STUDIES ON THE ELEMENTS OF THE CENTRAL NERVOUS SYSTEM OF THE HETERONEMERTINI.

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I. INTRODUCTION.

THE present paper gives the results of investigations upon the finer structure of the elements of the central nervous system of *Cerebratulus lacteus* (Verrill) and *Lineus gesscrensis* (O. F. Müll). It is more especially the structure of the ganglion cells and of the nerve tubules which has received attention; but

the distribution of the neuroglia, and of the ganglion cells II and IV, as well as the one or two posterior commissures of the ventral brain lobes, hitherto undescribed, have also been studied to a certain extent.

To the central nervous system of the nemerteans must be reckoned: (1) the dorsal and ventral brain lobes and their commissures; (2) the lateral nerve chords which, in both species examined, here unite posteriorly just beneath the end of the posterior intestine; (3) the paired oesophageal nerves; (4) the longitudinal nerves of the proboscis (two in number in each of our species); (5) the dorsal, unpaired, larger, median nerve of the body wall; and probably also (6) the lesser, unpaired, median nerve. Thus in the nemerteans the central nervous system, *i.e.*, that portion of the whole nervous system with which ganglion cells are in contact, has an extent and diversification which closely approach that of the Mollusca. Previous authors have limited the term "central nervous system" to the brain lobes and lateral chords, disregarding the fact that the other parts, mentioned above, are also provided with ganglion cells. My own investigations have been limited to the brain lobes, lateral nerve chords, and oesophageal nerves.

Before the appearance of M'Intosh's monograph ('73), no studies had been made upon the elements of the nervous system of the nemerteans. Since that time a considerable number of investigations have been published, only the more important of which will be specially mentioned here. Reference may be made to the papers of M'Intosh ('75, '76), Hubrecht ('74, '75, '79, '80, '87a, '87b), Mosely ('76), v. Kennel ('77), v. Graff ('79), Gulliver ('79), Dewoletzky ('80, '88), Salensky ('84, '86), Vogt and Yung ('85), Bateson ('86), Bürger ('88, '90a, '90b, '91a, '91b, '94a, '95), Haller ('89), Joubin ('90, '94), Dendy ('92), and Coe ('95a, '95b).

It is, however, v. Kennel, and more especially Hubrecht and Bürger, who have added most to our knowledge of the nervous system of the nemerteans. Hubrecht had especially studied the differentiation of the nervous system in its various layers, and had described the course of the larger nerves, etc.; he studied to less extent the cytological structure. Bürger considered not only the anatomy, but also the finer structure of the elements

of the nervous system. His more comprehensive papers, those to which reference will be made in the following pages, are '90b, '91b, '95; the latter paper really including the results of all his previous investigations, and furnishing also a number of new facts. Bürger first showed that all the ganglion cells of the nemerteans are unipolar and membraneless, and he divided the ganglion cells into four natural categories, which I follow him in adopting; he is also the discoverer of the colossal neurochord cells, and has been the first to recognize and distinguish the connective-tissue elements of the nervous system. This investigator has further been the first to apply the *intra vitam* methylene blue stain to this group, and by means of it has furnished most valuable contributions to the knowledge of the nervous system, especially with regard to the ganglion and nerve cells of the proboscis, and the course of the axis cylinders in the lateral chords and peripheral nerves. Though the results of my studies partly corroborate Bürger's conclusions, still in certain points I have reached views not in accord with his, especially in regard to the structure of the nerve tubules and of the dotted substance of the fibrous core, and of the genetic and structural relations of the neuroglia to the nervous elements.

My material was collected at Newport, where Dr. Alexander Agassiz had most kindly offered me a table in his private laboratory, and at Wood's Holl, where, through the kindness of Colonel MacDonald, I occupied a room in the Fish Commission Station. I would express my obligations to both these gentlemen. Colonel MacDonald's recent death was a sad shock to all who had known him personally or had experienced his generosity. *Lineus gesserensis* I collected in large numbers, it being abundant at both these localities; of *Cerebratulus lacteus*, however, I secured only a single specimen. In addition to these species I received a large *Lineus* from Norway, which I was unable to determine, and shall refer to simply as "*L. sp.*"¹

¹ This undetermined species of *Lineus* had, after preservation in alcoholic sublimate, a diameter of about 3 mm., and was of a cylindrical form; the color, above a dark olive, lighter ventrally, with a fine, median, dorsal stripe of a yellowish color, and a similar stripe on each side of the body. I am indebted to my friend Dr. Fritz Schaudinn of the Berlin zoölogical laboratory for collecting it for me at Bergen.

The best fixative for the ganglion cells I have found to be corrosive sublimate in alcoholic solution (50% alcohol); addition of acetic acid to this solution is to be avoided. The best differentiating double stain is Ehrlich's or Delafield's haematoxylin, followed by eosin. The Ehrlich-Biondi stain does not furnish as sharp differentiations as the preceding. For following the course of the nerve tubules, preparations fixed for $\frac{1}{2}$ –1 hour in Hermann's fluid (platinum chl. + osmic acid + acetic acid) may be especially recommended; Flemming's fluid (chromic + osmic + acetic acid, in the stronger solution) is also valuable. Osmic acid alone, as well as Kleinberg's fluid (picrosulphuric acid), Lang's fluid, Perenyi's fluid (chromo-nitric acid), and all single solutions of chromic acid are not to be recommended.¹ The gold-chloride method of Apáthy ('91) might also be applied with good effect to the nemerteans, though I have not had opportunity to use it.

II. GANGLION CELLS.

I follow Bürger's ('90b) precept in dividing these cells into: (1) the smallest sensory cells; (2) the medium-sized cells; (3) the large cells; and (4) the colossal neurochord cells (which are absent in *Lineus*). The cells of these different categories may be referred to respectively by the use of the roman numerals I, II, III, IV. Bürger's division of the ganglion cells I have found to be a very natural one, being based upon morphological differences as well as upon differences in regard to their relative positions in the central organs.

I can corroborate Bürger's ('90b, '91b) conclusions that all these cells are devoid of cell membranes, and that all are unipolar, — adopting his definition that a cell is unipolar when it has but one pole from which the cell processes depart, whether one or more processes are given off from the same pole. I have found only one process of the cell, namely, the true nerve tubule; and have never seen so-called "protoplasmic fibres" such as he has figured ('90b, Fig. 61 *g, h*). Haller's ('89) con-

¹ For more detailed results upon the action of different fixatives and stains, cf. Montgomery, '96b.

clusions that the nemertean ganglion cell is multipolar must either have been based upon the study of poor preparations or have been the result of preconceived views.

A. Cell I.

In *Lineus gesserensis* these smallest ganglion cells are usually densely massed together and of a shortened pyriform shape (Fig. 1). The nucleus is very large in proportion to the cell body, in fact nearly filling it; it is relatively very much larger, but varies less in size, than those of the other ganglion cells.¹ The nuclei vary from a spherical to an elongate-oval shape. Their chromatin is not limited to the periphery, but distributed in the form of nearly equally sized grains (of the number of ten or more in each nucleus), placed throughout the faintly staining nuclear sap; I have been unable to constate an achromatic network. In the nucleus one or two nucleoli may sometimes be found; these stain deeply with eosin, are of a spherical shape, and are larger than the chromatin masses. Sometimes an elongated "tail" of the nucleus penetrates for a short distance into the nerve tubule; but in none of the types of ganglion cells have I seen such branches of the nucleus as H. Schultze ('79) has described; it is to be noted that Leydig also never saw such structures. The cytoplasm usually stains very faintly, which is due to the excess of the hyaloplasmic vacuoles, these being enveloped by only a fine spongioplasmic meshwork.²

¹ Bürger has shown conclusively that these are sensory and not motor cells; and it would be interesting, in view of the relatively great size of their nuclei, to determine whether in other animal groups also the nucleus of the sensory is relatively greater than that of the motor cell; in other words, whether the size of the nucleus stands in relation to the function (sense, motion) of the ganglion cell.

² I shall employ in my descriptions of the cytoplasm the terms "hyaloplasm" and "spongioplasm" to denote respectively the homogeneous, unstaining, and the more or less granular staining constituents. Since Flemming ('82a) has by no means proved the fibrillar structure of protoplasm, I see no reason to adopt, as Rohde ('87) and Bürger ('90b) have done, his terms "paramitom" and "mitom." In a more recent paper ('92) Rohde has adopted Leydig's terms. The terms of Leydig, "hyaloplasm" and "spongioplasm," are more widely applicable, and thus preferable, since they express respectively the more fluid, homogeneous, and the more dense, more compound portions of the cytoplasm. I have never found a

Bürger ('90b, p. 107) describes a modification of these cells, "welche sich durch etwas grössere Kerne und lebhafteres Hervortreten des Zellplasmas von jener unterscheidet," and are situated around the cephalic clefts; but I have been unable to find any structural distinction between these two. However, two modifications of cells I may be distinguished as follows:

(a) A group of cells on the medio-dorsal side of the brain lobe, situated a little behind a frontal plane passing through the first ventral commissure. Their nuclei average larger, are as a rule more elongate-oval in form, and stain less deeply than the following.

(b) The greater number of the cells I on the dorsal brain lobe, *i.e.*, all with the exception of those in group (a); they have typically (though not always) spherical, deeply staining nuclei. But there is only a slight degree of difference between these two modifications, and intergradations are found between them.

In *Cerebratulus* these cells do not differ appreciably from those of *Lineus*, and occur in the same two modifications (Fig. 17 *a, b*).

B. Cell II.

Lineus gesserensis (Fig. 2).—These cells are usually more or less elongated, pear-shaped, with the greatest diameter proximally, becoming distally gradually more slender; seldom have they a shortened, oval form. The more or less centrally placed nucleus contains a relatively smaller amount of chromatin than that of I and III, and differs from the latter further in its elongate-oval, and not spherical, shape. One nucleolus (*n*) is sometimes found in it. The cytoplasm is of a coarsely vacuolar structure; sometimes the hyaloplasm fills the whole proximal portion of the cell as far as the nucleus. But a thin, peripheral layer (*Alv.*) of spongioplasm is always present, and a similar layer envelops the nucleus; these two layers, which may repre-

fibrillar structure of the spongioplasm of the ganglion cells. Further, these terms can be applied to denote the more fluid contents of the less fluid meshwork in describing a "honeycombed" structure of protoplasm (though Bütschli, '94, has endeavored to avoid the use of any such descriptive terms as might imply a difference between the substance of the meshwork and the substance contained within it).

sent alveolar layers (in the sense of Bütschli, '94), will be considered more in detail in treating of the ganglion cells III. In their distribution the cells II are limited to the ventral brain lobe and to the lateral chords, forming the greater part of the ganglion-cell layer of the latter. In their arrangement a radial grouping of a number of cells (thus giving rise to a cell cluster) around an opening in the inner neurilemma seems to be the rule; but the radial clusters are not as distinct, nor is there a symmetrical grouping of them in the lateral chords, as in *Cerebratulus*. Further, in *Lineus* II is not as distinct from III as in *Cerebratulus*, but these two types of cells closely approximate in appearance, so that a very small III may have a marked resemblance to a large II; but the form and structure of the nucleus usually serve to distinguish them.

In *Cerebratulus* the cells II (Fig. 18) differ quite noticeably from those of *Lineus*, in addition to their greater size. Thus the cytoplasm is usually denser, *i.e.*, there is a proportionately greater amount of spongioplasm, and a coarsely vacuolar structure is seldom found. The nucleus is usually oval and varies considerably in size; it contains a number of irregular chromatin masses, and one (sometimes two) larger, spherical nucleoli (*n*). The grouping of these cells into radial clusters, which Bürger ('90b) has shown to be characteristic for them, and which is much more pronounced in this genus than in *Lineus*, is due to the fact that the nerve tubules of a considerable number (approximately fifteen or more) of neighboring cells converge together and penetrate in a bundle through a single opening of the inner neurilemma to reach the fibrous core (Fig. 18). On a section, by which only a few of the cells of a cluster are cut, the arrangement is fan-shaped (Fig. 25, *Cl. II*). This grouping is especially characteristic for II, though sometimes cells I present this arrangement to a limited extent.

These cells occur only in the ventral brain lobes and in the lateral chords, as shown by Bürger ('90b). But their symmetrical arrangement in the lateral chords in *Cerebratulus*, a point hitherto unnoticed, is worthy of mention. In each lateral nerve chord, namely, the radial cell clusters occur as in the ventral lobe, but with a certain regularity of distribution which is not

expressed there. On a transverse section of a lateral chord one finds, both on the dorsal and on the ventral side (ganglion cells are absent on the median and lateral aspects, as stated by Coe, '95a), a right and a left cluster of these cells (Fig. 25). For each radial group is one opening in the inner neurilemma, serving for the transmission of its bundle of nerve tubules; the respective openings of two neighboring clusters are separated from one another by a distance equivalent to the greatest diameter of a cluster. Accordingly, an anterior opening is separated from the next following posterior opening, and an opening on the right hand from one on the left. Thus, both on the dorsal as well as on the ventral side of a lateral chord, there is a single linear series of cell clusters on the right, as well as such a series on the left; and, consequently, also two corresponding series of openings in the inner neurilemma. It is the rule, further, that the cell clusters on the right hand alternate with those on the left, on each side of the chord, and *pari passu* their respective openings on the right with those on the left; this alternation becomes more marked towards the posterior end of the chord, where, owing to the decreasing diameter of the latter, the distances between the successive clusters become relatively greater. So it is seen in Fig. 25, that on either side of the chord the cluster on the right does not lie in the same plane as that on the left. In other words, on either the dorsal or the ventral side of each lateral chord, the clusters of ganglion cells II and their respective openings in the inner neurilemma (these serving for the passage of their respective bundles of nerve tubules into the fibrous core) are symmetrically and bilaterally arranged. But this arrangement does not represent a true bilaterality, since the cell clusters on the right are not paired with those on the left, but rather alternate with them. To adopt the terminology of Bateson ('94), the relation of the two lateral nerve chords to one another would constitute a "major symmetry" (the one being a mirror image of the other); while that of the right and left sides of each chord would represent a "minor symmetry." Fig. 26 represents a diagrammatic longitudinal section (in the horizontal plane), through either the dorsal or ventral side of one

nerve chord: *Cl. II*, the cell clusters; *P*, their respective openings in the inner neurilemma; *x-x*, the imaginary median plane of symmetry.

