudad from the first metameres the following changes in distribution take place:

a. In each succeeding metamere, the organs become very gradually fewer in number up to and including the last caudal metamere. In metamere 41 there are only 1100 organs as against 2000 in the first metamere. In a few of the anterior metameres this decrease in number is accompanied by a decrease in size.

b. There are more sense-organs on the ventral than on the dorsal surface in a few anterior metameres. This difference becomes gradually less to about metamere 12 at which it disappears.

c. The sense-organs extend close to the posterior border of each metamere but are lacking over a narrow zone extending around the extreme cephalic border.

F. Function.

I do not find in the literature any experimental work on these sense-organs, neither have I been able to carry on such work myself. The parapodial, anal, and cephalic cirri, the tentacles and the retractile tips of the palps, from the way in which they are used, have always been regarded as tactile. *Nereis* possesses true eyes and other paired cephalic organs which probably serve for other special senses; it therefore seems to me that all of the diffuse sense-organs probably belong to the class of tactile organs. Those situated in the appendages and

therefore in the more exposed parts of the body probably receive stimuli for the most part through direct contact with external objects. Those situated in the body epidermis can probably, if necessary, function in the same way, but it seems more probable, since the surfaces in which they are situated are more or less protected by appendages and since their sense-hairs project but little above the general level of the body, that their function is to receive tactile, or possibly chemical stimuli, through the medium of the water. Nereis, when it leaves its burrow, is greedily eaten by various other marine animals. The motions of such animals in its neighborhood and perhaps the chemical substances thrown off by them may be conveyed to it through the water in advance of the animal and may thus enable Nereis to escape the threatened danger. The sense-organs found in the buccal cavity probably serve as gustatory organs.

The method by which mechanical stimuli are conveyed to the cells of the diffuse sense-organs appears to be as follows: If a living cirrus be watched under the microscope, it can be seen that, when a foreign body comes in contact with a sensory hair, the latter is bent passively to one side. This movement may be conveyed to the nerve-cell in one of two ways. Either the passive movement seen in the sensory hair is not confined to this part alone, thus mechanically stimulating the nerve-cell itself; or else the movement of the sensory hair causes a mechanical irritation of the end of the peripheral process on which it is borne, and this impression is conveyed to its cell by the protoplasm of the process as a nerve impulse—that is, each peripheral process is a nerve-fiber. The first method would necessitate a straight, stiff structure capable of purely passive movement. A peripheral process is always so delicate in structure and those in the cephalic cirri are so long and usually reach the cuticula by such an indirect course that it seems to be a mechanical impossibility for it to be a purely passive agent in the conveyance of a stimulus. It would, therefore, appear that each peripheral process, both from its structure, which exactly resembles that of the central processes, and from its probable

method of conveying stimuli from without, must be considered a nerve-fiber.

G. *Summary of the Literature.*

Claparède ('70) seems to have been the first to perceive these sense-organs in any species of *Nereis*. He studied the "terminaisons nerveuses" in "des tentacules, des palpes, et des rames pedieuses" of *N. peritonealis* and *N. cultrifera*. It is difficult to understand his description, but he probably merely saw the sensory hairs in an optical section.

Retzius ('92a and '95) studied the peripheral nervous system of various species of *Nereis*—of which the only one named is *Nereis diversicolor*—by means of the methylene blue and silver nitrate methods. He found a sensory system¹ of isolated, spindle or flask-shaped bipolar cells in the body wall, the parapodia, the tactile appendages and the buccal cavity. His figures and descriptions of these isolated bipolar nerve-cells in *N. diversicolor* closely resemble the bipolar nerve-cells of the diffuse sense-organs of *N. virens*. As before stated, with the exception of a few doubtful cases in the parapodial cirri, I have found that all of these bipolar nerve-cells in *N. virens* are grouped into definite sense-organs. Either two species of the same genus which live practically under the same conditions have the one a sensory system composed of isolated nerve-cells, the other one composed of the same kind of cells grouped into sense-organs or else, as seems to me more probable, the sensory cells described by Retzius are in reality grouped into definite organs. He does not describe any branching of a peripheral process or any especially modified area in the cuticula over these sensory cells, yet it seems probable that he has seen both. In one of his articles (see Retzius, '95, Plate II), he figures without remark a peripheral process which forks in the cuticula and also, in the cuticula above a nerve-cell, the outline of some structure which suggests the ovoid inner cuticular cavity of the sense-organs in the body epidermis.

Retzius describes the peripheral processes as usually ending just beneath the cuticula, sometimes in a little knob. Occasionally he found one ending in a yet finer part which ran partly through the cuticula in

¹ Retzius describes a system of branching nerve-fibers surrounding the setæ-fibers which he believes have no connection with the musculature of the setæ but probably form a second sensory nerve ending. In some of my preparations, these same nerve fibers have been richly stained, but they appear to me to be motor fibers innervating the muscles of the setæ.

a little canal and more rarely he found these finer processes raised above the cuticula. From these various positions in which he found the peripheral end of a peripheral process—beneath, in, or above the cuticula—he decided “dass sie vielleicht beweglich sind; man erhält nämlich den Eindruck, dass sie sich möglicherweise ausstülpen und wieder zurückziehen können.” From my own work, I judge that these finer processes are the sensory hairs of the nerve-cells, that the little canal in which one was occasional found must be one of the canals of a perforated membrane, that the end-knob in which a peripheral process occasionally terminates is purely an artefact—a varicosity which often forms at the tip of a sensory hair, that normally each peripheral process must project above the surface as a sensory hair, and that the retraction of these processes which Retzius regards as normal must be an abnormal processes—a process which takes place when the tissue is dying and which is usually caused by the formation of varicosities in the peripheral processes themselves.

Retzius states that the greater number of his bipolar nerve-cells lie beneath the epidermis—“die bei weitem grösste Anzahl derselben sich mit den eigentlichen zellenkörper aus der epithelschicht gelöst und in das unterliegende Gewebe eingesenkt hat.” He considers this true, not only in the tactile appendages in which the position of the cells in or beneath the epidermis depends upon one's definition of the limits of the latter structure, but also in the body itself. He considers that this position indicates an advance in organization of the sensory nervous system over that of *Lumbricus* (Retzius, '92b) and, therefore, uses *Nereis* as an illustration of the second stage in the passage of the sensory-cells from the epidermis to the central nervous system during the evolution of the vertebrate sensory system. In the early part of my work, I failed to perceive the true limits of the epidermis in the appendages and therefore fell into the error of supposing the bodies of the sense-cells in the diffuse sense-organs of these structures were “beneath the epidermis” (Langdon, '97). In my later work, I have been able to see that the bodies of the sense-cells in the tactile appendages always lie in the epidermis itself because, as previously stated, each of these appendages is purely an epidermal outgrowth and, therefore, all structures within one of them are in the epidermis, and that the bodies of the sense-cells in the body wall not only lie in the epidermis but generally *even nearer the cuticula than in Lumbricus*. I therefore consider that the sensory nervous systems of *Nereis*, if the position of the bodies of its bipolar nerve-cells can be taken as a criterion, is not higher but lower in organization than that of *Lumbricus* and that there-

fore in any series of animals arranged to illustrate the passage of the sensory cells from the epidermis to the central nervous system, *Nereis* would come before, not after, *Lumbricus*.

Racovitza ('96) states that in *Nereis dumerili* "la surface des deux antennes est hérissée de petits poils sensitifs"—probably the sensory hairs born by the cells of the diffuse sense-organs. He did not investigate these cells.

Hamaker ('98) is the only previous writer who has mentioned the bipolar nerve-cells in *Nereis virens* itself. He figures and briefly mentions *isolated* bipolar nerve-cells which generally lie partly or wholly beneath the epidermis of the body wall and the parapodia. He states that the cells of the sensory fibers of the third parapodial nerve—a nerve which receives the central processes from the diffuse sense-organs situated in the dorsal parapodial cirri and the dorsal gill lobes—"lie far beneath the hypodermis." As before stated, except for the doubtful cases in certain regions of the parapodial cirri, I have always found these bipolar sense-cells grouped into definite organs and, in all cases, have always found the bodies of these cells situated in the epidermis itself. In optical sections of living tissues or in thick microtome sections of methylene blue material, it is very difficult to perceive the unstained cells of a sense-organ and the limits of the epidermis. Even in thin paraffin sections, I have found that I could not feel sure of my results without the use of a secondary stain to define the limits of tissues unstained by the blue. Hamaker does not state from what kind of preparations his methylene blue figures are taken but his failure to use a secondary stain would in itself account for his failure to perceive the true arrangement and position of these sense-cells. Hamaker did not perceive the modified cuticular area over each sense-organ, and although he did not distinguish the sensory hairs as such, he noted that one of the peripheral processes enlarged "just beneath the cuticula into a small knob, from which a fine prolongation extended through the cuticula." This "fine prolongation" is, of course, a sensory hair and the "small knob" an artefact whose formation has partly retracted this hair.

There is a division of opinion concerning the final termination of the central processes from the bipolar nerve-cells—i. e., from the cells of the diffuse sense-organs—in *Nereis*. Retzius ('91) decided that these fibers entered the central nervous system, divided into an anterior and a posterior branch and each branch finally ended in an end-bush. Some of his figures of these end-bushes very closely resemble pericellular nerve-baskets. Among the branches of one of these end-bushes, he

often found an appearance of rounded glistening bodies which, it seems me, might be parts of the surface of an enclosed ganglion cell.

Hamaker ('98) decided that in *N. virens* each nerve fiber of his "set e" is "apparently centripetal, since no cell was found connected with it" and is equivalent to the sensory fibers of *Lumbricus*. These fibers enter the ventral nerve-cord through the fourth nerve, divide into an anterior and a posterior branch, the anterior branch divides again, and all three end in "fibrillations." Moreover some of the branches "lie side by side and are connected with one another by several ladder-like anastomoses." It seems to me unlikely that the sensory fibers should enter the ventral nerve-cord only by one of the five pairs of nerves found in each metamere of *Nereis*—unlikely both from the number and position of these organs and from the fact that in *Lumbricus* their central processes are found in all of the nerves in a metamere.

From his illustrations, I judge that his fibrillations are not the same as the appearances which I have called "apparent pericellular nerve-baskets"—appearances which are often found in the very ganglionic center to which the central fibers of the diffuse sense-organ can be directly traced and in which, as far as I have been able to determine, these same fibers are the only ones in my preparations that are stained by the blue. The mere fact that a given fiber is centripetal does not seem to me to be sufficient evidence that it is the central process from a cell in any epidermal sensory system. From the evidence now at hand it appears to me unlikely that the centripetal fibers described by Hamaker can be the central processes from the nerve-cells of the diffuse sense-organs. It will, however, need a careful tracing, on the one hand, of an individual centripetal fiber of the fourth nerve to its peripheral end, and on the other hand, of an individual central process from a single cell in a diffuse sense-organ to its central end in order to definitely settle this question.

As far as the final terminations of these central processes are concerned, my own observations make it seem possible to me that these will be found to be pericellular nerve-baskets rather than end-bushes or fibrillations.

The only previous accounts of pericellular nerve-baskets in the worms are those given by Retzius ('92c) and Simon ('96) for the leeches. Retzius figures and briefly mentions what appear to be undoubted nerve-baskets around ganglion cells in the brain of *Hirudo* and the ventral nerve-chain of *Aulastomum*. None of the appearances seen by me in *Nereis* have as closely resembled the nerve-baskets of vertebrates as those figured by Retzius. Some of the pericellular baskets figured

by Simon around the ganglion cells of the sub-oesophageal ganglia of the Hirudinea, exactly resemble the appearances found in *Nereis*. As he was not able to find the wall of these ganglion cells, he could not state positively whether the network lay upon the surface of the cell or was embedded in its peripheral protoplasm. Direct protoplasmic communication, however, between the nerve-basket and the ganglion cell, he considers as existing by means of a second, perinuclear, basket which is directly connected with the pericellular one. In *Nereis*, the wall of the ganglion cell may be plainly seen and is often stained; therefore it may be readily demonstrated that the apparent pericellular basket lies outside the wall itself and so far as I have been able to see, has no direct connection with the protoplasm of the enclosed cell. The only appearance I have seen in *Nereis*, which might at first sight be considered a perinuclear basket is one which proved to be the coarse, densely stained, chromatin network of the nucleus of the ganglion cell.

These diffuse sense-organs in *Nereis virens* are strictly homologous with the epidermal sense-organ described in *Lumbricus* by Hesse ('95) and myself (Langdon, '95) and also with those recently described in *Axiothea* and *Clymene* by Lewis ('98). The chief differences between the sense-organs in *Lumbricus* and those in *Nereis* are that in *Nereis* the cells of any one organ are smaller and fewer in number than in *Lumbricus*; in *Lumbricus* each cell bears but a single sense-hair, while in *Nereis* some of the peripheral processes branch and thus bear two or three; the slight concavity in the underside of the cuticula in *Lumbricus* is very much exaggerated in *Nereis* by the increase in thickness of the inner layer of its cuticula so that there results the ovoid cavity which is so characteristic a mark of the diffuse sense-organ of the latter form; in *Lumbricus* the external surface of the cuticula over each sense-organ is elevated, while in *Nereis* it is depressed; and in *Nereis* the perforated membrane appears to be formed only from the inner cuticular layer instead of from both, as in *Lumbricus*.

In *Lumbricus*, which entirely lacks any special tactile appendage, the diffuse sense-organs are apparently the only means the animal has of receiving tactile impressions. Living as it does in a comparatively dry burrow or crawling over the surface of the ground, it may be that it would more easily receive these impressions without injury to the rest of the body if the sensory hairs were borne on an elevated area. Since the surface of *Nereis*, whether in or out of its burrow, is always bathed by the sea-water, the sense-hairs, whatever their position, would also always be surrounded by this medium; stimuli conveyed through

the latter would be, therefore, just as quickly perceived if the external ends of these organs were more or less sunken beneath the surface, and the sensory hairs themselves would be thus better protected from injury. Nereis, as is well known possesses special tactile appendages which probably serve for all cases in which tactile impressions are to be received through actual contact with foreign bodies; the cuticular area over a sense-organ in these appendages resembles that over a sense-organ of *Lumbricus*.

The differences between the "diffuse sense-organs" of Nereis and the "epidermal sense-organs" of *Axiothea* and *Clymene* are as follows: In *Axiothea* and *Clymene*, the sense-organs as a rule "vary in size directly with the thickness of the cuticula;" the opposite is true in Nereis. A longitudinal section of the cuticular cavity over the sense-organs of the first named forms resembles more that found in the appendages of Nereis than that found in the body-wall, in that the inner cuticular cavity is shallow and wide at its inner end and the base of the outer cuticular cavity is elevated. As Lewis does not figure the two layers of the cuticula it is impossible to decide whether, as in Nereis, the perforated membrane is formed from the inner cuticular layer. In *Axiothea* and *Clymene* there is never but one sense-hair to a peripheral process; in Nereis there are sometimes two or three. Lewis considers these hairs probably normally retractile but states that she can give us no proof. She found two sensory hairs stained by the blue which seemed to move for a considerable time and change their position with reference to each other. This, it seems to me, was due to post-mortem changes taking place in the peripheral processes on which these hairs were born and not to any normal movement. She examined the removed cuticula of Nereis and concluded, from the likeness of the surface views of the cuticular areas over the sense-organs to those found over the sense-organs of *Axiothea* and *Clymene* that similar organs must exist in Nereis.

Blochmann ('95) and Zernecke ('95) have described and figured in the Cestodes and Blochmann and Bettendorf ('96) in the Trematodes a peripheral sensory system of isolated bi-polar nerve-cells lying partly in and partly beneath the sub-cuticular region. The peripheral processes of these cells are described as entering a "birnformigen Hohlraum" in the inner side of the cuticula and ending in this blind cavity in a "nagelkopfähnliche Platte" from which occasionally a small "Stiftchen" passes a little farther into the cuticula. Blochmann and Bettendorf regard this "Stiftchen" as probably always present but generally uncolored. Zernecke believes that, in the

Cestodes, it is probably an abnormal appearance caused by the silver nitrate deposit. All of these workers regard the end-knob of the peripheral process as a normal structure. Zernecke states that above these peripheral terminations in the Cestodes there is occasionally found a depression in the cuticula but does not think there can be any normal relation between the two. That is, according to all of these investigators the peripheral terminations of the bipolar nerve cells in the Cestodes and Trematodes are not external but lie in a small blind cavity which penetrates only the inner one-fourth of the thickness of the cuticula.

It seems to me probable, in comparing these peripheral terminations with those of the diffuse sense-organs of *Nereis*, that this blind cavity is but the lower part of such a modified cuticular area as has been described in preceeding pages for *Nereis*¹. It often happens in my preparations that the plane of the section is such that the ovoid inner cavity is cut obliquely (Plate II, Fig. 37). Then not only will the perforated membrane and outer cavity not appear in the section, but the inner cavity itself will often appear to extend but a short distance into the cuticula. In this case the appearance seen is similar to that figured by Blochmann and his pupils in the Cestodes and Trematodes and for some time I thought this appearance showed the correct structure of the cuticula over a sense-organ of *Nereis*. Even where the entire cuticular area appears in the same section, it is difficult without the use of a secondary stain in the methylene blue preparations to perceive the outer cuticular cavity even when the inner one is clearly defined.

The end-knob described by all these investigators as terminating each peripheral process, I regard as probably a varicosity formed during post-mortem changes—a varicosity whose formation caused the withdrawal of the “Stiftchen” which they occasionally found projecting from it. I believe that this “Stiftchen” is a sensory hair and that it normally passes through the cuticula and projects above the external surface. When the “Stiftchen” is not seen it is probably sometimes, as suggested by Blochmann and Bettendorf, unstained and sometimes wholly withdrawn; in the latter case the end-knob would be the abnormal swelling of the tip of the sensory hair so often found in *Nereis*. (See Plate I, Fig. 4.)

¹ If the modified cuticular area over the sensory cells of the Cestodes proves to be homologous with that in the cuticula of *Nereis*, it may be that this homology will tend to prove that the cuticula in the first named form is homologous with that of *Nereis* and that, therefore, the theory which claims the subcuticular tissue as epidermal is the correct one.

The sensory systems of these worms, as is known to be the case in other worms, would then come into direct relation with the external world—a condition which seems more probable than that this system should receive stimuli through a thick layer of resistant cuticula.

The nerve cells of the sensory system in the Cestodes and Trematodes closely resemble those of the diffuse sense-organs of *Nereis*. In several cases they are figured so close together that it would not be surprising if further research should prove that in some regions of the body these cells are grouped into small yet definite sense-organs.

Brode ('98) considers the metameric arrangement of the sense-organs of *Dero* of importance as a proof of the colonial theory of metamerism. My study of the distribution of the sense-organs of *Nereis*, especially when this distribution is compared with the form of the body and the movements of the worm itself, has led me to the opposite conclusion. The distribution in a given part of the body is so dependent upon the external form of this part and the form is so dependent upon the method of locomotion that I have been led to adopt the theory of Meyer ('91) that the metamerism of worms has been brought about by a secondary segmentation due to muscular activities. A further support of this theory is found in *Nereis* in that the external and internal metamerism do not agree with one another. It seems to me most probable that in the primitive worm the diffuse sense-organs—or what is probably their earlier form, isolated sense-cells—were evenly distributed over the general body and merely somewhat more numerous at the anterior end. Then as greater size and complexity of body brought metamerism with it through muscular activities, there became apparent a tendency for the sense-organs to become more pronounced in the more exposed portions of a given metamere and a tendency for the disappearance of these organs in regions in which they were of less use. There would thus be brought about a *secondary* arrangement of the diffuse sense-organs in girdles or longitudinal lines. I would therefore not lay stress upon the distribution of these sense-organs as a guide in tracing lines of descent.