C. Cell III.

a. *Lineus*.—These cells (Figs. 3-16) are of an elongated pyriform shape, largest and rounded proximally, seldom nearly spherical. It may be noted that while the cell bodies vary considerably in size, their nuclei remain of nearly uniform dimensions.

The nucleus (*N*) seldom lies in the proximal portion of the cell, but usually near the center, or even in the constricted, distal portion; this would show that it, as well as the nucleus of I (*v. supra*), stands in as close a physiological connection with the substance of the nerve tubule, as with the cytoplasm of the cell body itself; this fact might well be borne in mind by those who suppose the vitality of the cell process to be more or less distinct from that of the cell. The nucleus is usually spherical, and larger than those of any other somatic tissues, except a few of those of the outer neuroglia cells (Montgomery, '97). Its chromatin is more or less regularly distributed in granular form, but occasionally produces a thick peripheral layer, from which a few chromatic fibres pass towards the nucleolus. Such reticulation of the chromatin is especially discernible on preparations fixed with a fluid containing OsO_4 ; while the action of corrosive sublimate obliterates to a great extent whatever reticulation may exist, and imparts a granular appearance to the chromatin. One nucleolus (*n*) is always present; occasionally there are two, and then of unequal size; the single nucleolus is most frequently centrally situated, and then is enveloped by a sheath of chromatin.

The cytoplasm is, as a rule, coarsely vacuolar (vesicular), especially so towards the distal pole. A thin peripheral layer of finely granular cytoplasm is always present (Figs. 3-16, *Alv.*); this layer might compensate physiologically for the absence of a cell membrane, as has been suggested by Leydig ('64). Bürger ('90b), who has also noticed this layer, described it as more coarsely granular than the rest of the cytoplasm. This

compels us to refer briefly to the methods of fixation with which this investigator's material had been preserved. Part of it was fixed with weak chromic acid solutions, which are not to be recommended. He states, further, that "Die Behandlung derjenigen [*Cerebratulus marginatus*, *Langia*] aus der Zoologischen Station in Neapel ist mir unbekannt"; the fixative used for these, I presume, had been sublimate in alcoholic solution — a method much employed at the Naples laboratory. Thus Bürger had used neither Hermann's nor Flemming's fixation fluids, both of which demonstrate the fine-grained structure of the peripheral spongioplasmic layer much more clearly than does sublimate, which generally produces a fusion of the microsomes into larger granules.¹ A similar fine-grained layer of spongioplasm may almost always be found enveloping the nucleus.

As has been already remarked, the greater part of the cytoplasm is coarsely vacuolar, in that staining, non-fibrillar, spongioplasmic meshes envelop various-sized, unstaining, structureless vacuoles of hyaloplasm, which in life is probably fluid. There does not seem to be any concentric or other regular arrangement of these vacuoles around the nucleus, though Bürger has given two figures exhibiting such a distribution ('90b, Fig. 61 d, '91b, Fig. 18 a, the latter from life); this author considers that such an arrangement of the hyaloplasmic vacuoles is the natural one, and that preparations which show no such arrangement are artifacts. Now while I have never observed any such regular arrangement, I would not maintain that it does not occur, but merely that it must be very infrequent; but, on the other hand, the irregular grouping of vacuoles of unequal size must not be regarded as artificial, but as normal, since it is found after the use of the most diverse fixing reagents. I consider

¹ This peripheral, fine-grained layer of the cell had been seen by Leydig ('64), who quite correctly showed that it does not correspond to a cell membrane. But H. Schultze ('79), who found it to be continued along the axis cylinder, considered it a true cell membrane. Nansen ('87), as I understand him, was unable to decide whether the ganglion cells possess true membranes or only such as are formed by the encircling neuroglia fibres. Rohde ('90a, '92) supposed all the spongioplasm of the ganglion cells of *Polychaeta* and *Hirudinea* to be fibrillar, and composed of neuroglia fibres which had penetrated the cell.

the various groupings of these vacuoles within the cell as corresponding to the different physiological states of the latter. Rarely does the spongioplasm preponderate quantitatively throughout the cell, though this is the rule for the ganglion cells of the commissures of the oesophageal nerves.

To recapitulate : a fine-grained layer of spongioplasm forms the peripheral boundary of the cell, and a second similar layer envelops the nucleus. The remainder of the cytoplasm is usually coarsely vacuolar, especially distally, these hyaloplasmic vacuoles being of unequal size and without appreciable arrangement into concentric layers around the nucleus. Now the fine-grained layers around the periphery of the cell and encircling the nucleus I would consider *alveolar layers*, in the sense of Bütschli ('94), their microsomes thereby representing the nodal points of an alveolar meshwork, and the unstaining, hyaloplasmic spaces between these supposed nodal points the more fluid contents of the meshes ("Waben"). Whether similar alveolar layers also bound the larger vacuoles I have been unable to determine, even after careful investigation. According to Bütschli's conclusions, these larger vacuoles would not correspond to individual meshes, since they exceed the size of a primitive mesh ("Wabe," which, according to his studies, rarely exceeds 1μ in diameter, although occasionally it may measure 8μ). On the whole, however, the cytoplasmic structure of cells II and III, in both *Lineus* and *Cerebratulus*, and of IV in the latter (I being too small for investigation), gives the impression of a honeycombed meshwork, as described by Bütschli for the cytoplasm of especially vacuolar Protozoa, such as *Actinosphaerium*.¹ Even the presence of the two alveolar layers described by me would alone render it probable that this is the structure of these ganglion cells, since Bütschli has shown pretty clearly that the presence of such alveolar layers is only to be explained on the presupposition of a honeycombed meshwork.

¹ Schaudinn, in a number of papers upon Rhizopoda published in the last three years, has confirmed Bütschli's results on the structure of the protoplasm of the Protozoa. I would express the view reservedly that the honeycombed meshwork probably represents the structure of the less differentiated protoplasms, and is the more primitive structure; but that this structure may become radically changed in more differentiated cells.

In none of the nemertean ganglion cells are neuroglia fibres present; there seems to be no penetration of these elements into the cells, and the spongioplasm of the latter is certainly not produced by them.

There remain to be described certain bodies occurring in the cytoplasm of III in *L. gesserensis* and *L. sp.*, these bodies being restricted to these cells in this genus and absent in all ganglion cells of *Cerebratulus* (Gr. in Figs. 3, 6, 8, 9, 11, 12, 14, 15). These are frequently larger than the nucleolus and of a spherical or oval, regular shape, and are not refractive. After the use of a double stain, they stain usually with eosin, sometimes with haematoxylin, but always more intensely than the surrounding cytoplasm, though seldom as deeply as the nucleolus. Structurally they are homogeneous, with a peripheral membrane, which may be scarcely discernible, or in other cases of considerable thickness; this membrane always stains more intensely than the enclosed portion, and forms a boundary against the surrounding cytoplasm. These bodies do not occur in all cells, but only in about one-sixth of the total number; when they are present, it may be but a single one, more frequently four or five, apparently never more than about fifteen. There is also no regularity in their distribution, such as a concentric or radial arrangement, and in the same cell they are usually of various sizes and of different staining power; sometimes, however, two of equal size and similar staining power lie in contact (Figs. 11, 16), so that a distribution in pairs seems to be not infrequent. They are always absent in the nerve tubule. To these cytoplasmic bodies may be applied the term *chromophilic corpuscles*, to distinguish them from the *chromophilic granules* in the ganglion cells of other animals. These corpuscles are certainly not artifacts, since they become preserved equally well with Hermann's and Flemming's fluid and with sublimate (aqueous with or without acetic acid, alcoholic solutions). Further, they cannot be considered parasitic organisms, since they are found only in these cells in *Lineus*, and not in the other ganglion cells nor in the surrounding neuroglia; they are also not pathological, since I found them in all (about a dozen) of the individuals studied. Again, they cannot be regarded as aggregates of

nutritive substances which the cell has taken up from without, since they are never found within the nucleus.¹ I conclude that the chromophilic corpuscles are metamorphosed portions of the cytoplasm produced by a dense welding together of the microsomes of the latter at different points in the cell body; this would account for their power to stain deeply, and their homogeneous appearance. Again, some stain scarcely more deeply than the surrounding cytoplasm, and their bounding membranes are scarcely appreciable, while others stain intensely, and are provided with relatively thick limiting membranes; and all intergradations between these two stages occur. These facts are sufficient to show that the chromophilic corpuscles of *Lineus* are differentiated portions of the cytoplasm of the cell, the process of differentiation consisting in a compression or fusing together of the primitive microsomes. Analogical metabolic cytoplasmic changes are found, *e.g.*, in the formation of yolk particles in the egg cell of *Stichostemma* (Montgomery, '95).

Corpuscles, somewhat similar to these, I find described by Dehler ('95) for the sympathetic ganglion cells of the frog: "Diese Schollen . . . haben eine ziemlich unregelmässige Gestalt: von einer körnchenartigen Zusammensetzung an findet man sie bis zur Gestalt von flachen Dreiecken mit breiter Basis; auch grosse Schollen, die aus kleineren lose zusammengesetzt erscheinen, sind vorhanden; sie sind nicht kugelig und haben niemals scharfe Ecken, so dass der Ausdruck "Scholle" der einzig passende zu sein scheint. . . . Manchmal finden sich in kleineren Zellen wenig oder keine chromatischen Schollen; dafür ist dann die Zelle diffus und intensiver gefärbt. Flesch nennt dieses Verhalten Chromophilie. Ich erkläre mir das so, dass in solchen Fällen die chromatische Substanz nicht wie zu Schollen geronnen, sondern diffus in die achromatische Substanz verteilt ist; wahrscheinlich ist sie in den kleineren Zellen in derselben oder fast derselben Menge vorhanden, nur gleichmässiger verteilt wie in den grossen." Dehler finds these "Schollen," which differ from the corpuscles of *Lineus* in their

¹ Cf. Korschelt's studies, "Zur Morphologie des Zellkernes," and the observations of mine upon nutritive processes in mesenchym cells ('97).

irregular form and greater size and number, distributed in concentric circles around the centrosome (not around the nucleus), the largest "Schollen" being placed peripherally.¹

Three years previous to Dehler's researches, Vas ('92) studied the chromophilic bodies, which he termed "chromatin," in sympathetic ganglion cells of man, horse, dog, and rabbit; they are, in these forms, smaller than those observed by Dehler in the frog. Vas did not notice a concentric arrangement, but found the largest bodies peripherally situated. He makes the interesting observation that the granules are absent in the cells of the human foetus, and first appear after birth.

The *chromophilic granules* of ganglion cells, such as have been described (mainly for vertebrates) by Flesch ('86a, b), H. Virchow ('88), Nissl ('94a, b, and previous papers), de Quervain ('93), van Gieson, Lenhossék ('95a), Pflücke ('95), and others have but little resemblance to the chromophilic corpuscles of *Lineus*. For the "granules" are much smaller, usually spindle-shaped, and are arranged concentrically around the nucleus. One point of similarity may be referred to, however: the chromophilic granules as well as the corpuscles occur only in the cytoplasm of the cell, never in the nucleus nor in the axis cylinder. Lenhossék ('95a), who has studied the chromophilic granules in the multipolar spinal ganglion cells of *Homo*, *Bos*, and *Lepus*, states: "Es wäre allerdings möglich, dass sie, wie de Quervain ('93) vermutet, durchgehends Komplexe von feinen Körnchen sind, aber ein solcher diskontinuierlicher Aufbau lässt sich nur an einer kleinen Anzahl von Schollen nachweisen"; and notes that although the chromophilic granules do not enter the axis cylinder, they nevertheless penetrate the dendritic processes for a short distance.

The recent paper by Pflücke ('95), based upon studies on ganglion cells of *Lumbricus* and Mollusca (fixed with sublimate), describes as follows the arrangement of the chromophilic granules: "Der Zelleib der Nervenzelle besteht aus varikösen

¹ Centrosomes were discovered for the first time in ganglion cells in the frog by Lenhossék ('95b) and Dehler ('95), independently of one another; by the former in the spinal ganglion cells, by the latter in those of the sympathetic ganglia. I have not found centrosomes in the ganglion cells of the nemerteans.