V. SPIRAL ORGANS.¹

In the body epidermis, in the bases of the palps and cephalic cirri, and in the gill-lobes of the parapodia, are found com-

¹ These organs were called "ocular organs" in a brief résumé which appeared in *Science* (see Langdon, '97). I have since thought best to designate them by a term that will apply to them even if further research should prove my present conception of their function erroneous.

plicated epidermal organs to which I have given the name *spiral organs* because of the peculiar spiral arrangement of the peripheral processes of their cells. I have found these organs not only in *Nereis virens*, but also in the living parapodia of a second species—probably *N. limbata*, Ehlers.

A. Structure.

Each organ consists of a slender central tube around which are the spirally arranged peripheral processes from about 100 bipolar or multipolar cells whose bodies generally lie in the epidermis (Plate II, Fig. 41). The central tube and the peripheral processes arranged around it, whether seen in living material or in sections, form the most conspicuous part of one of these organs. This part is nearly ovoid, about $80\ \mu$ long, $40\ \mu$ wide at its widest part and has its smaller, somewhat pointed end pressed into a small cavity in the under side of the cuticula. This cavity is about $6\ \mu$ wide at the inner limit of the cuticula; from it a tubular opening or canal about $2\ \mu$ in diameter extends entirely through the cuticula, flaring a little at its outer end at which it becomes $4\ \mu$ in diameter (Plate II, Figs. 44 and 47).

The central tube is a cylindrical, flexible, thin-walled structure; it enlarges gradually from its peripheral to its central end and averages $2\ \mu$ in diameter (Fig. 43). The basal end of this tube appears to end blindly, but it is so covered by the lowest peripheral processes that it is difficult to determine this with certainty. The peripheral end of the tube passes into the shallow cavity in the under side of this cuticula above it. In the body epidermis and in the bases of the palps, the apical turn of the spiral formed by the peripheral processes lies in this cavity in the under side of the cuticula just where the cavity passes into the cuticular canal above it (Fig. 41.) In the gill lobes, the cuticula is very much thinner; in this region the apical turn of the spiral lies entirely below the cuticula and it can be seen that the central tube runs up to the cuticular canal and that the lumen of the tube is continuous with that of the canal and therefore opens to the exterior (Plate II, Fig. 43).

Quite often one of these cuticular canals contains a rod-like

body which takes a deeper stain than the inner cuticular layer—a stain like that of the outer cuticular layer. The inner end of this apparent rod joins the apex of the spiral organ; the outer end is sometimes bluntly rounded, but more often flares a little (Plate II, Fig. 45). Careful study seems to show that this apparent rod is an artefact. Very often the cuticular canal appears to be a mere opening through the cuticula without distinct walls of its own; then again it often appears to be lined by a distinct layer which takes a deeper stain than that of the surrounding cuticula. Finally cases are often found in which the lower parts of the more deeply stained lines along the two margins of the canal have separated from the inner layer of the cuticula (Plate II, Fig. 44). It may also be seen, both in sections of prepared material and in the surface views of living material, that the outer layer of the cuticula thins out and dips down into the flaring outer end of the canal; moreover, in macerations, the central tube always remains attached to the cuticula. All of these various appearances have led me to the conclusion that the central tube of the spiral organ passes entirely through the canal in the inner layer of the cuticula, the tube normally being closely pressed, perhaps actually joined to, the sides of the canal. The appearance of a rod in this canal is due to reagents, which cause the outer end of the central tube to shrink partly or wholly away from the cuticular canal in which it lies and to assume a rod-like form. This interpretation is borne out by the fact that this apparent rod has never been found in living material—the central tube always appearing empty throughout its length. The dipping down of the outer layer of the cuticula into the outer end of the cuticular canal suggests that the central tube of the spiral-organ is an invagination of the outer cuticula—an invagination probably formed before the formation of the inner layer of the cuticula. If, as now seems probable, the outer layer of the cuticula is either shed or worn away, the outer end of this central canal must each time either shift its attachment or else the inner surface of the canal itself must disappear and the cells of the spiral organ secrete new cuticular material.

The bodies of the cells of the spiral-organs may be found scattered among the basal processes of the epidermal supporting cells at a considerable distance and in any direction from the base of the central tube and in such cases the basement membrane of the epidermis is continuous beneath the organs. Sometimes, however, the cell-bodies lie in a group more or less directly beneath the central tube (Plate II, Fig. 41) and then the basement membrane of the epidermis is lacking under this group. Its place is taken by a thin membrane whose homology I have not been able to decide. It is formed of slender nucleated strands which resemble much flattened muscle-fibers, and is always convex on its inner surface. Sometimes all the cell-bodies of several spiral-organs lie in the same group and then the membrane under this group is so much curved as to form a sort of pouch projecting centrally. This is always the case in the bases of the palps, in which these pouches often extend beneath the epidermis a distance as great as the depth of the latter.¹ In the gill lobes, the bodies of the cells belonging to a single organ lie in a few groups beneath the central tube among the bases of the epidermal cells.

The body of each cell is quite large; its protoplasm is coarsely granular and its nucleus takes a uniform stain and contains a large nucleolus. The different cells of the same organ vary greatly in form. Some are oval or broadly elliptical bipolar cells, but by far the greater number are irregularly shaped multipolar cells (Plate I, Fig. 22 and Plate II, Fig. 41). All of the processes except two seem to be short slender processes which extend in various directions among the surrounding cells. One of the two longer processes is also slender. In living gill lobes taken from animals that have been injected by the methy-

¹ Retzius ('92a) figures, in the palps of *Nereis diversicolor*, the outline of large "Drüse" which exactly resemble the outline of one of the above mentioned pouches when a spiral organ appears in the same section and thus continues the outline of the pouch to the cuticula. The glands of *N. virens* are comparatively small and do not project centrally beyond the general level of the base of the epidermis. I at first looked upon these pouches in the palps of *N. virens* as glands and it may be that Retzius has fallen into the same error in *N. diversicolor*.

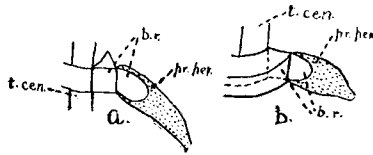
lene blue, this process is beaded or varicose and may be traced almost into one of the nerves of the lobe. It would, therefore, appear that this process is a central nerve-fiber. It may be seen also that consecutive sections always reveal a nerve in the base of the epidermis in the place occupied by several spiral organs in previous sections. There is never any appearance of a nerve passing to the central end of one of the pouches described in the palp, but one is always found passing to one side of its peripheral end. It seems that the central processes, in such a case, must pass peripherally into the base of the epidermis before entering a nerve. Everything indicates that these central processes always enter epidermal nerves but I have never been able to trace an individual process directly into a nerve. In living material the surrounding tissues render this tracing difficult and in mounted methylene blue material, the spiral organs are poorly preserved and have lost most of their stain. Without doubt these central processes in some regions of the body pass to the same ganglionic centers that receive the central processes from the diffuse sense-organs. The fact that they are, in all cases, stained by the blue for only a short distance centrally from the body of their cells would, I should judge, preclude the possibility of any of the apparent pericellular nerve-baskets found in these centers belonging to them. This does not, of course, preclude the possibility that these central processes also end in nerve-baskets—baskets unstained in my present preparations.

The second longer process from one of these cells is the peripheral one first mentioned. This process is always much stouter than the other processes from a given cell and enlarges at its end into a club-shaped part which terminates in a highly refractive body (Plate II, Figs. 41, 43 and 47). The peripheral processes pass toward the surface and at the same time toward the central tube in several small bundles and are generally attached on their own side of the tube. Sometimes, however, a single process, or even an entire bundle passes quite around the central tube and is attached to its opposite side. Either just before or just after enlarging into its club-shaped peripheral end

each process arches toward the central tube and its refractive body appears to be joined to a thick band which is wound spirally around the tube. The protoplasm of these peripheral processes as seen in living material, appears to be made up of transparent semi-liquid drops contained in the meshes of a very coarse, highly refractive network. In a few of my methylene blue preparations, there appears to be a nucleus lying close against one side of the enlarged end of a peripheral process. In material killed by alcohol or Müller's fluid, this appearance is never seen. The highest powers of the microscope and the most careful focusing never reveal any structure in a living peripheral process except the protoplasm previously described and the apical refractive body. As the nuclei in the cell bodies are clearly seen in living material, I believe, if one existed in the enlarged part of a peripheral process, it too could be seen. Moreover, in methylene blue preparations examined when the tissues are living, there is no trace whatever of the apparent nucleus seen in the permanent methylene blue preparations. In the latter, the spiral organs are poorly preserved. Each peripheral process is much vacuolated and its protoplasm is consequently reduced to mere threads or films which are forced against the wall of the process. The apparent nucleus seen in these preparations seems to me to be merely a thicker place of one of these threads.

The refractive bodies are clear, lens-like structures which take the stain but faintly, if at all. Each, when viewed from above, is generally rounded at the end away from the central tube and tapers from this end toward a slender rod-like part which rests upon the outer surface of the spiral band previously mentioned (Pl. II, Fig. 43). These rod-like parts give this band an appearance resembling the rim of a cog-wheel. (Pl. II, Fig. 49 g). The refractive bodies belonging to the peripheral processes, which pass to the deep end of the central tube seem to rest, when seen in living material, directly upon the tube itself. Sections, however, show that the spiral band is also present here, making its last turn around the base of the tube. When viewed from the side, it is seen that each refrac-

tive body really consists of two parts—an ovoid part embedded in the protoplasm of the peripheral process and continuous with a somewhat wedge-shaped block which extends quite to the central tube. (Text-figure 4). It is therefore clear that the spiral band is really not a separate structure, but is formed of



Text-figure 4. Lateral views of the tips of two peripheral processes in a spiral organ. *a* shows a refractive block with a ridge on its upper surface; *b* shows one which lacks this ridge and thus builds a smooth turn of the spiral.

b. r. refractive body; *pr. per.* peripheral process; *t. cen.* central tube.

the wedge-shaped blocks of the refractive bodies, arranged side by side in a spiral manner around the central tube. One of these blocks has usually seven surfaces. (Text-fig. 4, *a*, and Pl. II, Fig. 46). The two lateral surfaces are closely joined to the corresponding surfaces of adjacent blocks. In living material this plane of union is not visible; under the influence of reagents the blocks separate a little from one another and the component parts of the spiral band may then be seen. (Plate II, Fig. 41). The outer surface of each block is continuous with the ovoid part of the refractive body and with the protoplasm surrounding the latter. The lower surface is free and forms the lower surface of the spiral band; the upper surface is also free and usually bears an angular ridge which gives the cog-like appearance previously described upon the outer surface of the spiral. The inner surface of one of these blocks usually consists of two parts; the lower part is concave from side to side and closely joined to the central tube while the upper is free and forms an acute angle with the tube. It is these free upper parts of the inner surface that form the upper border of the spiral band. Sometimes the entire inner surface of several blocks joins the central tube and then the angular ridges on the upper surfaces are lacking. (Text-figure 4, *b*), and the part of the spiral band formed by these blocks appears smooth. In

a side view, the ovoid part of the refractive bodies, often does not show. (Pl. II, Fig. 46). These parts are, however, so generally found in views from above and in macerations that I am inclined to think they are always present; probably when apparently absent, they are concealed by a thick layer of protoplasm. The different appearances presented by these refractive bodies do not seem to be limited to any particular part of a spiral organ or to the organs of a definite region of the body. Occasionally I have seen in the gill lobes peripheral processes which contained refractive bodies of abnormal size or shape or even accessory bodies which were entirely unconnected with the apical one. (Pl. II, Fig. 48). As far as I can judge, these accessory bodies always have the same optical properties as the normal refractive bodies.

The refractive bodies might be either a hardened secretion of the cells with which they are connected or the metamorphosed tips of the peripheral processes. The protoplasm of the peripheral process is usually found to entirely surround the ovoid part of a refractory body and sometimes even the wedged-shaped blocks. This shows that, whatever its method of formation, a refractive body is an inclusion of the cell which produces it.

Under the influence of macerating fluids, the peripheral processes swell and soon go to pieces. The central tube not only remains attached to the cuticula but the refractive bodies remain firmly attached to the tube although component blocks of the spiral band sometimes separate a little from one another. It has therefore so far proved impossible to obtain for study a perfect detached element of a spiral organ—i. e., a cell with all its processes and its refractive body. The small size of the refractive bodies and their peculiar spiral arrangement around a tube of so small diameter produces many optical effects which render difficult the study of these bodies. The foregoing account however contains only descriptions which have been tested by repeated observations.

The spiral band may be either a left- or a right-handed spiral but the two never occur in the same organ. The en-

larged parts of the peripheral processes in consecutive turns of a spiral usually touch each other, but consecutive turns of the spiral band itself are always separated by a space about of the width of the band.

In sections from material killed by alcohol, the peripheral processes appear to be very slender and to be separated by very large clear spaces. These spaces are really enormous vacuoles which have formed within the processes themselves forcing the protoplasm to one side. The strands of protoplasm between these vacuoles thus present the appearance of very slender peripheral process separated by large clear cells (the vacuoles). In some material killed by Müller's fluid, a few of the upper peripheral processes and the cells to which they are attached are much more deeply stained than the lower processes in the same organ. (Plate II, Fig. 41). The protoplasm of such processes always appears more poorly preserved—i. e. more shrunken and more disintegrated—than others. The only explanation I can offer is that this appearance may be due to a different physiological condition of these processes or of the cells which bear them at the time of death. I am certain that it is not due to any morphological difference or to any difference in function. In living material and in some material killed with alcohol no essential difference whatever can be observed between cells or peripheral processes in different regions of a given organ; in material injected with methylene blue, the cells which take the blue may lie in any part of the organ. I therefore consider *that a spiral organ is composed of but one kind of cell and this cell is a nerve cell.*

Pigment is never present either in or around the peripheral processes. It is sometimes found in and among the bodies of the cells belonging to the spiral organs but never in any larger quantities than are found associated with other structures in the base of the epidermis.

C. Distribution of the Spiral Organs.

The number of the spiral organs is comparatively small. They are most numerous on the head; in the body itself they

are apparently confined to the first 20 metameres. The only appendages in which they are found are the gill lobes and the bases of the palps and cephalic cirri.

A reconstruction of the head and first metamere shows that in this region the spiral organs have a definite arrangement which may be summarized as follows. (Plate I, Fig. 28):

1. On the base of each palp about 43 organs are scattered over the outer or lateral surface; they are entirely lacking on the inner surface.

2. A few organs are found in the outer surface of the bases of the cephalic cirri.

3. On the dorsal surface of the prostomium are two broad irregular bands of 15 or 16 organs each, which extend, one on either side, from the base of the tentacles almost to the anterior eyes. Each of these bands is thus practically in line with the true eyes on its own side of the prostomium. No spiral organs are found on the ventral surface of the prostomium.

4. About 372 organs occur in the peristome in the raised surfaces between the grooves. In the mid-ventral region these organs extend to the posterior margin, but not to the anterior one. Passing dorsad they may be said to be distributed in a wide band which occupies about the median two-fourths of the peristome. In the mid-dorsal region, this band is narrow and is found only at the anterior border. Just caudad of the base of the cephalic cirri this band is extended to the anterior margin by a group of about 33 organs.

5. In the first metamere about 56 organs are found in a narrow median zone which passes over the dorsal and lateral surfaces between the parapodia of opposite sides. Just ventrad of each parapodium is a group of 8 or 10 organs. About 6 organs are found in the anterior half of the mid-ventral region of this metamere.

Although the above statements rest on a study of but one reconstruction, my study of sections of other worms shows that the main facts of distribution must be generally true. Variations in the whole number and exact location of each organ

in a given region always exist in the two sides of the same worm and probably in the same side of different worms.

A study was also made of the distribution of these organs by means of surface views of the epidermis. As the results thus obtained did not appear to be strictly accurate they were not included in the chart. This study, however, tended to show that the median zone of spiral organs occurred in the dorsal surface of every metamere as far back as the twentieth and that the number of organs in each zone back of the first became gradually less.

From a study of living parapodia it was found that the spiral organs are found in the tips of each gill-lobe of every parapodium; the number found in a given parapodium depends directly upon the size of the latter. As many as 15 are sometimes found in a single gill-lobe.

C. Function of Spiral Organs.

The spiral organs of *Nereis* suggest three different classes of organs—compound glands, phosphorescent organs whose structure is similar to ocular organs, and ocular organs themselves.

The component cells of these spiral organs not only differ in structure from the isolated gland-cells in the epidermis of *Nereis virens*, but also when tested by a special stain like Biondi-Ehrlich never take the stain of gland-cells. They always stain more like undoubted nerve-elements. Moreover the most careful study under the oil-immersion has failed to reveal any secretion in the central tube or any opening from a peripheral process into this tube. A refractive body always fills the tip of each process. Sometimes the secretion from one of the mucous gland cells hardens under the influence of reagents in the peripheral end of the cell. But such a hardened glandular secretion always takes an intense stain, while the refractive bodies of the spiral organ remain almost if not quite colorless. Moreover they are found to be hardened structures even in the living condition. As far as present observations go I therefore

consider it impossible that these spiral organs should be glands of any kind whatever.

The phosphorescent organs of some invertebrates have practically the same structure as simple ocular organs. The two have often been mistaken for one another and are supposed to be derived from the same primitive organ. From its structure the spiral organ might belong to either class.

I have not found in the literature any record of phosphorescence in *Nereis*. Moreover, as much as I have worked with the living spiral organs, crushing them in sea-water, exposing them to the air, and watching them for hours under the microscope, I have never seen any trace of luminosity. Experimenters on phosphorescent organs have found that an organ becomes luminous when removed and crushed in water, even, according to Vallentin and Cunningham ('88), in the day time. It therefore seems to me, that the possibility of these organs functioning as phosphorescent organs can be set aside until some direct proof of this function is brought forward.

This leaves the ocular, or at least the light perceptive, function as the only probable one.

The simplest form of ocular organs among invertebrates is that described by Hesse ('95) for the *Lumbricidæ* and closely related forms. Each organ consists of but a single cell. Each cell possesses a basal process which is probably a nerve fiber, a nucleus in its basal end, and an irregularly prolonged peripheral part which contains a refractive body. If one imagined this peripheral process drawn out into a longer process with the refractive body confined to its extreme tip and changed in shape by the pressure of surrounding parts, one would have an individual cell of the spiral organ of *Nereis virens*.

Sharp ('84) has described in *Solen* ocular organs each of which consists of a group of cells arranged around a central invagination. These cells have clear peripheral ends, pigmented middle portions, and a basal part containing a nucleus. Except for the pigment, this would correspond in general with the spiral organs.

Andrews ('91) has studied the "branchial eyes" of several

sedentary Polychætes. He found these organs in *Potamilla* to consist of an area of cells each of which has a basal process, a nucleus in the basal part of the cell, and a larger peripheral process containing a large refractive body. Each refractive body is usually firmly attached to the cuticula. There are sometimes other "inclusions" between this apical refractive body and the nucleus. Each cell is covered with pigment granules. Andrews experimented with these eyes to see if they were phosphorescent organs with but negative results. Here then, in the Polychætes, is a case of a simple eye whose cells closely resemble those of the spiral organs of *Nereis*. If the simple area in *Potamilla* became invaginated, the peripheral ends of its cells spirally arranged, and the bodies of its cells farther removed from the cuticula, we should have, except for the presence of pigment, the spiral organ of *Nereis*.