Fibrillen, die sich im Umkreis des Kernes, unter Bildung zahlreicher Queranastomosen in ein Netzwerk auflösen. Die Varikositäten sind eine besondere Eigenschaft der Plasmafibrillen, da sie denjenigen des Achsencylinders fehlen oder doch nicht durch die Färbung nachzuweisen sind. . . . Die Kernmembran besitzt knötchenartige Verdickungen von gleicher Beschaffenheit, wie diejenigen der Plasmafibrillen. Diese Knötchen bilden die Vereinigungspunkte der sowohl vom Plasma, als auch vom Kerngerüst ausgehenden Endfäserchen" (p. 538). In justice to that excellent observer Leydig must be stated that he was the first to figure such varicose, concentric fibrils ('85). What Pflücke describes as varicosities of supposed concentric cytoplasmic fibrils (which he states compose the "primitive fibrils" of the axis cylinder) correspond to the chromophilic granules of other authors. A certain similarity is to be noticed between his conclusions and those of Nansen ('87). Thus Nansen, although he had not seen the chromophilic granules, described the primitive tubes of the axis cylinder as encircling the nucleus concentrically; the concentric fibrils of Pflücke might correspond to the sheaths of such primitive tubes, or *vice versa*. Pflücke's paper reopens up a field which certainly deserves reinvestigation.

In the ganglion cells of *Unio*, H. Schultze ('79) found "grössere, doppelcontourirte, myelinähnliche Tropfen," which became browned by osmic acid; if these really contain myelin, which is doubtful, they would correspond neither to the chromophilic granules nor to the chromophilic corpuscles.

b. *Cerebratulus*. — The cells III in this genus differ slightly from those of *Lineus* and are considerably larger (Figs. 19–21, 29, III); they resemble closely those described by Bürger ('90 b) for *C. marginatus*. They are usually flask-shaped, swollen and rounded proximally, distally tapering to the axis-cylinder pole; sometimes even retort-shaped, ovoid, or nearly spherical; in the lateral chords they may be even angular in outline.

The nucleus (Fig. 22 a–e) is usually proximal or central in position, seldom distal (this being the frequent position in *Lineus*). It is usually nearly spherical or spherico-oval, sometimes kidney-shaped; but I have never seen one of a horse-

shoe shape, as found by Bürger ('90b, Fig. 61 *b, c*). Usually a coarse-grained peripheral layer of chromatin (*Chr.*) is present, each of these larger grains being apparently composed of finer microsomes; and centrally, fine-grained chromatin is distributed in the nuclear sap. In only a few nuclei were evidences of a delicate achromatic reticulation to be found. Occasionally the chromatic granules are limited entirely to the periphery, the central portion of the nucleus containing only nuclear sap; on the other hand, sometimes the whole nucleus appears to be nearly filled with chromatin. The different ways in which the chromatin may be distributed probably correspond to different physiological states of the nucleus, and cannot be considered artifacts, since the same differences are found after the use of various reagents.

Each nucleus contains one large spherical nucleolus (*n*), which is usually centrally placed, rarely peripherally, and never in close contact with the nuclear membrane; this latter position is typical for the nucleoli of cells IV. A layer of chromatin granules usually surrounds the nucleolus, and from this layer fibres radiate towards the peripheral masses of chromatin. Not infrequently two nucleoli are present, which are then usually of different size and placed at varying distances from each other; but in only one case did I find the two nucleoli stained differently (Fig. 22 *b*). I never found more than two nucleoli, and never saw evidences of nuclear division, though I had paid particular attention to these points.

Bürger states ('90b, p. 113): "Bei I habe ich immer mehrere [nucleoli] beobachtet," which shows that he had confounded chromatin masses with nucleoli. By the term *nucleolus* I understand, in accord with most cytologists, a body contained within the nucleus, usually of a spherical form, which stains intensely with eosin (after the use of the double stain, haematoxylin + eosin). It should not be confused with the irregular masses of chromatin, which stain with haematoxylin, and each of which is composed of finer microsomes. Bürger has also described for *C. marginatus* and *Langia* slightly staining, but little refractive ("von mattem Glanz") globules (Bläschen) continued within the nucleus. Thus ('90b, p. 113):

"Dasselbe liegt fast immer dicht neben dem Nucleolus oder umfasst selbst denselben. Zuweilen sah ich auch viele kleine Bläschen um den Nucleolus gelagert oder an der Membran des Kernes kranzförmig angeordnet, in einem besonders grossen lag alsdann der eigentliche Nucleolus. War der Kern, d. h. der gefärbte Bestandtheil desselben nierenförmig oder ähnlich gestaltet, so umschloss er das Bläschen." In *Langia* he found the "Bläschen" of an enormous size, nearly filling the nucleus. Rhumbler ('93) has reproduced four of Bürger's figures showing these Bläschen, in support of his theory of the formation of the "Binnenkörper." Such structures as these "Bläschen" of Bürger are positively absent in the nuclei of all ganglion cells which I have examined. Bürger's "Bläschen," such as he described them, can be only artifacts, that is, artificially centralized portions of the fluid nuclear sap, and their apparent globular form is due to an optical illusion. In other words, I would regard them, not as distinctly defined spherical bodies, but merely as portions of the nuclear sap which fills all interstices between the chromatin granules. This is shown by my Fig. 22 *b, e*. Whenever the chromatin forms a sharply bounded peripheral layer and the central portion of the nucleus is filled entirely with nuclear sap, as is not infrequent, it is only an optical illusion which could lead to the assumption that a large, unstaining globule nearly fills the nucleus. It has been necessary to refute Bürger's observations on this point, since he has described a nuclear structure, which would be nearly unique in the Metazoa, had it been accurately portrayed. Rohde ('90a) described similar globules in the nuclei of the ganglion cells of Polychaetes.

I have found only one cell containing two nuclei (Fig. 21) among the hundreds of ganglion cells examined. These nuclei differed both in size and structure, which moots the question whether this particular cell should not be considered a fusion of two cells, rather than a cell whose nucleus had divided into two, while the cell body remained intact. For in the latter case it would be probable that both nuclei should exhibit the same size and structure.

In *Cerebratulus* the cytoplasm of cells III is not, as a rule, as vesicular as in *Lineus*, but both hyalo- and spongioplasmic constituents are pretty evenly distributed. In some cases the hyaloplasm nearly fills the whole cell body, though even in such cells a peripheral, fine-grained, spongioplasmic layer envelops the cell, and a similar layer surrounds the nucleus. Occasionally, also, I found a large, flattened vacuole, resembling in shape a concavo-convex lens, situated between the nucleus and the proximal end of the cell; the structure of the cytoplasm in the rest of the cell being finely granular.

The cells of the commissures of the oesophageal nerves are a modification of the cells III of the brain, from which they differ in their inferior size and denser cytoplasm (Fig. 20). In the lateral chords, two or three cells III often surround a cell IV, and such enveloping cells are often difficult to distinguish in structure from the enclosed IV (Fig. 29).

Bürger ('90b) has already shown that the cells III occur both in the dorsal and ventral lobes of the brain and in the lateral chords. It may be noted that in *Lineus* they are comparatively more numerous on the periphery of the ventral lobe than in *Cerebratulus*; while in the latter genus they are relatively more abundant on the medial side of the dorsal lobe than in *Lineus*. Only in *L. sp.* do I find a few cells III on the lateral aspect of the lateral nerve chord; this, as well as the median side of the chords, being always devoid of ganglion cells in *Lineus gessserensis* and *Cerebratulus*.

D. Cell IV (*Cerebratulus*).

These colossal cells, termed by their discoverer, Bürger ('94b), "neurochord cells," on account of their similarity to the neurochord cells of other forms, have been found by him to be limited to the genera *Cerebratulus*, *Langia*, *Drepanophorus*, and *Prosadenoporus*. They are absent in *Lineus*, but I have found them in *Cerebratulus lacteus*. Coe ('95a) did not observe them in the latter species, which is a strange oversight, since they are the largest cells of this nemertean, with the exception of the ova; however, it is possible that this author classed them together with cells III.

a. *Distribution*. — In *Cerebratulus marginatus* and *Langia formosa*, Bürger found one pair of these cells in the ventral lobe of the brain, and a considerable number placed irregularly along the lateral nerve chords. In *Drepanophorus* and *Prosa-denoporus* he found only one pair, situated in the brain, and none along the lateral chords.

In *C. lacteus* I have made a more detailed investigation of their distribution, based upon a study of several series of transverse sections (of about 5μ thickness) through an immature individual of approximately 6 in. in length. In this way about four-fifths of the worm was sectioned. Since it was not my intention to determine the total number of neurochord cells in the body, — a number which probably varies in different individuals, — but rather to determine their proportionate number in the two lateral chords and on the dorsal and ventral sides of each chord, it would have been an unnecessary consumption of time to cut the whole animal into thin sections of 5μ thickness. Even had this been done, the total number of cells could have been given only approximately, since quite a number of cells occur which are structurally intermediate between III and IV, putting the calculator into the quandary of not knowing whether to count them in or whether to leave them out; and whichever way he should determine upon, he could not be certain of the correctness of his resulting figures.

Three pairs of neurochord cells are present in the ventral lobes of the brain (three cells in each lobe). The cells of the first pair (Fig. 24, *C. IV*) lie close beneath the dorsal blood vessel (*D.V.*), on the medial sides of the ventral brain lobes, in a frontal plane which cuts the oesophageal nerves about the point where they begin to pass out of the fibrous core of the lobes. Both cells lie in the same frontal plane. This was the only pair found by Bürger in the brain of *C. marginatus* and *Langia*. The second pair of cells do not lie in one and the same plane: the first cell lies on the right hand, one section behind the first pair of cells, the second cell lies on the left hand, five sections behind the first pair of cells; thus the cells of the second pair are three sections apart. The third pair of cells are placed two sections behind the most posterior cell of

the second pair (six sections behind the first pair); both cells of the third pair, just as those of the first, lie in the same frontal plane. These three pairs lie in nearly the same horizontal plane, and the distance separating the cells of the first pair is about equal to that between the cells of the third pair; but the space between the cells of the second pair is greater, since they are three sections apart.

Behind the brain no neurochord cells are found in the lateral nerve chords until the anterior region of the posterior intestine is reached, being absent in the chords in the oesophageal region of the body, as noticed by Bürger ('90b); in *C. lacteus* this is a distance of several centimeters.

Counting from before backwards, I find the first neurochord cell of the chords just behind the oesophageal region on the ventral side of the left chord; the second on the dorsal side of the right chord; the third on the ventral side of the left chord; the fourth on the dorsal side of the same chord; the fifth on the ventral side of the same chord; the sixth and seventh on the dorsal side of the right chord; the eighth on the dorsal side of the left chord; the ninth and tenth on the same section, on the dorsal sides of the right and left chords respectively. With the exception of the last two, the cells enumerated are separated (in the longitudinal axis) by considerable, though varying, distances. The sequence of the first ten cells of the lateral chords has been given as an example of their irregularity of arrangement. It is unnecessary to reproduce here the distributive sequence of the approximately 159 cells whose position I have determined, and it will be sufficient simply to state the general results of this study of their arrangement. The following table gives, for the four-fifths of the worm sectioned, the numbers of these cells in both chords, and of each side of each chord, all cells which are not typical neurochord cells being excluded:

RIGHT CHORD.		LEFT CHORD.	
Dorsal	Ventral	Dorsal	Ventral
68	16	55	20
<i>Totals</i>	84		75

These figures show: (1) that the number is not equal in both chords, and (2) that there are about three or four times as many cells on the dorsal sides of the chords as there are on their ventral sides.

The neurochord cells are absent in the oesophageal region, and also in the caudicle; thus both ends of the lateral chords are devoid of them.¹ They increase in number from the anterior to the posterior end of the chord, and, in which I can also corroborate Bürger's observations, only dorsally situated cells occur in the region just anterior to the caudicle. They are always situated medially, close to the circular musculature, as Bürger states, but are frequently more or less lateral in position. The cells in the left chord are seldom paired with those in the right, though it is not infrequent, through a short extent, for those of the one to alternate with those of the other. But it is more usual for three or four to succeed one another in the one chord, while the corresponding portion of the opposite chord is devoid of cells, this order being reversed further on. Then, too, in the same chord dorsal and ventral cells do not alternate, and seldom occur together on one section (I found only two sections of a ventral chord, each of which contained a dorsal and a ventral cell); similarly, two cells in the same section, both on the dorsal side of a chord, I found only twice, and have figured one of these cases (Fig. 32). With these exceptions, the neurochord cells were separated, as a rule, by considerable, though irregular, distances, so that in a series of forty consecutive sections from the middle of the body, seldom were more than six neurochord cells to be observed in both nerve chords.

The only apparent regularity in their distribution is that, in certain portions of the chord at least, zones may be distinguished in which they follow one another in comparatively close sequence, alternating with areas (of approximately equal extent) where they are much less abundant. These alternating areas

¹ I have shown previously ('97) that in the caudicle the fibrous core of the lateral chord is directly enveloped, on all sides except the median, by a mass of true mesenchym cells, and that no ganglion cells accompany the chord in this region.

do not correspond to the number or position of the lateral nerves ("spinal" nerves) of the lateral chords. It would be important to determine whether the sequence of such zones corresponds, for instance, to the metamerism of the gonads; since my specimen was immature with undeveloped gonads, I could not determine this point. If such a regular metamerism of the areas could be proved, then the lateral chords of the nemerteans—in which no segmental localization of ganglion cells producing ganglia has as yet been shown—could be considered as in the inceptive stage of producing such ganglionic localizations. Unfortunately, however, the determination of this point, which has a certain phylogenetic importance, would necessitate the preparation of many thousand sections, since the adult worm should furnish the basis for such a study. But it might more easily be investigated on smaller species of the genus.

b. *Structure*.—The structure of the giant ganglion cells IV of *Cerebratulus* (Figs. 27–29, 32) has much resemblance to that of cells III of the same species, though there are certain differences which may usually serve to distinguish them.