In a later paper, Andrews ('92) gives an account of the true eyes of many Polychætes. In all of the forms studied macerations showed that the retinal cells were the nerve-cells, that the base of each cell was prolonged into a nerve-fiber, and that the peripheral end bore a slender refractive rod. In the Syllidæ, it could be further seen that the lens was made up of the refractive peripheral ends of the retinal cells and that the entire organ was attached to the cuticula by a stalk which probably represented an invagination. There is also strong evidence that the lens of the eyes of all Polychætes is composed of separate elements—elements which are but the transformed peripheral ends of the retinal cells. Andrews' figure of the eye of *Lepidonotus* is strikingly like the appearance shown in a section of a poorly preserved spiral organ. Each of the retinal cells of this form bears a refractive body at its tip and these bodies, closely packed together, constitute the lens.

Hesse ('99) has lately re-investigated the eyes of Polychætes. One of the simpler ones—the "Augenflecken" of *Ranzania sagittaria* in several respects closely resembles the spiral organ of *Nereis*. It has a central solid cylinder which appears to be an invagination of the outer layer of the cuticula and which corresponds to the central tube of the spiral organs.

Closely investing this central cylinder is a clear zone which is continuous with the inner layer of the cuticula and which appears to consist of separate elements each of which belongs to the peripheral end of a visual cell. These elements correspond to the refractive bodies of the spiral organs. Between the bodies of the visual cells and this clear zone is a layer of pigment.

A comparison of the figures and descriptions of these various eyes with the spiral organs of *Nereis* leads me to the conclusion that the latter must be simple epidermal eyes; that their cells are retinal cells; the ovoid and wedge-shaped parts of the refractive bodies, rods and lens elements; and their central tube merely an invagination of the cuticula. These spiral organs need only a close packing of their lens elements and the addition of pigment to be strikingly like the eyes of several of these Polychaetes.

The absence of pigment might be taken as evidence against the ocular character of these organs, or at least as evidence that they were not at present functional. However, both Whitman ('89) and Nagel ('96) have arrived at the conclusion that pigment is not a necessary part of a functional eye.

The main difference in structure, besides the absence of pigment, between these spiral organs and the ocular organs previously described is the spiral arrangement of the peripheral processes around the central tube—an arrangement which, so far as I know, has never been described for any sense-organ. This spiral seems at first to be the result of an actual whirling around of the entire cells but the position of the cell-bodies precludes this possibility. In reality I believe this spiral is due simply to two processes which take place during development—the increase in depth of the epidermis by a growth in length of its elements and the sinking of the bodies of the cells belonging to a spiral organ below their former level. In the eyes of Arthropods, Patten ('89) found that the clear refractive tips of the visual cells were hexagonal and fitted closely together. In *Nereis* the outer ends of the epidermal cells are hexagonal and fit closely together. If a tubular invagination of such an area of simple epidermal cells should take place, the invagin-

ated cuticula would form a central tube and the peripheral ends of the epidermal cells, being attached to this cuticula, would arch inward to this tube. The surface of the latter would thus be covered with the hexagonal ends of these cells. If now an increase in the depth of the epidermis should take place by an elongation of its cells and if also the nucleated parts of the cells attached to the tube should grow downward and laterally so as to lie among the bases of the other epidermal cells, there would be two forces pulling upon the peripheral ends attached to the central tube. One force would tend to pull the cuticular tube outward away from the cells attached to it; the other force would tend to pull the peripheral ends of these cells downward away from the tube. If the strain from these two forces continued long enough it would tend to pull the peripheral ends of the cells away from the central tube. As a result of either force it would be the upper part of each process which would first loose its connection with the cuticular tube, because this part is more convex and thus being under a strain due to its own form is less able to resist the downward pull of its own cell-body or the upward pull of the cuticular tube to which it is attached. It will be remembered that, in these organs, there is a space between two adjacent turns of the spiral and that the upper half of the inner face of each component block of the spiral is usually free while the lower half is still joined to the tube. Such a process as that described above would account for both of these—the free upper half of the upper face of the block would be the half of the peripheral end which had been pulled away from the surface of the central tube; the space between two adjacent turns of the spiral would be the space thus left upon this tube, increased probably by a stretching of the thin cuticular tube itself. It will be remembered that some of these component blocks of a spiral bear ridges upon their upper surfaces while some are smooth. This is probably to be accounted for by the fact that all of the cells in any epidermal area are not true hexagons. In some cases it may also be accounted for by the possibility of some of the refractive blocks being still in a plastic condition when the separation

above described takes place and thus being still able to change their form under the influence of surface tension and also of external forces.

When the upper halves of the peripheral processes became pulled away from the tube, they would also be separated from the lower halves of the processes next above them *and this line of separation would be a line passing spirally around the central tube.* The truth of this statement can be easily demonstrated. If a surface be covered with hexagons, it will be at once seen that the line of least resistance—the line along which these hexagons would most easily separate—is an oblique one. If the surface of a thin plate of clay be marked with hexagons and the plate carefully invaginated so that the hexagons are on the outer surface of the invagination, and then a line be traced through the hexagons along the line of least resistance, *this line will pass spirally around the invagination and if the hexagons are very small, it will need but one such spiral to take in every hexagon on the invagination.* This shows that in an invaginated surface formed of small hexagonal cells, the line along which these cells will tend to break apart under strain is a spiral one winding around the invagination. This, it seems to me, accounts for the spiral arrangement, characteristic of the spiral organ.

The above explanation needs to be tested by a study of the development of these organs. It is, however, an explanation built upon general facts of development, for it will be conceded that ocular organs come from simple epidermal areas which often become invaginated, that epidermis increases in height during development, and that the bodies of epidermal cells, especially nerve-cells, often wander from their original positions. The truth of the mechanical principle involved can easily be tested. In ocular organs of other forms in which the refractive bodies are massed together, the cell bodies lie close to the refractive bodies and there has been no change of position which would cause the refractive bodies to separate from one another.

The position of these spiral organs on the dorsal and lateral surfaces of *Nereis* and in the tips of the gill-lobes is that

best suited to enable these worms to receive luminous impressions from above and from either side—as would be necessary when they leave their burrows. The greater number of these organs on the prostomium, palps, and peristome and also their presence on the ventral surface of the peristome would be a great protection when the animal simply thrusts its head from its burrow. Since *Nereis* possesses true eyes, these spiral organs probably serve, not for the perception of distinct images, but of difference in intensity of light. Nagel ('96) has shown that animals which lie buried in the sand with only a small portion of their body exposed have this portion supplied with ocular organs. Experiments show that, in such cases, this part is extremely sensitive to differences in intensity of light and is quickly withdrawn when a faint shadow is cast upon it. Nagel therefore concluded that these organs give warning of the approach of enemies by the perception of their shadows. In the absence of direct experiments on the spiral organs of *Nereis* it may be concluded that the general explanation given by Nagel is also applicable to *Nereis*—that the spiral organs are ocular organs which have for their function the perception of differences in intensity of light.

VI. Paired Cephalic Sense-Organ.

A lack of the necessary material and time has prevented me from making a thorough study of the paired sense-organs found in the head of *Nereis virens*. I can, therefore, merely give the few facts of interest which have come under my observation during the foregoing study.

The two pairs of *eyes* have been described in *N. virens* by Andrews ('92) and I can add but little to this description. In some of my methylene blue preparations, the retinal cells were well stained and it could be distinctly seen that, in many cases, the peripheral protoplasmic ends of the retinal cells themselves passed through the pigment layer and appeared within the cup. The lens was shrunken and connected with the retinal rods by strands as described by Andrews. When the apex of a retinal cell appeared within the cup, it, too, was connected

with the lens by a delicate strand. According to Hesse ('99) the cells thus so connected with the lens are not visual cells but "Sekretzellen" by which the lens has been formed. In several eyes the striations always apparent in preserved lenses passed obliquely to the longitudinal axis of the lens and their arrangement strongly suggested the ovoid part of a spiral organ—the part formed by the enlarged ends of the peripheral processes, the refractive bodies, and the central tube—as seen in poorly preserved material. The structure and the probable function of these spiral organs and their position in line with the eyes, suggests the possibility that they represent the more primitive type from which the true eyes have developed. If the true eyes were derived from the spiral organs, or both are derived from the same more primitive organ, it is probable that the lens of the true eye is, as Andrews rather doubtfully suggests, actually composed of closely massed refractive bodies, each of which is but the transformed peripheral end of a retinal cell, and that the striations so often observed in preserved eyes are caused by the shrinking apart of the lens elements under the influence of reagents—a shrinking apart directly comparable to the separation of the component blocks of the spiral band in a spiral organ.

In *Nereis diversicolor*, Retzius ('95) was unable to find the optic nerves. In my preparations of *N. virens* it has been very easy to trace all four of these nerves from their respective eyes into the lateral surface of the brain and thence to its posterior part in which, according to Racovitza's ('96) investigations in *N. dumerili*, lie the four optic ganglia. The nerve fibers from the retinal cells are extremely delicate and in the methylene blue preparations each is always broken up into a row of minute, disconnected granules.

A number of very large unipolar ganglion cells are found beside each of the anterior eyes. The greater number of these cells are ventral to their eyes, but some are anterior and some lateral to them. A few of the cells extend so far peripherally among the epidermal cells as to almost touch the cuticula. Several of them lie in the main dorsal branch of the circum-

oesophageal commissure and some are found in this branch even after it has entered the brain itself. Each of these cells is plainly a ganglion cell and from each a single process can be seen passing into the main dorsal branch of the commissure just mentioned and then turning ventrad in this branch. I have not been able to trace the further course of these axis cylinders, but Hamaker ('98) states that they pass to the commissural ganglion and he apparently considers it possible that they are the ganglion cells which give rise to the "three giant fibers which traverse the ventral cord throughout its entire length." Each cell is itself enclosed in a fibrous capsule and its process or axis cylinder is surrounded by a large sheath which is a prolongation of this capsule. Retzius ('95) noted these ganglion cells in *N. diversicolor* and considered it possible that they were concerned with the innervation of the anterior eyes. Although Hamaker ('98) considered that this could not possibly be true, yet he has designated each of these groups of ganglion cells as an "optic ganglion." Such a designation is not only incorrect in itself since given to a ganglion having no connection with the eye except, in some species, the accidental one of position, but also leads to confusion since Racovitza ('96) has already designated as optic ganglia the regions in the posterior brain which receive the central fibers of the retinal cells.

The anterior paired cephalic organs are situated in the prostomium, one on either side, just at the angle which this part of the head makes with the palps (Plate I, Fig. 28). In a surface view of the prostomium taken from a worm injected with methylene blue, this organ appears as a deeply stained, ovoid body apparently formed of very coarse fibers whose peripheral ends branch in a twig-like manner just beneath the cuticula. Sections reveal the fact that this ovoid is really formed of very large bipolar cells which are mostly spindle-shaped (Plate I, Fig. 29). The central processes from each group of cells form a small nerve which passes directly to the anterior margin of the brain slightly mesad and ventrad of the palp nerve. This nerve now joins other nerves from the anterior part of the prostomium and the common nerve thus formed can be traced along the lateral

margin of the palp ganglion (see Text-figure 3). The peripheral processes from the cells of one of these organs usually branch several times. The ultimate ends of all of these branches come together in a small area just beneath the cuticula and each, as far as I have been able to make out, terminates in a little end-bush. The cell-bodies and peripheral processes of these organs lie in a large mass of fine, interwoven connective tissue. The dorsal part of this mass is cone-shaped and the apex of this cone appears to reach the cuticula and to contain the peripheral ends of the peripheral processes of one of these anterior organs. If this be correct, the peripheral processes of the cells in this organ would have no direct connection with epidermal cells or with the exterior. My sections, however, are not such as to enable me to decide this point with certainty. These organs were first seen by Retzius ('95) in *N. diversicolor*. He says concerning them: "Es findet sich in den Palpen, und zwar an ihrem inneren Umfange, jederseits ein eigenthümlicher Nervenzweige welcher aus einer beschränkten Anzahl von Fasern besteht, die ein grob-variköses Aussehen darbieten und vorn einen kolbenförmigen Klumpen bilden. In diesem treten starke Verdickungen der Nervenfasern hervor, die jedoch nicht als kleine kernhaltige Nervenzellen imponiren, sondern eher das Aussehen von motorischen Nervenendigungen darbieten." An organ lies so close to a palp that a surface view would mislead one as to its position. My sections of *N. virens* plainly show that, in this species at least, this organ lies in the prostomium and also that the "starke Verdickungen der Nervenfasern" are nerve cells. It is evident that Retzius supposed these nerve-fibers to be motor fibers innervating the palps. The peripheral situation of the cells that give rise to these fibers, the appearance of the organs as a whole, and the fact that the peripheral processes appear wholly unconnected with muscles, would all tend to prove that this is a true sense-organ. Of its probable function I can at present only conjecture.

I have several times seen an appearance that suggests that the surface of the palp adjacent to the organ just described is modified into some sensory structure. In the base of the epi-

dermis of a small area are a number of apparently isolated, spindle-shaped, bipolar nerve-cells. The peripheral process of each cell appears to pass in a small canal through the cuticula and to project above the surface as a sensory hair. The central processes from these cells join each other to form small nerves which later unite and pass to the brain. If this observation should be verified, there would be proved to be on the base of the inner side of each palp a small sensory area thickly covered with cilia which are born by nerve cells apparently identically like the component cells of the diffuse sense-organs.

Each of the *posterior pair of cephalic organs* lies on the anterior surface of a little pocket-like invagination which is situated between the prostomium and peristome just caudo-laterad and somewhat ventrad of the posterior eyes (Plate II, Fig. 28). Retzius ('95) has briefly described these organs in *Nereis diversicolor*; Racovitza ('96) has made a somewhat extended study of them—he calls them "*Organe nucae*"—in *Nereis dumerili* and in many other Polychætes. Hamaker ('98) has given a partial description of them in *N. virens* itself. These organs in *Nereis virens* are practically the same as those described for the two species studied by Racovitza. Each is an elongated area of very long epidermal cells among whose peripheral ends lie the free terminations of the peripheral processes from a group of bipolar nerve-cells situated in the posterior brain. I have, however, found among the central ends of the epidermal cells of this area the wandering cells bearing yellow pigment which Racovitza has described in other genera but not in *Nereis*. I have not been able to see that the final ends of the central fibers from the nerve-cells end in fine branches as described by Retzius nor that the epidermal cells bear cilia as described by Racovitza and Hamaker. My failure to observe the latter is, I am sure, due to my material, not to the absence of these cilia. Racovitza states that these organs are difficult to see in the living animal because "*ils sont cachés sous un repli du bord antérieur du premier segment*," a view also held by Hamaker. It is, however, more than these folds which conceals these organs. Each is really situated on the anterior surface of a pocket-

like invagination—an invagination which is easily seen in the removed cuticula. To the cuticula in the base of each invagination is attached a large muscle which is probably one of the muscles of the proboscis, and it is, I believe, the pull of these muscles which has caused these invaginations: the two posterior sensory organs have come to lie in these pockets through the accident of their position. It appears to be generally true in *Nereis* that muscles are often attached to the cuticula and that such lines of attachments become the bases of grooves. These posterior cephalic organs have been supposed by different writers to serve every special sense except that of sight. Răcovitz (1906) concludes that they are olfactory organs. Their structure, position, and innervation correspond to the so-called olfactory organs of other worms in which undoubted otocysts are also present (see Gamble and Ashworth's account of *Arenicola marina*); but the presence in *Nereis virens* of one and possibly two other pairs of cephalic organs of unknown function renders necessary an extended study of the latter before the function of any of them can be absolutely decided for this worm. In any case the presence of a sensory area in an invagination which is apparently due to muscular action gives a very suggestive theoretical explanation of the primary cause of such invaginations as are found in some otocysts—invaginations which merely serve to increase the sensory epithelium in higher animals in which the proboscis has disappeared.

VII. *Epidermal Anchoring Cells.*

I have given this name to certain epidermal cells which seem to be intimately connected by one end with the cuticula and by the opposite end with muscle fibers passing to the epidermis. Each of these cells, when stained by methylene blue, is seen to have a very slender somewhat cylindrical or prismatic body, one, two, or three diverging basal processes, and a large number of peripheral processes. (Plate II, Fig. 49). The body of an anchoring cell extends from the cuticula centrally about to the middle height of the epidermis and contains a more deeply stained oval nucleus at or beneath the middle of

its height. Above its nucleus, each cell-body is of almost uniform width; below, it tapers to its central end. The part of the cell which touches the cuticula is always deeply stained and enlarged. This enlargement has the appearance of a varicosity and from it a number of fine strands run into the cuticula just above, passing almost or quite through the inner layer of the latter. At first sight these strands appear like sensory hairs but a comparison of their appearance with that usually presented by a sensory hair reveals several important points of difference. Each sensory hair lies in a special canal of its own whose outline, in some cases at least, can be clearly distinguished. Some of the sensory hairs are always found passing through to the exterior in methylene blue preparations. Some are irregularly varicose and some are always stained continuously for their whole length; when one is broken up into small separate parts, these parts are always rounded. I have never found a peripheral process from one of these anchoring cells stained continuously or presenting any varicosities—each process is evenly broken up into minute cylinders placed end to end; I have never found one of these processes passing through the cuticula to the exterior—they all lie in the inner cuticular layer; neither have I found any trace of a special canal around any of these process—each seems to be simply inclosed in and almost a part of the cuticula. The appearance presented by a group of these processes suggests that delicate strands have grown out into the cuticula from the apex of each anchoring cell and have become intimately connected with the latter and that, under the influence of reagents, a decided contraction had taken place. Then, because the peripheral processes were too intimately connected with the inner layer of the cuticula to become wholly withdrawn beneath the latter, some of the protoplasm in the apex of the cell, and perhaps a little from the very base of the peripheral processes, became gathered into the varicosity usually found just beneath the cuticula and the processes themselves became broken up into tiny cylinders.

If the outer layer of the cuticula is shed, these protoplasmic strands must either constantly grow from the apex of their cells

at the same rate as the cuticular layer grows by addition to its inner surface, or else the strands must shift their attachment. The former appears the more probable at present but it can only be decided by further study.

The basal processes from these anchoring cells are never beaded or varicose as are the central processes from the nerve-cells. Over the surface of each one can always perceive either a single row or two parallel rows of small blue cylinders like those of the peripheral processes only slightly larger. This appearance I have never seen in a nerve-fiber of *Nereis virens* but have often found on the surface of a muscle-fiber. The fact that these broken cylinders, instead of the varicosities usual in nerve tissue, are found in the central processes which are free from other structures except at their ends, shows that their form can not be due to the processes being firmly embedded in a surrounding tissue, as one might suppose from a study simply of the peripheral processes, but must be due to some intrinsic difference in the tissues themselves. These basal processes can be traced directly past the nerves in the base of the epidermis *to the peripheral end of one of the muscles which pass in large numbers to the epidermis.* Sometimes these processes appear to enter the muscle itself and sometimes to pass onto its outer surface. It would, therefore, appear that *these anchoring cells serve for the attachment of muscles to the cuticula.* The peripheral strands embedded in the cuticula anchor the cells at their peripheral ends; the basal processes are either interwoven with the connective tissue at the peripheral end of the muscle or else actually form this tissue itself, thus forming a sort of muscle tendon.