The nucleus (Fig. 31 *a–e*) may be nearly spherical, but is more frequently spherico-oval. It usually has a proximal position within the cell, close to the cell membrane, is seldom central, and never distal in position. In it small masses or granules of chromatin (*Chr.*) of adequal size are arranged peripherally on the inner surface of the well-marked nuclear membrane; and these do not form a continuous layer, as is frequently the case in the nucleus of III, but are placed at more or less regular distances apart. The central portion of the nucleus, which Bürger ('90b, cf. my remarks on the nucleus of III) has erroneously supposed to be filled with a "Bläschen," is mainly filled with the nuclear sap; this sap, in contrast to that of the other ganglion cells, stains faintly with haematoxylin. In it vestiges of a finely granular, achromatic reticulum (mesh-work?) may be observed (*Achr.*). A thin mass of chromatin envelops the nucleolus (*n*). The latter is never absent, is of large size, and almost always peripherally situated; it has thus the same position in the nucleus as the latter has in the cell.

I have found only three or four cells containing two nucleoli apiece, and in each case the latter were unequal in size; these cells were placed about the middle of the lateral chords. Thus, it is not the case in *C. lacteus* that "die Zellen im hintersten Ende der Seitenstämme besitzen . . . häufig zwei gleich grosse Nucleoli," as Bürger ('90b, p. 117) has stated for *C. marginatus*; on the contrary, I found the most posterior cells to contain only one nucleolus. Nor yet, in the species described here, are the nucleoli of the first pair of neurochord cells in the brain directed towards one another.

The cell (Figs. 27-29, 31) is usually of a shortened, pyriform shape, occasionally nearly spherical, or again elongated (this is the case with the first pair in the brain). The cell, together with the thickened, proximal portion of its nerve tubule, often resembles an Italian wine-flask. As a rule, though not always, these cells are much larger than III.

The cytoplasm is, especially distally, coarsely vacuolar, more so than in any other ganglion cell; this gives the cell much the same appearance as a slime-producing gland cell. It is characteristic for the neurochord cells that the hyaloplasm (*Hl. Pl.*) usually stains slightly with haematoxylin. There is always a fine-grained, peripheral, spongioplasmic, supposedly alveolar layer, and a similar layer immediately invests the nucleus (*Alv.*). The mass of cytoplasm is never finely granular throughout, such as is sometimes the case in III, but the distal portion at least is always vacuolar; and as in III, there is no special linear, radial, or concentric arrangement of the hyaloplasmic vacuoles. In IV also the general structure of the cytoplasm apparently corresponds to that of a honeycombed meshwork (Bütschli, '94).

E. Comparison of the Ganglion Cells.

In *Lineus* the ganglion cells are not so strongly differentiated, *i.e.*, represent a lower stage of development than in *Cerebratulus*. Thus in the former genus there are no neurochord cells, and the cells II and III approximate much more closely than in the latter.

In both these genera cell I differs markedly from the others in (1) its small size, (2) the relatively great size of its nucleus, and its large proportion of chromatin (Figs. 1, 17). Bürger ('90b, '91b) has shown these cells to be sensory in function, which their position, etc., renders very probable.

The cell III in structure closely resembles II, especially in *Lineus*. Cell III (Figs. 3-16, 19-21, 29, III) is structurally intermediate between II and IV, and even grades into them; while II (Figs. 2, 18) and IV (Figs. 27-29, 32) never intergrade, but are always to be sharply distinguished.

III resembles II in: (1) its usually elongated form, (2) its more or less marked radial arrangement around the fibrous core (in *Lineus* it is occasionally even grouped in radial clusters), (3) in the usually central or distal position of the nucleus.

III resembles IV in: (1) its size (very large examples being fully as large as small specimens of IV), and (2) in the usually peripheral distribution of the chromatin within the nucleus. Some cells intermediate in structure between III and IV occur in the lateral chords. Thus the cell reproduced in Fig. 23 resembles IV in the coarse vacuolization of its cytoplasm, and in the peripheral, proximal position of its nucleus; but it is similar to III in its small size, the arrangement of the chromatin, and the position of the nucleolus within the nucleus.

Since it is the rule in most of the higher Metazoa that the larger ganglion cells are motor cells, and since III, which is the largest cell in *Lineus* and next to the largest in *Cerebratulus*, shows structural resemblances to II on the one hand, and to IV on the other, I would conclude that these three types of cells are related in function, as well as in structure, and that they are probably all motor cells. Bürger ('91b, '95) has already produced good evidence to show that IV cannot be sensory cells, since he found that their axis cylinders do not pass out of the lateral chords; and having found that they occur only in genera which have the power of swimming, he makes the suggestion that they are directly concerned in this form of motion. I give the following diagram to represent my views on the morphological and physiological, though not necessarily histo-

genetic, relationships of the four types of nemertean ganglion cells:

It may be noted that in the nemerteans the size of the ganglion cells stands, as a rule, in proportion to the size of the body. Thus *Cerebratulus lacteus*, the largest species examined here, has larger cells than has *Lineus sp.*; and the latter species has larger cells than the still smaller *L. gesserensis*. And I find in the *Metanemertini* also that *Amphiporus glutinosus* and *A. virescens* have larger cells than the smaller species, *Tetrastemma catenulatum*, *T. vermiculum*, and *Stichostemma eilhardi*. An exception to this rule is *Carinella annulata*, with smaller cells than *Lineus sp.*; but *Carinella* is a most primitive form, in which the ganglion cells and the whole nervous system have become but little differentiated.

III. NERVE TUBULES.

A. Cell III.

In *Lineus gesserensis* I have studied the nerve tubules on thin sections (c. 3μ thickness) on material prepared with sublimate (aqueous, alcoholic solutions), Flemming's and Hermann's fixatives, and treated with different stains.

Each ganglion cell has one axis-cylinder process, and I have been unable to find dendritic (so-called "protoplasmic," or "Deiter's") processes.

The cytoplasm of the ganglion cell (Figs. 3-14) is usually most vacuolar distally, where the cell tapers towards the axis-cylinder pole. But even here the mass of cytoplasm is always bounded by a peripheral, fine-grained layer (*Alv.*). This peripheral layer is directly prolonged along the axis cylinder, and produces the very fine spongioplasmic sheath of the latter (Figs. 3-14, *Alv.*). This sheath is, with the exception of the sheath of Schwann (to be described later, cf. "Neuroglia"), the only staining portion of the nerve tubule, and also the only part in which a fine-grained structure can be discerned. This fine

outer spongioplasmic sheath of the nerve tubule immediately envelops the axis cylinder, which cylinder composes the greater part of the tubule, and is a direct continuation into the latter of the hyaloplasm (*Hl. Pl.*) of the cell. Thus the axis-cylinder process is a *nerve tubule* and not a *nerve fibril*, since by the term "fibril" is implied a very fine thread of more or less dense (*i.e.*, non-fluid) composition, which is also of equal density in its whole diameter. In short, the typical structure of the ganglion-cell process in *Lineus* is that of a nerve tubule, consisting of a very fine-staining, fine-grained, spongioplasmic sheath, which envelops the unstaining, hyaloplasmic axis cylinder.¹ The hyaloplasmic axis cylinder never stains with any of the methods employed by me; an exception is found in the *intra vitam* methylene blue staining; thus Apáthy's ('91) investigations show that the axis cylinder (his "Primitivfibrille") stains as well as its sheath; and since Bürger's ('91b) Fig. 18 a. shows that both hyalo- and spongioplasm stain within the ganglion cell, it is allowable to conclude that both the axis cylinder and its sheath become stained with methylene blue. I might also refer to my Fig. 41, from a preparation of *Tetrastemma* fixed with sublimate and afterwards stained with aq. sol. of methylene blue; here the structure lettered *N. T. ?*, which probably represents a nerve tube (*i.e.*, a bundle of nerve tubules), has become deeply stained throughout with the methylene blue. Further, the axis cylinder is always non-refractive and homogeneous, and does not contain longitudinal "primitive fibrils," nor other fibrous or granular structures; nor yet have I found any evidences of a meshwork structure, as described by Bütschli ('94). The substance of the axis cylinder is always homogeneous and structureless, and is identical with the hyaloplasm of the cell. This hyaloplasm must be a fluid, or at least a viscid, substance in life; but it certainly cannot be dense, since in that case we would expect to find it refractive, and to

¹ The very fine membrane around the axis cylinder in vertebrate nerve fibres, as figured by Koelliker ('89), might correspond to such a spongioplasmic sheath as that described by me in nemerteans. The "primitive nerve fibrils," such as have been described for a large number of forms, lie within the substance of the axis cylinder.

find it showing evidences of a finer structure. It is strange that Apáthy ('91), whose description of the axis cylinder (his "leitende Primitivfibrille") of the *Hirudinea* closely corresponds to mine of the *Nemertini*, should acknowledge that the axis cylinder is homogeneous, and yet conclude that it is solid and non-fluid in consistency. He reached this result as to its density simply from observations with polarized light; for the axis cylinder would be capable of isolation, provided that its sheath remained intact, even if it were fluid in consistency. Not, I think, that the best reason for the correctness of the assumption, that the substance of the axis cylinder has a fluid or viscid, and not a dense, consistency, is to be given by the fact that this substance is in every way identical with the hyaloplasm of the cell; and all observations tend to prove that the hyaloplasm of the cell cannot be of solid (dense) consistency, but is fluid, or at least viscid.

The structure of the nemertean nerve tubule, as just described, may be seen after preparation with corrosive sublimate, but is rendered much more distinct after fixation in Flemming's or Hermann's fluids. The fluid of Hermann especially renders the course and structure of the nerve tubules very plain, and for this purpose cannot be too highly praised. Thus, after fixation of half an hour in this fluid, the spongioplasmic sheaths of the tubules and all the neuroglia fibres (or "fibrils," as one will) of the fibrous core of the brain and lateral chords become stained a deep bronze-brown, while the hyaloplasmic axis cylinders remain unstained, and are easily traceable as fine, colorless lines. And this result is reached after sectioning in paraffine and mounting in Canada balsam, — a course of procedure much deprecated by Apáthy ('91). Hermann's fluid, accordingly, produces just the very opposite effect of the impregnation method of Golgi: by the former only the axis cylinders become stained, while by the silver method it is especially these parts which become blackened. But Hermann's fluid is always precise in its effect, while, as Friedländer ('89) has shown, the Golgi method is far from reliable, since frequently neuroglia, as well as the strictly nervous elements, become stained by it.

The nerve tubule is best studied in its proximal portion (Figs. 3-14), since it has the greatest diameter at this part; and further, owing to its somewhat tortuous course within the fibrous core, it is only this portion which may be traced to the ganglion cell (cf. Fig. 3). In a small number of cases I have found spongioplastic strands or fibres prolonged from the cytoplasm of the cell for a short distance into the hyaloplasm of the axis cylinder (Figs. 4, 5, 7, 11, 13, *F.*). These strands of spongioplasm are found only in the most proximal portion of the axis cylinder, and are not continued distally. The observation of such fibres as these might have led Nansen ('87) to the conclusion that the axis cylinder represents a bundle of "primitive nerve tubes," and that these fibres correspond to their supposed sheaths. For my part, however, I consider that the nemertean axis-cylinder process represents a single nerve tubule, and not a bundle of parallel "primitive nerve tubes." And the spongioplastic strands or fibres which I have described in the axis cylinder, (1) being found in but a small proportion of the large number of axis cylinders examined, (2) being even then present only in their most proximal portions, and (3) varying both in number and size (Figs. 4, 5, 7, 11, 13), would lead to the justifiable conclusion that they do not represent sectioned sheaths of "primitive nerve tubes," but are merely spongioplastic prolongations of the cytoplasm of the ganglion cell, which penetrate but a short distance into the hyaloplasm of the axis cylinder.

On cross section, studied with high powers of the microscope, the nerve tubule appears as a minute, circular, unstaining disc, bounded by a fine, staining line (Fig. 39, *Ax. Cl.*, also Figs. 36, 37).

As noted above, the nerve tubule has the greatest diameter proximally, and distally gradually decreases in size (Figs. 3, 4). There are apparently no dichotomic divisions by which two branches of equal diameter are produced. But the diminution in calibre is due, partly at least, to the giving off of collaterals from the nerve tubule, which always have a smaller diameter than that of the nerve tubule at the point of division (Fig. 39, *Coll.*). I have never been able to trace these collaterals for

more than a very short distance, nor have I found them branched; my observations corroborate those of Bürger ('91b) on methylene blue preparations, who discovered the collaterals (his "ungleichwerthige Nebenfortsätze"), and found them always unbranched. After the nerve tubule has given off a number of collaterals, it is greatly decreased in diameter, becoming almost invisible. In this distal portion of its extent, the finer structure can necessarily be no longer determined; but there is no adequate reason for supposing that the structure of the nerve tubule here differs from that in its proximal portion, as maintained by Bürger ('91b). The nerve tubule, after entering the fibrous core, certainly does not divide into a brush of fine branches, as figured by Rohde ('90a) for polychaetes.