It will be remembered that a number of rather large pores were found in the cuticula around the perforated membranes belonging to the diffuse sense-organs in the tentacles and the tips of the palps. (See Plate I, Fig. 8). In the palps many small muscles pass toward the cuticula among the bodies of the epidermal cells. It seems to me probable that these muscles are attached to the cuticula by just such anchoring cells as are described above and that this attachment is strong

enough to tear an opening entirely through the cuticula when the latter is removed. Since the cuticula in the palps is much thinner than that over the body it may be that the peripheral processes of the anchoring cells in the former region extend entirely through the inner cuticular layer, into the outer layer, or it may be that there is a more intimate connection between the two layers of cuticula themselves than between those of the the body. Either supposition would account for the fact that these openings are so often found in these two appendages and so rarely in the body. As only a very few anchoring cells were stained in the palps, I was not able to decide this question by actual study. In the tentacles there are no muscles, but a number of very coarse connective tissue strands pass from the base of the tentacles toward the cuticula and these strands may be basal processes of anchoring cells, processes connected with muscles at the base of the tentacles. When the cuticula is removed from the ventral surface of *Nereis*, there is sometimes found in it large circular openings in those places to which the ventral oblique muscles pass; these openings, it seems to me, are also due to the firm attachment of groups of anchoring cells.

I have been able to examine only the head and first metamere for these anchoring cells. In these regions, they are present in the epidermis wherever muscle fibers pass to or into the latter. They are especially numerous in the epidermis of the grooves which pass across the prostomium and to which large numbers of muscle-fibers are attached. I have found them at the bases of the cephalic appendages, at the insertion of the muscles moving these appendages, and at the point of insertion of the ventral oblique muscles of the first metamere.

I have found no description of cells exactly like these anchoring cells of *Nereis* but I have found two references to epidermal cells which may be, I think, such cells. Andrews ('92) after describing the apparent connection of the retinal cells in the eye of *Eunice* with the lens itself states that: "Some views of the common epidermis of the head lead one to infer that here also the attenuated cells amongst the larger epidermal cells have a close connection with the cuticula like

that of the above cells with the lens." Zernecke ('95) has figured and described in the subcuticular region of Ligula cells from whose narrowed peripheral ends a number of fine processes pass into the cuticula without any definite canals and sometimes, though not always, end under an insinking from the exterior; from the basal end of each cell one or two processes are given off which never appear to be connected with nerves. Zernecke calls these cells "Korbchen-zellen" and says they "stehen vielleicht im Dienste der Nahrungsaufahme." It seems to me not impossible that both the "attenuated cells" of Eunice and the "Korbchenzellen" of Ligula may be anchoring cells for the attachment of muscles to the cuticula. If this proves true, the insinking sometimes seen in the cuticula of Ligula over one of these cells, will probably be found to be due to a contraction of these cells and their muscles—a contraction due to the influence of reagents and strong enough to tear the peripheral processes of the cells and the cuticula to which they are attached away from the surrounding cuticula.

SUMMARY.

I. The Diffuse Sense-Organs.

1. The epidermis of *Nereis virens* contains a peripheral sensory system composed of bipolar nerve-cells, which, except for some doubtful cases in the parapodial cirri, are always grouped into definite sense-organs.
2. The bodies of the cells in these sense-organs, in all regions of the body, are always situated in the epidermis itself.
3. From the peripheral end of each sense-organ a bundle of nerve-fibers—the peripheral processes of the nerve-cells—passes to the cuticula and into a differentiated area in the latter—an area composed of a deep inner and a shallow outer cavity separated by a perforated membrane of cuticula. In the inner cuticular cavity some of the peripheral processes branch. Each finally terminates in a sensory hair. All of the sense-hairs from a single organ pass to the exterior by means of the canals in the perforated membrane belonging to the organ in question and are, therefore, in direct communication with the external world.

4. From the central end of each organ, a second bundle of nerve-fibers—the central processes of the nerve-cells—passes into the central nervous system or into peripheral ganglia connected with the latter and seem to form pericellular nerve-baskets around the ganglion cells there present.

5. The diffuse sense-organs are most numerous in those regions of the body that are most exposed to contact.

6. It is probable that these organs serve for the perception of chemical and mechanical stimuli. Similar organs which exist in the epithelium lining the buccal cavity probably serve as gustatory organs.

II. The Spiral Organs.

1. The epidermis of the gill-lobes, of the enlarged bases of the palps and cephalic cirri, and of about the first twenty metameres of *Nereis virens* contains complicated organs which probably form a second system of sense organs.

2. Each of these spiral organs consist of about 100 bi- or multipolar cells—apparently nerve-cells—whose peripheral processes are arranged spirally around a central tube—a tube apparently formed of invaginated cuticula.

3. The bodies of the cells composing the spiral organs lie in the base of the epidermis or in special pouches which project centrally from this base.

4. The peripheral processes are club-shaped and the tip of each contains a refractive body. The terminal halves of these refractive bodies are so arranged as to form a spiral band around the central tube.

5. The central processes have been traced only a short distance centrally; it can be seen that they pass toward and almost into the epidermal nerves.

6. The spiral organs are most numerous on those portions of the body which are likely to be most directly exposed to the light.

7. They resemble the epidermal eyes of Invertebrates and some of the simpler true eyes of the Polychætes; their function is probably the perception of difference in intensity of light.

III. *The Paired Cephalic Organs.*

1. The prostomium contains four pairs of special sense-organs, two pairs of eyes in its dorsal surface, one pair of problematical organs in its anterior margin, and a second pair in its posterior margin. There also appears to be present near the base of the inner side of each palp a ciliated area which may prove to be a second pair of anterior cephalic organs.

2. The evidence at hand goes to prove that the true eyes are derived either from the spiral organs themselves or some more primitive type common to both. It also supports Andrews' suggestion that the lens in the true eyes is composed of the transformed tips of the retinal cells—the "Sekretzellen" of Hesse.

3. The anterior pair of cephalic organs are each composed of a group of large bipolar nerve-cells whose peripheral processes branch and finally terminate in end-brushes just beneath the cuticula, apparently without any connection with epidermal cells, and whose central processes pass into the brain.

4. The posterior pair are also each formed of a group of bipolar cells, but these cells have their bodies situated in the brain itself and their peripheral processes terminate among special epidermal cells which lie on the anterior face of two invaginations. These invaginations appear to be due to the pull of large muscles—not to the necessities of the sense-organs contained in them.

IV. *The Epidermal Anchoring Cells.*

1. There are also found among the common epidermal cells of *Nereis virens* modified epidermal cells which I have called anchoring cells.

2. The body of one of these cells does not appear to differ from the bodies of the supporting cells of the epidermis.

3. From the peripheral end of each anchoring cell a large number of fine processes pass into and are firmly embedded in the inner layer of the cuticula just above the cell.

4. From the basal end of each cell a small number of slender processes pass to or into the latter.

5. These anchoring cells apparently serve for the attachment of muscles to the cuticula.

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DESCRIPTION OF PLATES.

Figs. 2-4, 12, 13A, 13B, 18-20, 22-27, 33, 35, 36, 38, 42, 43, 47 and 48 are free-hand drawings made from material studied under the 2 mm. oil immersion objective and compensating oculars 8-12. Except where noted, all the other figures were made from camera outlines and filled in with the 2 mm. oil immersion obj. and comp. os. 8-12.

REFERENCE LETTERS.

- | | |
|---|---|
| <i>a</i> —area of attachment of anchoring cells | <i>c. s.</i> —sensory cell. |
| <i>ax. cy</i> —axis cylinder. | <i>cap. g.</i> —capsule of ganglion cell. |
| <i>b. r.</i> —refractive body. | <i>can. cu.</i> —cuticular canal of spiral organ. |
| <i>bl. v.</i> —blood-vessel. | <i>cav. cu¹.</i> —outer cuticular cavity. |
| <i>c. anch.</i> —anchoring cell. | <i>cav. cu².</i> —inner cuticular cavity. |
| <i>c. ep.</i> —epidermal supporting cell. | <i>cav. ep.</i> —epidermal cavity in tactile appendage. |
| <i>c. g.</i> —ganglion cell. | <i>cir.</i> —cirrus. |
| <i>c. gl.</i> —gland cell. | |

<i>cu.</i> —cuticula.	<i>o. ceph. p.</i> —posterior cephalic organ.
<i>cu</i> ¹ .—outer layer of cuticula.	<i>or. s.</i> —diffuse sense-organs.
<i>cu</i> ² .—inner layer of cuticula.	<i>or. sp.</i> —special organ.
<i>cu. a.</i> —modified cuticular area.	<i>pal.</i> —palp.
<i>e.</i> —eye.	<i>par.</i> —parapodium.
<i>f. nv.</i> —nerve-fiber.	<i>pers.</i> —peristome.
<i>f. s.</i> —sensory fiber.	<i>pig.</i> —pigment granules.
<i>gr. inter.</i> —intersegmental groove.	<i>pr. bas.</i> —basal process.
<i>h. s.</i> —sensory hair.	<i>pr. cen.</i> —central process.
<i>m. bas.</i> —basement membrane.	<i>pr. per.</i> —peripheral process.
<i>m. cu.</i> —perforated cuticular membrane.	<i>pros.</i> —prostomium.
<i>met.</i> —metamere.	<i>p.s.</i> —sensory pore.
<i>n.</i> —nucleus.	<i>t. cen.</i> —central tube.
<i>nv.</i> —nerve.	<i>ten.</i> —tentacle.
<i>o. ceph. a.</i> —anterior cephalic organ.	

DESCRIPTION OF PLATE I.