It remains to state that even after the use of fluids containing OsO_4 I have been unable to find any evidences of a myelin sheath, such as has been described by Retzius ('89b) and Friedländer ('89) for other invertebrates. And as little as H. Schultze ('79) and Apáthy ('91), have I found varicosities of the axis cylinder.

In *Cerebratulus lacteus* I could not make as thorough a study of the nerve tubules as in the preceding species, since I had but one specimen, and that fixed with alcoholic sublimate. But it may be stated that these preparations of *Cerebratulus* showed the same structure, as those of *Lineus* fixed by the same method. The spongioplasmic, peripheral layer of the ganglion cell is produced to form the sheath of the nerve tubule, and its hyaloplasm is in direct connection with that of the axis cylinder (Figs. 20, 21, 23, 29, III). As in *Lineus*, spongioplasmic strands sometimes penetrate from the cytoplasm of the cell into the proximal portion of the axis cylinder (Fig. 23); but though found in a comparatively larger number of cells than in that genus, they are nevertheless restricted to relatively few cells. Such strands are of varying thickness, and have a greater diameter proximally than distally; further, they vary in number from one to about six, and, though more or less parallel in position, are not placed at equal distances apart. Accordingly, there is apparently no regular distribution of the spongioplasmic and hyaloplasmic substances in the proximal portion of such an

axis cylinder, *e.g.*, no alternating, concentric, or linear zones of these substances. In short, the nerve tubule in the proximal and distal portions of its extent consists, as in *Lineus*, of a thin spongioplasmic sheath and an enclosed, homogeneous, unstaining, hyaloplasmic axis cylinder; only in a small number of cases are spongioplasmic fibres or strands, which vary in size and number, continued from the framework of the cell for a short distance into the hyaloplasm of the proximal portion of the axis cylinder.

The nerve tubules of cells I are so minute in diameter that their structure can only be studied in their wider, proximal portion (Figs. 1, 17); as far as I could determine, they have the same formation as those of III. In Fig. 37, representing a cross section of the fibrous core of the dorsal brain lobe, the unstained axis cylinders are probably of both cells I and III (these two types of cells forming the ganglion-cell layer of the dorsal lobe). The structure of the nerve tubules of cells II (Figs. 2, 18) may be more easily studied than those of I, and have exactly the same structure as the nerve tubules of III, from which they differ only in size.

It will be well to review briefly Bürger's representations of the structure of the nerve tubules of cells III before describing those of IV.

Bürger's observations ('90b, '91b, '95) differ quite essentially from mine, though his direct observations less so than his generalizations. For the terms "spongioplasm" and "hyaloplasm" used here, he adopts Flemming's expressions, "mitom" and "paramitom." The following quotations will show his views on the ganglion-cell processes ('95): "Die Fortsätze der Ganglienzellen, welche den Stammfortsätzen von Retzius ['90] entsprechen, zeigen mit Ausnahme derjenigen der Neurochordzellen perlschnurartige Verdickungen" (p. 332). . . . "Die Nervenfasern der Centralsubstanz d. i. der in ihr enthaltene Abschnitt des Stammfortsatzes stellt nämlich nicht einfach den in den Seitenstamm der Nemertine verlängerten Fortsatz der Ganglienzelle dar. Denn der Fortsatz einer Ganglienzelle verjüngt sich in der Centralsubstanz oft bis in eine recht feine Spitze und tritt mit dieser an die Nervenfasern heran, die häufig

diesen Fortsatz überhaupt, jedenfalls aber sein verjüngtes Ende sehr an Dicke übertrifft" (p. 334). The "Nervenfibrillen" of all cells but IV possess "Nebenfortsätze": "Unsere Nebenfortsätze entspringen von den Verdickungen [varicosities] der Fibrillen. . . . Ich halte den Stammfortsatz der Ganglienzelle, obwohl ich an ihm zwei Abschnitte ["Ganglienzellfortsatz," "Fortsatzfibrille"] unterschied, keineswegs für ein zusammengesetztes Gebilde im Sinne von Dohrn [91, the view has since been relinquished by Dohrn] und Apáthy" (p. 335).

Now the Göttingener investigator distinguishes on the "nerve fibre": (1) the true prolongation of the ganglion cell, and distally (2) the "nerve fibril," which he claims is sharply bounded off from the former, though both should stand in the same genetic relationship to the cell! He found, with the *intra vitam* methylene blue staining, that the distal "Fibrille" stains more intensely than the proximal "Ganglienzellfortsatz"; he gives no structural details of its formation, but his term "Fibrille" leads us to suppose that he conceived of it as a dense fibril with a structure different from that of the proximal process. His descriptions would give the idea, further, that there is an abrupt local as well as structural demarcation between the two, *i.e.*, that they do not merge gradually into each other. Already in a former paper Bürger (90b) had distinguished ganglion-cell process and nerve fibril on the study of sections fixed with chromic acid and with alcoholic sublimate (?); of the structure of the ganglion-cell process, he states (p. 112): "Bei III und IV ist das Paramitom vorherrschend. Es ist in mehreren Säulen im Fortsatze gelagert, jede Säule wird von einer Mitomscheide umgeben, das gesammte Bündel umfasst eine besonders körnige Mitomschicht, wie sie als Rindenschicht des Zelleibes charakterisirt wurde." This representation of the structure of the proximal portion of the axis cylinder, namely, as a nerve tube composed of a bundle of "primitive nerve tubes," is in close accord with the descriptions of Nansen (87) for other forms; and Bürger's Fig. 56, Taf. IV, bears marked resemblance to certain of Nansen's figures. Finally, of the nerve fibril, he states (90b, p. 118): "Als Formelement der centralen Fasermasse habe ich eine

feinste, kaum messbare Fibrille verfolgen können, die in den Ganglien einen verschiedenen Verlauf besitzt, in den Commissuren von einer Gehirnhälfte zur anderen ihren Weg nimmt und in den Seitenstämmen entschieden längsgerichtet ist."

Now I have found that the nerve tubule, as far as it can be followed, consists of a thin spongioplasmic sheath and an enclosed, homogeneous, hyaloplasmic axis cylinder (Figs. 3, 36-39). The axis cylinder is not a bundle of "primitive nerve tubes," as held by Nansen, and as Bürger's ('90b) Fig. 56 would show. The assumption of the existence of the "primitive nerve tubes" has probably had its origin in that those spongioplasmic strands, which I have shown to be sometimes prolonged for a short distance into the axis cylinder, had been regarded by Nansen and his followers as the sheaths of such primitive tubes; that such a structure is not present in the nemertean axis cylinder I have already shown. My results would show that the axis-cylinder process in its whole extent represents a single nerve tubule; and that a structural distinction into a proximal "ganglion-cell process" and a distal "nerve fibril" is not present. A "kaum messbare Fibrille," in the sense in which Bürger uses the term, namely, as a dense, deeply staining, non-tubular fibril, I have never found. And in fact, I have found only a number of parallel nerve tubules at the roots of the spinal nerves and in the first ventral commissure of the brain,—points where Bürger stated his "nerve fibrils" to be most easily demonstrable. Therefore, Bürger, in those studies ('90b) of his based upon stained sections, had either: (1) supposed the true hyaloplasmic axis cylinder to be simply an unstaining space between two "fibrils," and then had mistaken the sheaths of the axis cylinders for "fibrils"; or (2) what, however, seems to be a less probable explanation, had confused neuroglia fibrils with "nerve fibrils." But we must conclude that in the fibrous core he had not seen the true axis cylinders. This critique cannot be considered unjust, since Bürger had neglected to employ the two methods best qualified to demonstrate the axis cylinders in the fibrous core, namely, Flemming's fluid and, better still, the fluid of Hermann.

But does the nerve tubule consist of two separate parts, — a proximal ganglion-cell process and a distal "Nervenfibrille"? Bürger's ('91b) figures drawn from preparations stained in life with methylene blue certainly seem to support such a view. But his descriptions do not mention any difference of structure between the two parts, but simply a difference in dimension and a slight distinction in staining power; and my own observations have taught me that there is no structural distinction between the proximal and distal portions, but only a gradual difference of diameter. Thus, if the nerve tubule be divisible into a proximal ganglion-cell process and into a distal portion, this distinction will probably be found, not to be one based upon differences of structure in the nerve tubule itself, but either upon differences of dimension or of differences in the structure of its connective-tissue envelope (sheath of Schwann). And with Apáthy ('91), I think the supposed varicosities of the nerve tubule might also be referred to the sheath of Schwann.

B. *Cell IV.*

The nerve tubules of the cells IV are the largest in the nemerteans, and deserve the term "neurochords" applied by their discoverer, Bürger ('90b), with reference to their similarity to the neurochords (Eisig, '87; "Leydig'sche Fasern," Friedländer, '89) of the annelids and crustaceans.

This colossal nerve tubule (Figs. 27-29, 32, *Ax. Cl.*) is composed of a thin spongioplasmic sheath, which is a continuation of the peripheral alveolar layer of the cell; and of an enclosed, unstaining, homogeneous, hyaloplasmic axis cylinder, which is in direct communication with the hyaloplasm of the distal portion of the cell. The neurochord nerve tubule differs from the tubules of the other ganglion cells mainly in its superior size. I have never found any evidences of a finer structure in the hyaloplasmic axis cylinder, but always found it to be homogeneous; my results being in accord with those of Friedländer ('89) on annelids and crustaceans, and with those of Apáthy ('91) on *Hirudinca*. But it is to be noted that on studying, for example, a longitudinal section of such a neurochord by elevating or

lowering the tube of the microscope, *i.e.*, with a focus a little too high or too low, the enveloping sheath of Schwann is brought into view, presenting the illusory appearance of a stained structure lying in the axis of the neurochord. It is possible that Bürger ('90b) had experienced such an optical illusion when he described an irregular, staining structure lying in the axis of the nerve tubule in *C. marginatus*; otherwise it must have been an artifact, as I found no positive evidences of such a structure in *C. lacteus*. On cross section (Figs. 30, 40, *Ar. Cl. IV*), the neurochord is found to consist of an unstaining, homogeneous disc (the hyaloplasmic axis cylinder); this is immediately bounded by a very fine spongioplasmic layer, and outside of the latter is the thicker, granular sheath of Schwann, which stains with eosin. I have been unable to find traces of a myelin sheath; but since the individual examined had been fixed in 50% alcoholic solution of sublimate, alcohol having the property of dissolving myelin, the nemertean neurochord must be studied after the action of a fixative containing OsO_4 (this acid blackening myelin) before it can be determined whether such a sheath is present or absent. And this point is worth investigation with regard to the possible homologies of these neurochords with those of the annelids, crustaceans, *Amphioxus*, and even *Myxine*.¹

The neurochord of cell IV divides dichotomously, though the points at which it divides are situated at considerable distances apart. Fig. 42 *a, b* shows such dichotomic divisions on longitudinal sections. It is the rule that each of the branches has one-half the diameter of the neurochord before the point of division, so that it is a strictly equal dichotomy. In an exceptional case (Fig. 42 *c*) were two branches given off at the same point from the one side of the neurochord, though the diameter of the latter behind this point was not diminished; this should, perhaps, be regarded as a pathological case, and these two branches would not correspond to collaterals, since Bürger ('91b)

¹H. Schultze ('79) first discovered myelin in the nerves of invertebrates within the substance of the axis cylinder (between his "primitive fibrils") in *Unio* and *Anodonta*. Myelin sheaths of the nerve fibres of vertebrates have been described by Leydig ('85), Retzius ('89b), Friedländer ('89), for annelids and crustaceans, and by Apáthy ('91) for *Hirudinea*.

has found the absence of collaterals characteristic for the neurochords. Leydig ('85) has figured a dichotomic division of the neurochord in *Dytiscus*. Another peculiarity of these neurochords I find in their constrictions, which may be compared to the "anneaux constricteurs" ("Ranvier'sche Einschnürungen") of the vertebrate axis cylinder. To wit, just anterior to a point of division, such a constriction of the axis cylinder may always be found (Fig. 42 *a, b*); and in one case (Fig. 42 *d*) I found a constriction far removed from any point of dichotomy. Such segmental constrictions of the neurochords have been observed by Friedländer ('89) in the polychaete *Mastobranchus*; but in this annelid the constrictions are of greater extent than in *Cerebratulus*. It will be recalled that three pairs of cells IV occur in the ventral lobes of the brain, and none at all in the lateral chords in the oesophageal region; each lateral chord, therefore, derives three neurochords from the respective side of the brain. But these most anterior neurochords do not pass undivided through the lateral chord in its oesophageal region, but divide here dichotomously; so that in studying a series of transverse sections from this region, they are found to increase in number and decrease in size posteriorly. Since, however, on a cross section of the lateral chord in the posterior portion of this region it is not infrequent to find a neurochord fully as large in diameter as one in the more anterior portion, we must suppose, either (1) that a neurochord or one of its branches may vary in diameter in different portions of its course, or (2) that a number of neurochords may fuse together, posteriorly, to produce a larger, compound neurochord (or neurochord "bundle"). Though the first alternate would appear to be the more probable, I was unable to determine this question, even on longitudinal sections.

Bürger first ('90b) maintained that the neurochords of *Cerebratulus* and *Langia* divide dichotomously, after observing their numerical increase on successive cross sections. Later ('91b) he abandoned this view, and finding on *intra vitam* methylene blue preparations no branching of the neurochords, concluded that the latter pass to the posterior end of the lateral chords without division. My observations, which are epitomized in

Fig. 42 *a-e*, corroborate his former view, and show that the neurochords possess equal dichotomic divisions.

Though I have followed Bürger ('90b) in applying the terms "neurochord cells" and "neurochords" to nemerteans, — terms introduced by Eisig ('87) for the colossal ganglion cells and their fibres in annelids (which structures had been recognized first by Leydig, '64, as nerve tubules), — yet I would not intend to express, by the use of similar terms, homologies between these structures in different animal groups. Friedländer ('89) maintained such a homology in different animal groups, or at least declared the neurochords of different groups to be "fundamentally the same" structures (p. 258). But what is meant by the expression "fundamentally the same," if not homology? But though the neurochords may present similar structural relations in the different animal groups (*Nemertini*, *Annelida*, *Arthropoda*, *Leptocardia*), their homology is not thereby proved; for there is as much probability for the assumption that they have been developed independently by these various forms. And notwithstanding the large number of investigations already made upon neurochords,¹ it is still necessary to subject them to renewed study, with the aid of the newer histological technique, and to treat them from the comparative standpoint.

IV. NEUROGLIA.

As Bürger ('90b) has demonstrated, the brain lobes and lateral chords are compounded of the following layers: (1) the outer neurilemma (Fig. 25, *o. Neur.*), a connective-tissue capsule enveloping (2) the ganglion-cell layer, and (3) the inner neurilemma (*i. Neur.*), which separates the latter layer from (4) the central fibrous core (composed of "dotted substance"). Bürger had also described the connective-tissue elements of the ganglion-cell layer, and termed it "intracapsuläres Bindege-webe" or "Hüllgewebe"; he discovered, also, a layer of cells of this tissue situated between the inner neurilemma and the

¹ A nearly complete bibliographical list of papers dealing with neurochords has been given by Friedländer ('89).

fibrous core. In a paper ('97) on the cytology and comparative distribution of the connective-tissue elements in the nemerteans (*Carinella*, *Cerebratulus*, *Lineus*, *Amphiporus*, *Tetrastemma*, *Stichostemma*), I have given detailed descriptions of the cellular elements forming the neurilemmatic capsules, and the "Hüllgewebe" (this latter I termed "neuroglia"); for fuller structural details of these elements, I must refer to the paper in question.

Now I agree with Bürger's conclusion ('90b, p. 137): "Das Pigment führende Hüllgewebe der Ganglienzellbündel . . . und der faserig-zellige Mantel des Faserstammes . . . sind ursprünglich ein und dieselben Gewebsgebilde, örtlich von einander getrennt und differenziert." But he adds (p. 138): "Sie sind vielleicht als mit dem Neurilemma in Gemeinschaft entstanden zu denken, jetzt aber so sehr von den Bildungen desselben verschieden, dass sie für sich zu betrachten sind. So sind sie auch mit der Glia (Hatschek's) unvereinlich, da sie ihrem vornehmsten Kriterium Scheiden- oder Röhrenbildnerinnen niemals entsprechen." I have shown in my previous paper (*l. c.*), however, that the elements of the neuroglia (Bürger's "Hüllgewebe") and those of the neurilemmatic sheaths must be considered as distinct for the following reasons: (1) because the tissue of the neurilemma is identical with the connective tissue forming the basal membranes of all epithelia, with that enveloping the muscle bundles, etc., and consists of branched cells lying within a dense intercellular substance, while the neuroglia is restricted to the nervous system, and its cells are not imbedded in an ectoplastic, intercellular substance; and (2) because no intergradations between these two tissues occur, not even in that primitive form *Carinella*. Further, as shall be described, the branching fibres of the multipolar neuroglia cells not only produce a loose network around the ganglion cells (III, IV), but also form the outer connective-tissue sheaths of their nerve tubules. Thus Bürger's "Hüllgewebe" is a typical neuroglia tissue, and can stand in no histogenetical relationship to the tissue of the neurilemmatic sheaths. It is more probable, indeed, in the light of our knowledge of the ependyma (embryonal neuroglia) in vertebrate histogenesis, that the neuroglia of the nemerteans stands in closer genetical relation

to the ganglion cells themselves than to the cells of the neurilemma (cf. Rohde, '90b).

I have ('97) found that the neuroglia of the central nervous system occurs in two or three modifications, according to structural differences: thus (1) the "outer neuroglia," which is situated between outer and inner neurilemma, and (2) the "inner neuroglia," in and around the fibrous core, may be distinguished in all nemertean genera; while in a few genera the outer neuroglia may be subdivided into (a) the outer neuroglia of the brain lobes, characterized by the presence of pigment, and (b) the outer neuroglia of the lateral nerve chords, in which pigment is absent.

The membraneless, multipolar cells (Figs. 35 *a-c*, 40, *NgL. C.*) of the outer neuroglia, which are situated between the outer and inner neurilemma of the brain and lateral chords, possess long, fine, branching fibres which produce loose fibrous sheaths around each of the ganglion cells of the types III and IV. In the Figs. 3-16, 19, 21, 23, 27-29, 32 the fibres alone of the sheaths (*NgL.*) are reproduced, the cells from which they arise, and which usually are more peripherally situated, having been figured in my preceding paper (*l. c.*). Bürger ('90b) first described these fibrous sheaths of the ganglion cells; but he had overlooked the more important fact that they are continued along the nerve tubules also, producing an outer connective-tissue sheath of the latter, which is fully comparable to the sheath of Schwann ("Schwann'sche Scheide") of, *e.g.*, the vertebrate axis cylinder, and for which the same term may be applied. The number of fibres composing the sheath of the ganglion cell is greatest and they are most loosely arranged around the enlarged proximal portion of the cell (Figs. 3-8, 10-13, 19, 21, 23, 27-29, *NgL.*). Towards the distal pole of the cell—the point of origin of the nerve tubule—the number of enveloping neuroglia fibres diminishes, and they commence to place themselves much closer to this portion of the cell. Finally, on each side of the proximal portion of a nerve tubule, as seen on a thin longitudinal section, one neuroglia fibre may be seen, and can be traced to one of the fibres forming the fibrous sheath of the ganglion cell. Thus the nerve tubule is enveloped by a

sheath of Schwann (*S. Sh.*), the separate longitudinally directed fibres of which are derived from the fibrous sheath of the cell itself. As far as I could determine, the sheath of Schwann consists of a single layer of longitudinal neuroglia fibres, the fibres being parallel to, but not in contact with, one another, *i.e.*, they apparently do not produce a continuous membrane. I could not determine along how great an extent of the nerve tubule this sheath continues, since its fibres decrease in size distally. Certainly, however, in its proximal portion the following components of the nerve tubule may be distinguished: (1) the axial, hyaloplasmic axis cylinder, (2) the spongioplasmic sheath of the latter, and (3) on the outside of this sheath, the sheath of Schwann. On a distal portion of the nerve tubule the axis cylinder is found to be bounded by a very fine, scarcely visible envelope (Fig. 40); the latter is so minute that one cannot determine whether it corresponds to the spongioplasmic and the neuroglia sheath, or whether to merely one of the latter.

On longitudinal sections of the neurochord nerve tubules (Fig. 42 *a-e*) the separate fibres of the sheath of Schwann are mostly found to be bisected; this fact might be explained on the ground that they describe a spiral course around the nerve tubule.

As just described, the sheath of Schwann is formed by a continuation along the nerve tubule of certain of those outer neuroglia fibres which produce the loose sheath around the proximal portion of the ganglion cell. But whether fibres from the cells of the inner neuroglia also take part in the construction of the sheath of Schwann, I have been unable to decide; this might appear probable in those cases where the distal pole of the ganglion cell lies close to the layer of the inner neuroglia cells. Further, I cannot state positively that an additional sheath, derived from the inner neurilemma, is added to the nerve tubule; though in support of there being such a sheath around at least the proximal portion of the tubule, I may refer to the left-hand cell portrayed in Fig. 29, where a thin plate of the inner neurilemma is split off from the latter, and accompanies the proximal portion of the nerve tubule for a short distance. This was the only case in which I found evidences of such a neurilemmatic sheath.

V. DOTTED SUBSTANCE OF THE FIBROUS CORE.

The fibrous core (Figs. 25, 30, 35 *a-c*, 40, *F. C.*) of the brain and lateral chords is composed of the so-called "dotted substance" ("Punksubstanz" of Leydig), and is divided from the outer ganglion-cell layer by the inner neurilemma (*i. Neur.*). The only cells occurring within the fibrous core are the branched cells (*Ngf. C.*) of the inner neuroglia tissue, and these are situated mostly peripherally, just beneath the inner neurilemma, though a small number penetrate also into the dotted substance.

The fibrous core is composed of: (1) fibres of the cells of the inner neuroglia, which compose its greater part, (2) nerve tubules and their sheaths, (3) irregular spaces containing body fluid. Apparently no fibres or strands of the inner neurilemma penetrate for any considerable distance into it. It cannot be too strongly emphasized, that in order to arrive at a clear understanding of this much-discussed portion of the central nervous system, comparisons must be made between preparations fixed in different fluids (especially Hermann's fluid and sublimate solutions), and between those differentiated by different stains. Since the structure of the fibrous core differs somewhat in *Lineus* and *Cerebratulus*, it may be described separately for these two genera.

A. *Lineus*.

In this genus there is a proportionately larger number of inner neuroglia cells around the fibrous core than in *Cerebratulus*, and their fibres are also coarser and hence more easily followed. These fibres, as well as the cell bodies, are of a dense, granular structure, and stain intensely with eosin; and though they branch excessively, I have never found anastomoses between the fibres of adjacent cells.¹ The fibres of the peripheral inner neuroglia cells radiate into the fibrous core, producing the fibrillar, staining substance of the latter. A single neuroglia fibre with its branches may often be traced for a considerable

¹ If it were necessary to be precise in our terminology, the term *fibre* could be restricted to the branch of the cell, and *fibril* employed for secondary branches of these fibres; but these distinctions are of doubtful value, and need not be employed here.

distance in the fibrous core, and is always to be distinguished from the really nervous elements by (1) its granular, refractive appearance, (2) its staining power with eosin, (3) its irregular branches. On cross section, after fixation in sublimate, such a fibre appears as a refractive, staining granule or group of smaller granules (depending upon its size).

The nervous elements in the fibrous core, or dotted substance, are the nerve tubules, and their course and grouping is to be best studied on sections of material fixed with Hermann's fluid (in Figs. 36-38 I have tried to reproduce the appearance of such preparations, though the ground color should be more of a bronze than green). The axis cylinder of the nerve tubule never stains (except with methylene blue, and probably with gold chloride: cf. Apáthy, '91), is circular on cross section, and its fine, staining envelope is the spongioplasmic sheath. After fixation in Hermann's fluid for half an hour, when studied with high magnifying powers (Fig. 39), the fibrous core is seen to consist of a deeply stained, very finely granular matrix (of neuroglia fibres), throughout which the unstaining axis cylinders lie; with a lower power of magnification (Figs. 36-38) the staining matrix appears homogeneous, deeply staining, and the axis cylinders as fine, colorless lines, or dots on cross section. Sublimate produces a more coarsely granular appearance of the fibrous neuroglia matrix than does Hermann's fluid, probably owing to the faculty of the former reagent to produce coagulation.

In the fibrous core of the dorsal (Fig. 37) and ventral lobes of the brain and in the dorso-ventral commissure the unstaining axis cylinders are more or less regularly distributed, and are not united into special bundles. In the dorsal commissure of the brain (commissure of the dorsal lobes) and in the ventral commissures (Fig. 38), they all take a parallel course, but here also are not grouped into bundles.

There is in the lateral chord, however, a more specialized arrangement of the nervous elements (Fig. 36). Here, namely, a short distance behind the ventral lobe of the brain, about the region of a frontal plane passing through the posterior end of the cephalic sense organ, a large tube arises (Fig. 36, *N. T.*) which is situated a little lateral from the center of the fibrous

core and courses towards the posterior end of the chord, where it becomes gradually indistinguishable, owing to decrease in diameter. On cross section it is more or less circular or oval in outline, and is bounded by a fine sheath; its contents do not stain and are homogeneous, except that occasionally vestiges of a very fine, reticular structure may be found within it. On account of its large size and general appearance, especially on longitudinal sections, it bears a close resemblance to a neurochord; but neurochord cells are absent in *Lineus*. This structure certainly can represent nothing else than a bundle of nerve tubules, and accordingly may be termed a *nerve tube*; the fine reticulation which its contents sometimes show would correspond to the sheaths of the individual nerve tubules composing it. It is the "Faserstrang" found by Bürger ('90b, '91b), but it is not composed of a bundle of "nerve fibrils." The fine membrane surrounding the nerve tube is so minute that I cannot determine whether it is a neuroglia product *sui generis*, or whether it is formed by a coalescence of the sheaths of the outermost layer of enclosed nerve tubules. This tube is not continued, anteriorly, into the ventral lobe of the brain, nor into the first commissure of the latter. Further, it does not persist as a single, unbranched tube through the whole length of the lateral chord. For on following a series of cross sections, the first section may show a single tube, the second two tubes (each half the diameter of that on the foregoing section), further sections may show three or four tubes, and a consequent section the disc of but one tube again (Fig. 33 *a-d* shows the branching of the nerve tube as seen on four consecutive cross sections). That the tube branches, apparently dichotomously, can be observed on longitudinal sections also. Thus the nerve tubules in the nerve tube do not pass singly out of the latter into the peripheral nervous system, but smaller tubes (each containing a number of nerve tubules) branch off from the main tube. It is possible that towards the posterior end of the lateral chord, where the diameter of the main nerve tube becomes much reduced, the nerve tubules pass out of it singly; but I do not attempt to decide this point, which has no direct bearing upon the questions at issue.