The drawings were made in ink and were reduced slightly more than one-half linear in the plate.

Fig. 1. The diffuse sense-organs in a cephalic cirrus as shown in a longitudinal section. Only the organs on one side of the axial nerve are shown. The base of the cirrus is toward the left. From a methylene blue section restained by alum cochineal. (The outlines were made with the Zeiss projection apparatus, obj. 35 mm., no ocular).

Fig. 2. Two diffuse sense-organs whose cell-bodies lie in one group. From an optical section of a living, unstained cephalic cirrus.

Fig. 3. Epidermal cavity and normal sense-hairs of a diffuse sense-organ in a cephalic cirrus. From an optical section of living, unstained material.

Fig. 4. Epidermal cavity and abnormal sense-hairs and peripheral processes of a diffuse sense-organ in a cephalic cirrus. An optical section from dying material injected with methylene blue.

Fig. 5A. A longitudinal section of the modified cuticular area of a diffuse sense-organ in a cephalic cirrus. From a methylene blue section restained by alum cochineal.

Fig. 5B. A longitudinal section of the modified cuticular area and peripheral processes from a diffuse sense-organ in a ventral parapodial cirrus. From a methylene blue section restained by alum cochineal.

Fig. 6. A surface view of the modified cuticular area belonging to a diffuse sense-organ in the cephalic cirri. From a surface view of the removed cuticula.

Fig. 7. A longitudinal section through the base of a dorsal parapodial cirrus showing *apparently* isolated sense-cells. From a methylene blue section restained by alum cochineal. A sense-cell which was unstained by the blue is shown at the right.

Fig. 8. A surface view of the modified cuticular area of a diffuse sense organ in retractile tips of the palps. From a surface view of the removed cuticula.

Fig. 9. A longitudinal section of the modified cuticular area of a diffuse sense-organ in the peristome. The portions of the peripheral processes in

the inner cuticular cavity and the sense-hairs appear to be nearly normal. From material killed in Müller's fluid and stained with Kleinenberg's hæmatoxylin.

Fig. 10. Omitted from the plate.

Fig. 11. A surface view of the modified cuticular area of a diffuse sense-organ in the body epidermis. From a surface view of the removed cuticula.

Fig. 12. Normal shape of the bodies of the sense-cells of the diffuse sense-organs in the cephalic cirri. From living unstained material.

Figs. 13 A and B. Two optical longitudinal sections of the epidermal cavities of the diffuse sense-organs in the cephalic cirri. From living, unstained material. In *Fig. 13 B* the position of the peripheral processes of an epidermal cavity is shown.

Fig. 14. A longitudinal section of a diffuse sense-organ in the tentacles. From methylene blue material restained by alum cochineal.

Fig. 15. A longitudinal section of a diffuse sense-organ in the palps. From methylene blue material restained by alum cochineal.

Fig. 16. A longitudinal section through the modified cuticular area of a diffuse sense-organ in the cephalic cirri. From methylene blue material restained by alum cochineal.

Fig. 17. A longitudinal section of a diffuse sense-organ in the base of the dorsal border of a dorsal parapodial cirrus. From material killed in alcohol and stained with Kleinenberg's hæmatoxylin.

Fig. 18. The outline of a longitudinal optical section of a dorsal parapodial cirrus showing the arrangement of the sense-hairs in definite groups along the dorsal and ventral borders and the apparently isolated ones at the tip of the cirrus. From living, unstained material.

Fig. 19. The surface view of one-half the surface of the distal part of a cephalic cirrus. The location of the modified cuticular areas of the diffuse sense-organs is marked by the circles over the surface and by the groups of sense-hairs around the margin. The tip of the cirrus was so transparent that the location of the sense-organs in it could not be seen. From living, stained material.

Fig. 20. A group of sense-hairs which have become swollen into balls resting on the cuticula. From a diffuse sense-organ in unstained dying material.

Fig. 21. A surface view of one side of a dorsal parapodial cirrus. The distribution of the modified cuticular areas of the diffuse sense-organs in the surface is shown by the circles. The sense-hairs around the margin did not show (see *Fig. 18*). A camera drawing from living stained material.

Fig. 22. A few of the cells of a spiral organ in a gill-lobe. From an optical view of living material that had been injected with methylene blue. In this organ only the cells shown in the figure took the blue.

Fig. 23. The sense-hairs of the diffuse sense-organs along the dorsal border of a dorsal parapodial cirrus. The hairs near the base appear to be isolated, those nearer the tip appear to be arranged in groups. The base of the cirrus is toward the left. From living unstained material.

Fig. 24. Sense-hairs in diffuse sense-organs from a parapodial cirrus. Each hair has its tip swollen into a little ball. From dying unstained material.

Fig. 25. A sense-hair which has become thickened at its base. From a diffuse sense-organ in a dying parapodial cirrus.

Fig. 26. Four views of a single sense-hair of a diffuse sense-organ showing successive stages in the withdrawal of a hair which has its apex already swollen into a ball. From a dying parapodial cirrus.

Fig. 27. The normal sense-hairs of three diffuse sense-organs situated in the dorsal border of a dorsal parapodial cirrus. From living, unstained material.

Fig. 28. A diagram showing the distribution of the spiral organs as far back as the first metamere. A wax model was constructed from sections and the position of each spiral organ marked on the surface. Tissue paper was then carefully fitted over the surface of the left half of the model and the position of each organ, as seen through the tissue paper, was marked in pencil on the latter. The tissue paper was then straightened and the chart thus obtained transferred to drawing paper. The right hand margin of the figure represents the mid-dorsal line and the left one the mid-ventral line. The position of the spiral organs is shown by the black dots. The broken lines mark the position of grooves in the surface.

Fig. 29. The cell-bodies and a few of the peripheral processes of one of the anterior cephalic organs as seen in a longitudinal section of the prostomium. From methylene blue material restained by alum cochineal.

DESCRIPTION OF PLATE II.

Figs. 30-32. Longitudinal sections of diffuse sense-organs in the peristome. The sensory hairs were mostly withdrawn. *Fig. 30* shows the connection of a central process with an epidermal nerve and *Fig. 32* shows an organ in which but one of the nerve cells has taken the blue. From methylene blue material restained with alum cochineal.

Fig. 33. Optical view of a diffuse sense-organ in a cephalic cirrus. The under side of the perforated membrane is shown. From living, methylene blue material.

Fig. 34. A longitudinal section of the modified cuticular cavity of a diffuse sense-organ in the peristome. One sense-hair retains its normal position. The rest have been withdrawn into the inner cuticular cavity. From methylene blue material restained by alum cochineal.

Fig. 35. A single nerve cell belonging to a diffuse sense-organ in the cephalic cirri. The peripheral process of this cell has four branches. Varicosities have formed at the tips of the sensory hairs and one large one in the peripheral process itself. From dying, methylene blue material.

Fig. 36. An optical longitudinal section through the tip of a cephalic cirrus. The sense-hairs belonging to two diffuse sense-organs are shown and one peripheral process which took the blue and which has a large varicosity. From dying, methylene blue material.

Fig. 37. An oblique section of a modified cuticular area of a diffuse sense-organ. The outer cuticular cavity does not appear in this section. One peripheral process branches in the inner cuticular cavity. From methylene blue material restained by alum cochineal.

Fig. 38. Optical view of the peripheral processes of the diffuse sense-organs whose cells lie in a single group. The perforated membranes are shown from underneath. From a living cephalic cirrus stained by methylene blue.

Figs. 39 and 40. Apparent pericellular nerve-baskets around ganglion cells in a cirrus ganglion. Fig. 39 shows the position of this basket in relation to both the ganglion cell and its capsule. The protoplasm of the cell has shrunk. Fig. 40 shows the centripetal nerve-fiber around the axis-cylinder of the ganglion cell. From sections of methylene blue material restained by alum cochineal.

Fig. 41. A longitudinal section of a spiral organ in the peristome. From material killed in Müller's fluid and stained with Kleinenberg's hæmatoxylin.

Figs. 42 and 43. Optical sections of parts of two spiral organs in the gill lobes. In Fig. 43 the whole of the central tube and a surface view of its external opening is shown. Fig. 42 shows the base of an organ. From living, unstained material.

Figs. 44 and 45. Two abnormal appearances sometimes seen in longitudinal sections of the outer ends of spiral organs, appearance apparently due to the central tube contracting away from the surrounding cuticula. From material killed in Müller's fluid and stained with Kleinenberg's hæmatoxylin.

Fig. 46. A lateral view of a tip of one of the peripheral processes belonging to a spiral organ. In this tip only the apical block of the refractive body could be seen (see Text-figure 4). From material killed with alcohol and stained with Kleinenberg's hæmatoxylin.

Fig. 47. An optical section of the summit of a spiral organ showing the apical turn of the spirally arranged peripheral processes. The cuticula is shown in surface view. From living, unstained gill lobes.

Fig. 48. Several peripheral processes containing abnormal or accessory refractive bodies. From spiral organs in living, unstained gill lobes.

Fig. 49. Two of the epidermal anchoring cells as seen in a longitudinal view of the peristome. From methylene blue material restained with alum cochineal.

DESCRIPTION OF PLATE III.

This chart was made from the removed cuticula by means of the Zeiss projection apparatus fitted with obj. 35 mm. and no eye piece. It was drawn to a scale of 1 dm. for 2 mm. and has been much reduced in the plate.

Fig. 50. A chart showing the distribution of the diffuse sense-organs. This chart is from one half the cuticula extending from the mid-dorsal line to the mid-ventral line. The metameres are separated by heavy black lines which represent the intersegmental grooves; other grooves are shown by broken lines. The small black dots represent the cuticular areas over the sense-organs.

Fig. 51. The arrangement of the modified cuticular areas belonging to the diffuse sense-organs as shown in a bit of the cuticula from near the base of a cirrus (compare with Fig. 19).