A large number, though by no means all and perhaps not even one-half, of the nerve tubules of the lateral chord are enclosed in this nerve tube. For a glance at Fig. 36 demonstrates that a considerable number of cross-sectioned axis cylinders are distributed pretty evenly throughout the fibrous core, without being grouped together as nerve tubes. In fact, there appear to be nearly as many nerve tubules scattered throughout the fibrous core of the lateral chord, and not enclosed in its central nerve tube, as we find in the fibrous core of the dorsal and ventral brain lobes, where no nerve tubes occur (cf. Fig. 36 of a lateral chord with Fig. 37 of the dorsal brain lobe).

For each nerve tubule of cell III there is usually a special opening in the inner neurilemma, while, as already noted, for each radial cluster of cells II (Fig. 25) there is but a single opening through which all their nerve tubules penetrate to the fibrous core. Fig. 36 shows that the bundle of nerve tubules from such a cluster of cells II penetrates nearly to the center of the fibrous core, where the individual nerve tubules then diverge and bend towards the posterior end of the chord. Fig. 37, representing a transverse section of the core of the dorsal brain lobe, exhibits the same phenomenon in regard to clusters of cells I. Probably new accessions of nerve tubules are being continuously added to the central nerve tube of the lateral chord from such metameric bundles of nerve tubules of the radial cell clusters of II.

Attention may be drawn to Fig. 41, from a preparation hardened in sublimate, afterwards stained with methylene blue followed by brasilin, of *Tetrastemma vermiculum*. In the longitudinally sectioned fibrous core (*F. C.*) of the lateral chord, I find a rod-like structure which had been stained a deep green. This body probably represents just such a nerve tube as I have described for *Lineus*.

I must not be misconstrued into supposing that all the unstaining portions of the dotted substance represent axis cylinders. On the contrary, I have found irregular, even more or less tubular, unstaining spaces in the fibrous core which can represent nothing more nor less than spaces filled with body fluid, just as the unstaining spaces enclosed by the muscle

bundles of the body wall.¹ Thus in those frequent points in the brain lobes and lateral chords where "strings" of the inner neuroglia cells penetrate into the fibrous core, these cellular ingrowths do not form compact masses, but their individual cells are separated by irregular, unstaining spaces, which branch out into the substance of the fibrous core. Often such irregular, branching cavities are present beneath those inner neuroglia cells which occur on the periphery of the fibrous core (Fig. 37, *Sp.*). The clefts or spaces produced by these accumulations of body fluid may readily be distinguished from cross-sectioned axis cylinders by their superior size, irregular form, and absence of a limiting sheath.

The results of Bürger's ('90b, '91b, '95) observations on the finer structure of the fibrous core differ quite essentially from my own. For he supposed its nervous elements to be dense, staining "nerve fibrils," a view which my investigations would show to be erroneous, and which has been sufficiently criticised above. He consequently considered that the minute, unstaining spaces of the fibrous core did not represent axis cylinders, but clefts filled with body fluid, showing that he had overlooked the true nerve tubules. Again, the nerve tube (*mili*) of the lateral chord, which he discovered and termed the "Faserstrang," he stated to be composed of a bundle of deeply staining "nerve fibrils," whereas I was able only on a few preparations to find evidences of a structure in it, and then in the form of a faintly staining reticulation (never "nerve fibrils"), which probably represents the sheaths of enclosed nerve tubules. Bürger may have employed a fixing reagent which had caused such an excessive coagulation of the contents of the nerve tube as to have given the appearance of fibrils; but, as already stated, I have never found any evidence whatever of the

¹ As a rule, the body fluid of the nemerteans can be considered to be a thin, homogeneous, unstaining fluid, which fills the very numerous, usually minute, clefts in the different tissues; but I have shown ('97) that that portion of it enclosed in the bundles of the longitudinal musculature, where it is found in great quantity, becomes to a certain degree coagulated by corrosive sublimate, and then presents a finely granular appearance. Before this observation was made, no one had actually seen the body fluid, although previous investigators had assumed its existence.

existence of such fibrils, though I have worked with a larger number of preserving and staining reagents. He described the "Faserstrang" of the lateral chord in *Cerebratulus marginatus* as continued directly into the fibrous core of the ventral brain lobe; in *Lineus* I have found no such anterior continuation. Lastly, Bürger had not noticed the branching of the nerve tube (his "Faserstrang").

Rohde, who previously maintained ('90a, '90b) that the fibrillar structures of the dotted substance were the true nervous elements, has later ('92) abandoned this view and, following Leydig ('64), assumed the hyaloplasm to represent the nervous elements.

B. *Cerebratulus*.

The dotted substance of *C. lacteus* was studied on sections fixed with alcoholic solution of sublimate; and since I had no material hardened in Hermann's fluid I could not determine the course of the smaller nerve tubules, and only to a certain extent that of the neurochords.

The structure of the fibrous core of the lateral chords is illustrated by the Figs. 30, 35 *a-c*, 40; the same structure is found in the brain lobes, except that here the neurochords are absent. As may be seen in Fig. 40, which represents a lateral segment of a cross section out of about the middle point of the fibrous core of the lateral chord, the dotted substance consists, as in *Lineus*, of: (1) the staining fibres of the inner neuroglia cells (*NgI.C.*); (2) axis cylinders (*Ax.Cl.*) and their sheaths; (3) irregular, unstaining spaces between the latter which, in reference to what we have learned in *Lineus*, are probably filled with body fluid. But the fibrous core of the lateral nerve chords in *Cerebratulus* differs especially from that of *Lineus* in the presence of the colossal nerve tubules (neurochords of cells IV, *Ax.Cl. IV*, Figs. 30, 35 *b*, 40). I have found these neurochords to be pretty equally distributed throughout the fibrous core, though they are more numerous centrally and laterally than medially (Fig. 30). In the oesophageal region I traced for a considerable distance a neurochord, which was situated at the latero-ventral corner of the chord. The fibrous core pre-

sents a somewhat different structure in different portions of the lateral chord: thus anteriorly (Fig. 35 *a*) the finer nerve tubules preponderate in number, and but few neurochords occur, while more posteriorly (Fig. 35 *b, c*) the neurochords increase in number, which is due to their dichotomic divisions as well as to the accession of new neurochords from the cells IV placed along the chord, these cells becoming more numerous posteriorly.

Thus I have found no nearly central bundle of neurochords, such as Bürger (91b) has described, but rather individual neurochords of various diameters as well as the smaller nerve tubules (of cells II and III) throughout the whole diameter of the lateral chord. Although I did not observe a nerve tube in the lateral chord, such as has been described for *Lineus*, I would not thereby maintain the absence of such a structure in *C. lacteus*, since it might here easily be confounded with a neurochord.

VI. BRAIN COMMISSURES, OESOPHAGEAL NERVES.

The large ventral commissure of the brain which had been distinguished by the pioneers of nemertean anatomy, Delle Chiaje (1823) and Quatrefages (1846), has been supposed by all succeeding investigators to be the only ventral commissure. This large commissure may be termed, however, the *first ventral commissure* to distinguish it from two posterior commissures which are described here for the first time, and which may be termed the *second* and *third ventral commissures* respectively. In *Cerebratulus lacteus* the second ventral commissure arises from the fibrous core of each ventral lobe, just ventral to the oesophageal nerves, and one section behind the first pair of neurochord cells of the brain. It has scarcely one-fifth the diameter of the oesophageal nerve at this point, and, though it apparently has no special neurilemmatic envelope, is separated from this nerve by the neurilemmatic sheath of the latter. The nerve tubules of which this commissure is composed (probably those of cells II and III) are derived from the fibrous core of either ventral lobe. In *Lineus gessnerensis* (Fig. 43) this second ventral commissure (*Comm. 2*) has the same position and struc-

ture as in *Cerebratulus*; but in *L. sp.*, in addition to this second commissure, there is also a third ventral commissure (absent in the two preceding species) which is placed two sections (about 7μ) behind the second.

The paired oesophageal nerves of *Cerebratulus lacteus* ("vagus nerves," according to Hubrecht, who sought to homologize them with the vertebrate vagi), I find to have three commissures, as Bürger ('90b) has described for *C. marginatus*; while Coe ('95a), who also studied *C. lacteus*, saw only the third (largest) commissure. Each oesophageal nerve has its origin on the median side of the fibrous core of the ventral brain lobe, a short distance behind the first ventral commissure of the latter; the nerve is therefore, in point of origin, a posterior continuation of part of the fibrous core of the ventral lobe. In this core the nerve has its own sheath, which is a derivative of the inner neurilemma of the former. About five sections behind the second ventral commissure of the brain lies the *first commissure* of the oesophageal nerves, the latter commissure being but little thicker than the former. From this point on, these nerves are situated outside of the fibrous core of the brain lobe. Three sections behind the first lies the *second commissure* of the oesophageal nerves, which has the same diameter as the first. An equal distance behind the second is situated the *third commissure*, which is the last and much the largest of the three, both in length and diameter. Behind this last commissure the oesophageal nerves diverge from each other, as described by Hubrecht and Bürger, each passing downwards and outwards to occupy a latero-ventral position in the inner longitudinal muscle layer of the body wall, close to the oesophagus; in their course they give off a number of smaller nerves. The oesophageal nerves, both in the fibrous core of the brain as well as posteriorly, are enveloped by a neurilemmatic sheath, beneath which a few inner neuroglia cells lie (Fig. 43, *Oes. N.*). Ganglion cells are present only around the commissures of the nerves, most abundantly (though only in a single layer) around the third; these all are modifications of cells III of the brain lobes and have been already described (Fig. 20). The neurilemmatic sheath is absent only around the commissures.

In both species of *Lineus* examined the oesophageal nerves have four commissures, of which the fourth (last) is the largest, and accordingly corresponds to the third of *Cerebratulus*. The commissures are more widely separated in *Lineus*; otherwise the oesophageal nerves have the same structure as in *Cerebratulus*.

VII. GENERAL CONCLUSIONS.

1. To the central nervous system of the nemerteans belong the dorsal and ventral brain lobes, the lateral chords, the oesophageal and proboscidean nerves, and the dorsal, unpaired, longitudinal nerves.

2. All ganglion cells are membraneless and unipolar, and may be naturally divided into the four categories adopted by Bürger ('90b).

3. In all the ganglion cells one or two (never more) spherical nucleoli are present, which are readily distinguishable from the chromatin masses of the nucleus; in the latter an achromatic reticulation is also present. I found only one cell with two nuclei.

4. The cytoplasm of the ganglion cells consists of staining, more or less granular, but not fibrillar, spongioplasm, and unstaining, homogeneous hyaloplasm, the latter usually in excess, especially in the distal portion of the cell. The cell is bounded by a thin peripheral layer of fine-grained spongioplasm not in connection with the external neuroglia, and a similar layer envelops the nucleus; these probably represent superficial alveolar layers, and the structure of the cytoplasm a honeycombed meshwork, in the sense of Bütschli ('94).

5. In the cytoplasm of cells III in *Lineus*, homogeneous, deeply staining, more or less spherical bodies occur, which are never numerous, and have no regular arrangement in the cell; to these bodies, which cannot be classed with the chromophilic granules of other forms, the term *chromophilic corpuscles* has been applied here.

6. The axis-cylinder process is the same in all the ganglion cells; it represents a nerve tubule and not a "nerve fibril," and is composed of: (1) the homogeneous, unstaining axis

cylinder, which is probably of a fluid (or at least a viscid) consistency in life, and of (2) a fine spongioplasmic sheath enveloping the latter. The hyaloplasm of the axis cylinder is in direct connection with that of the cell, and its spongioplasmic sheath with the peripheral spongioplasmic layer of the latter. "Primitive nerve fibrils" are absent in the homogeneous axis cylinder, and the nerve tube is not composed of a bundle of separate "primitive nerve tubes" (Nansen), though in a few cases irregular strands of spongioplasm may penetrate from the cell into the most proximal portion of the axis cylinder. The nerve tubule gives off fine, unbranching collaterals, and decreases in diameter distally; it does not terminate in a number of brush-like processes. There is no structural difference between the proximal and distal portions of the nerve tubule, *i.e.*, no structural distinction into a proximal "ganglion-cell process" and a distal "nerve fibril."

7. The colossal nerve tubules of *Cerebratulus*, the so-called neurochords, differ from the other tubules (1) in their superior size; (2) in that they do not give off collaterals but divide dichotomously, the two branches formed by such division being of equal size; (3) in their segmental constrictions.

8. I found no substance resembling myelin in the nervous system.

9. The colossal ganglion cells (IV) of *Cerebratulus* (absent in *Lincus*) are present in three pairs in the ventral brain lobes, and are distributed irregularly along the lateral chords, but are wholly absent in both ends of the latter (namely, in the oesophageal region and in the caudicle). In the lateral chord they increase in number posteriorly, and are dorsally more abundant than ventrally; those in the one chord do not regularly alternate with, nor are they paired with, those in the other. The only apparent regularity in the distribution is that areas where they are comparatively numerous alternate with zones where they are relatively scarce.

10. In each lateral chord of *Cerebratulus*, but apparently not of *Lineus*, both dorsally and ventrally the radial clusters of cells II show a bilateral arrangement.

11. Ganglion cell III has structural affinities on the one hand to II, on the other to IV ; these three are probably motor cells.

12. In the fibrous core representing the so-called dotted substance the following components may be distinguished : (1) staining, dense, branching fibres of the inner neuroglia cells, these being the only fibrillar constituents of the dotted substance ; (2) nerve tubules and their sheaths ; (3) irregular, branching spaces filled with body fluid. In the lateral chord of *Lineus* is situated a longitudinally directed *nerve tube* near the center of the fibrous core, composed of a large number of individual nerve tubules. This nerve tube gives off smaller nerve tubes which pass to the peripheral nervous system ; anteriorly it is not continued into the brain. By no means all, probably not half, of the nerve tubules in the fibrous core are enclosed in this nerve tube, since a large number are distributed pretty evenly throughout the fibrous core.

13. The fibres of the outer neuroglia cells produce not only loose sheaths around the ganglion cells III and IV, but are also continued distally to form a sheath of Schwann around the nerve tubule ; this sheath, which is never occupied by nuclei, is not a continuous membrane, but apparently consists of a single layer of parallel fibres, which are separated from one another. The neuroglia of the nemerteans is fully comparable to that of the annelids or vertebrates, and stands in no relationship to the elements of the neurilemmatic sheaths.

14. In *Cerebratulus* and *Lineus gesserensis* there is a second ventral commissure of the brain uniting the ventral lobes, situated behind the first massive commissure, and of much smaller diameter. In *L. sp.* there is, in addition to the second, also a third ventral commissure.

15. In *Cerebratulus* there are three commissures of the oesophageal nerves, the third (most posterior) being the largest. In *Lineus* there are four such commissures, the fourth of which is the largest, corresponding to the third of *Cerebratulus*.

At the close of this brief study of the elements of the central nervous system of *Lineus* and *Cerebratulus* it is not my intention to enter into a discussion of the many views in regard to

the structure of the nervous elements in general; any one wishing to consult the rather voluminous literature on this subject may find more or less complete bibliographies given by H. Schultze ('79), Eisig ('87), Nansen ('87), Rohde ('90), and Friedländer ('89). But one point may be mentioned, namely, that the newer researches are tending to prove that the nervous element of the so-called "dotted substance" is a *nerve tubule* and not a *nerve fibril*; and that the fibrillar elements of this substance are derivatives of the neuroglia, or of other connective tissues. Whether, however, as Leydig ('85) maintains, the hyaloplasm alone represents "die eigentliche Nervenmaterie," we are not as yet in position to decide; for the nerve tubule consists not only of hyaloplasm (though this substance may preponderate), but also of spongioplasm. And unless one would side with Rohde ('90a, '92) in assuming — what seems very improbable — that the spongioplasm of the ganglion cell is formed entirely by neuroglia fibres, we must consider the spongioplasm as much a vital substance of the cell as the hyaloplasm, and therefore as much a vital part of the nerve tubule. Further, the dotted substance would appear not to be a "spongy meshwork" with confluent meshes, but to consist of nerve tubules (which do not anastomose), between which a fibrous neuroglia network is situated.

The structure of the axis cylinder has also been a subject of much controversy, and has been described (1) as homogeneous, (2) as fibrillar, (3) as consisting of a number of parallel "primitive nerve tubes," (4) as having a honeycombed meshwork structure. This difference of opinion is due to two reasons: (1) the study of different objects, and (2) the use of different technical methods on the part of the observers; for seldom has an investigator studied a number of different organisms and at the same time employed various reagents. Now because I have found the axis cylinder of the nemerteans to be homogeneous, it would be false reasoning for me to conclude that this structure holds good also in other forms. On the contrary, the researches on the vertebrate axis cylinder would show it to be fibrillar (with "primitive fibrils" enclosed in hyaloplasm); while in some of the invertebrates it would seem to be fibrillar,

in others homogeneous. *A priori* we would expect the axis cylinder, as any other organ, to be more highly differentiated in the higher forms than in the lower; and the facts would seem to be, indeed, that in some of the invertebrates it is homogeneous, while in the (higher) vertebrates it may be fibrillar. And at any rate it is always unsafe to conclude that if the axis cylinder, or any other nerve element, has a particular structure in one organism, the same structure must exist also in but distantly related forms.

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PHILADELPHIA, May 26, 1896.

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EXPLANATION OF PLATES.

The outlines of all figures, with the exception of the diagram 26, have been drawn with the camera lucida of Zeiss; and unless otherwise stated, have been made with homogeneous immersion $\frac{1}{2}$ of Zeiss, with ocular 4. The following abbreviations have been employed in the figures:

<i>Achr.</i>	achromatic substance.	<i>L.</i>	lateral.
<i>Alv.</i>	alveolar layer.	<i>l. Musc.</i>	longitudinal musculature.
<i>Ax. Cl.</i>	axis cylinder.	<i>L. V.</i>	lateral blood vessel.
<i>Ax. Cl. IV</i>	neurochord.	<i>M.</i>	medial.
<i>C. II</i>	ganglion cell II.	<i>Musc.</i>	musculature.
<i>C. IV</i>	ganglion cell IV.	<i>N.</i>	nucleus.
<i>Chr.</i>	chromatin.	<i>n.</i>	nucleolus.
<i>Cl. II</i>	cluster of cells II.	<i>Ngf.</i>	neuroglia.
<i>c. Musc.</i>	circular musculature.	<i>Ngf. C.</i>	neuroglia cell.
<i>Coll.</i>	collateral of nerve tubule.	<i>N. S.</i>	nuclear sap.
<i>Comm. 2</i>	second ventral commissure of brain.	<i>N. T.</i>	nerve tube.
<i>D.</i>	dorsal.	<i>Oes. N.</i>	oesophageal nerve.
<i>D. V.</i>	dorsal blood vessel.	<i>o. Neur.</i>	outer neurilemma.
<i>F.</i>	spongioplasmic fibre.	<i>P.</i>	pore (opening) of inner neu- rilemma.
<i>F. C.</i>	fibrous core.	<i>Prob.</i>	proboscis.
<i>G. C.</i>	ganglion-cell layer.	<i>Sp.</i>	space containing body fluid.
<i>Gr.</i>	chromophilic corpuscle.	<i>Sp. Pl.</i>	spongioplasm.
<i>Hl. Pl.</i>	hyaloplasm.	<i>S. Sh.</i>	sheath of Schwann.
<i>i. Neur.</i>	inner neurilemma.	<i>V.</i>	ventral.

EXPLANATION OF PLATE XXIV.

FIG. 1. *Lineus gesserensis*: ganglion cell I. Sublimate, Del. haematoxylin + eosin.

FIG. 2. *Ibid.*: ganglion cells II. Sublimate, Del. haematoxylin + eosin.

FIGS. 3-10. *Ibid.*: ganglion cells III. Sublimate, Del. haematoxylin + eosin.

FIGS. 11, 12. *Ibid.*: ganglion cells III. Sublimate with acetic acid, Ehrl. haematoxylin + eosin.

FIG. 13. *Ibid.*: ganglion cell III. Flemming's fluid, Del. haematoxylin + eosin.

FIG. 14. *Ibid.*: ganglion cell III. Hermann's fluid, Ehrl. haematoxylin + eosin.

FIGS. 15, 16. *Lineus sp.*: portions of ganglion cells III. Sublimate, Del. haematoxylin + eosin.

FIG. 17. *Cerebratulus lacteus*: The two modifications of ganglion cells I. Sublimate, Del. haematoxylin + eosin.

FIG. 18. *Ibid.*: ganglion cells II, from the ventral side of the ventral brain lobe. Sublimate, Del. haematoxylin + eosin.

FIG. 19. *Ibid.*: an unusually large ganglion cell III from the dorso-ventral brain commissure. Sublimate, Del. haematoxylin + eosin.

FIG. 20. *Ibid.*: ganglion cell III from third commissure of the oesophageal nerves. Sublimate, Del. haematoxylin + eosin.

FIG. 21. *Ibid.*: ganglion cell III with two nuclei, from lateral side of ventral brain lobe. Sublimate, Del. haematoxylin + eosin.

FIG. 22a-c. *Ibid.*: nuclei of ganglion cells III. Sublimate, Del. haematoxylin + eosin.

FIG. 23. *Ibid.*: ganglion cell intermediate between III and IV, from the ventral side of the lateral chord. Sublimate, Del. haematoxylin + eosin.

FIG. 24. *Ibid.*: part of a cross section of the ventral lobe of the brain, showing the position of the first pair of ganglion cells IV of the brain. Obj. A, oc. 4.

FIG. 25. *Ibid.*: cross section of a lateral nerve chord, close behind the mouth region, showing radial clusters of ganglion cells II. Obj. C, oc. 2. Sublimate, Del. haematoxylin + eosin.

FIG. 26. *Ibid.*: diagram to illustrate the regular arrangement of the cell clusters of cells II (*Cl. II*) and their respective openings (*P.*) in the inner neurilemma, on either the dorsal or the ventral side of the lateral nerve chord; *X-X*, the imaginary median plane of symmetry.

EXPLANATION OF PLATE XXV.

FIGS. 27, 28. *Cerebratulus lacteus*: ganglion cells IV (neurochord cells) from the lateral chord. Sublimate, Del. haematoxylin + eosin.

FIG. 29. *Ibid.*: ganglion cells III and IV, from the dorsal side of the lateral chord. Sublimate, Del. haematoxylin + eosin.

FIG. 30. *Ibid.*: portion of a horizontal, longitudinal section of the fibrous core of the lateral nerve chord, from the middle body region. Sublimate, Del. haematoxylin + eosin. Obj. C, oc. 4.

FIG. 31. *Ibid.*: Nuclei of ganglion cells IV. Sublimate.

a, b, from the lateral chord. Ehrl. haematoxylin + eosin.

c, d, of the right and left cells IV of the first brain pair. Del. haematoxylin + eosin.

e, from the lateral nerve chord. Del. haematoxylin + eosin.

FIG. 32. *Ibid.*: two contiguous ganglion cells IV, from the lateral chord; their respective nerve tubules not situated in the same plane. Sublimate, Del. haematoxylin + eosin.

FIG. 33 *a-c*. *Lineus gesserensis*: outlines of the nerve tube of the lateral nerve chord on four consecutive cross sections, to show its manner of branching. Hermann's fluid.

FIG. 34. *Ibid.*: outline of a cross section of the fibrous core of the lateral nerve chord, to show the position of the nerve tubes (*N. T.*). Hermann's fluid. Obj. C, oc. 4.

FIG. 35 *a-c*. *Cerebratulus lacteus*: transverse sections of the right lateral nerve chord. Obj. C, oc. 4. Sublimate, Del. haematoxylin + eosin.

a, from the oesophageal region.

b, behind the middle body region.

c, from the anterior portion of the caudicle.

FIG. 36. *Lineus gesserensis*: cross section of the fibrous core of the lateral chord, in the anterior oesophageal region. Hom. immers. $\frac{1}{2}$, oc. 2. Hermann's fluid, Ehrl. haematoxylin + eosin. In this, and in Figs. 37, 38, the appearance of the preparation has been reproduced, the white lines representing the unstained axis cylinders, and the dark ground (which should be of a bronze color) the deeply staining, non-nervous substance of the fibrous core; seen with this magnification, this staining matrix appears nearly homogeneous.

FIG. 37. *Ibid.*: cross section of the fibrous core of the dorsal brain lobe. Hom. immers. $\frac{1}{2}$, oc. 2. Hermann's fluid. (Cf. explanation of Fig. 36.)

FIG. 38. *Ibid.*: frontal section of the fibrous core of the first ventral commissure of the brain. *a*, the branch towards the dorsal lobe; *b*, that to the ventral lobe. Hom. immers. $\frac{1}{2}$, oc. 2. Hermann's fluid. (Cf. explanation of Fig. 36.)

FIG. 39. *Ibid.*: portion of a thin cross section of the fibrous core of the dorsal brain lobe. Hom. immers. $\frac{1}{2}$, oc. 4, tube extended. Hermann's fluid $\frac{1}{2}$ hour, Ehrl. haematoxylin + eosin.

EXPLANATION OF PLATE XXVI.

FIG. 40. *Cerebratulus lacteus*: segment of a cross section through the lateral side of the fibrous core of the lateral nerve chord, from about the middle body region. Sublimate, Ehrl. haematoxylin + eosin.

FIG. 41. *Tetrastemma vermiculum*: portion of a horizontal, longitudinal section of a lateral nerve chord (only the outlines drawn), showing a supposed nerve tube (*N. T. ?*) stained with methylene blue. Sublimate, aq. sol. of methylene blue 10 minutes, aq. sol. of brasilin 40 minutes.

FIG. 42 *a-e*. *Cerebratulus lacteus*: portions of longitudinal sections of neuro-chord tubules, from the fibrous core of the lateral nerve chord, behind the middle body region. Sublimate, Del. haematoxylin + eosin.

FIG. 43. *Lineus gesserensis*: portion of a cross section of the posterior ventral portion of the brain, showing the second ventral commissure. Obj. C, oc. 2. Hermann's fluid.