THE BRAIN OF THE BEE

A PRELIMINARY CONTRIBUTION TO THE MORPHOLOGY OF THE NERVOUS SYSTEM OF THE ARTHROPODA.

By F. C. Kenyon, Ph.D.,
Fellow in Biology, Clark University, Worcester, Mass.

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Introduction.

Since Viallanes' (88) monograph on the brain of the grasshopper (*Oedopoda* and *Caloptenus*) and the smaller but as excellent work of Cuccati on the organization of the brain of *Somomya* appeared nothing has been added to our knowledge of the structure of the hexapod brain. In fact no one seems to have worked at the subject. Such being the case, my endeavor by an application of one of the more recent histo-neurological methods to bring this subject into line with what is now known relative to the stucture of the central nervous system of several other *invertebrates* and more especially of the *vertebrates* will doubtless be appreciated. Here, as elsewhere, an application of the chief of the two recent methods, namely that of Golgi, brings to light facts before known only from inference, and also often materially alters conceptions based wholly upon the older methods of staining. A detailed history of the matter in hand is therefore needed, but since it would add too much to the length of the present paper, the pretentions of which as indicated in the title are very limited, little more than a reference here and there will be given. This course is doubtless excusable since Retzius (**90**) has already given a summary to which the reader may be referred. Three papers that have appeared since the publication of this author's work may, however, be noted.

The first of these is the paper by Saint-Remy (**90**) on the brain of tracheate arthropoda. In this the author describes the brains studied histologically of myriopods, chilopods, arachnids and *Peripatus*; but although the work is comprehensive and fills a void in our knowledge of the arthropod nervous system, it is far from treating the subject with sufficient depth, a deficiency mostly due to the method of staining employed. The nerve cells, or cell bodies, following Dietl, he divides into two groups, one composed of large cells well supplied with extra-nuclear protoplasm and with relatively small nuclei having few chromatin elements, the other of small cells having little or no extra-nuclear protoplasm and relatively large nuclei richly supplied with chromatin elements and restricted to certain cerebral areas. To the latter he applies the term chromatin cells in preference to the ganglionary nuclei of Dietl and others.

Two small nerves that he describes for the myriopods may be passed by with the remark that one, namely the nerve of Tömösvary appears to have no homologue in the hexapods unless it be the small nerve mentioned by Newton (**79**) as arising from the front of the brain of the cockroach and terminating in a small organ near the base of the antenna. The other, or tegumentary, nerve may be the homologue of the tegumentary nerve described by Viallanes (**88**) for the grasshoppers and consequently, as will be shown in subsequent pages, the homologue of the salivary nerve that I have traced out in the bee.

The most interesting discovery recorded in the paper is that of structures found in the brain of *Scutigra* that he describes as mushroom bodies. The term he bases upon their form and not upon an idea of their being the homologues of the organs of the same name found in the hexapods. But from the fact that their cells are of the chromatic cell type and similarly situated and also from the fact that he seems able to recognize nearly all the parts generally described in the organs in the hexapods it may here be suggested that they may possibly be the homologues of these latter organs. There is needed, however, a more minute and painstaking study than St. Remy has given the structures before one should come to a definite conclusion as to their homologies.

The second of the three papers is that by Viallanes (93) on "The neural centers and sensory organs of articulates" and is mainly of interest here in showing this author's conception of the minute structure of the nervous system. In his earlier papers he did not touch upon the matter, but in his last paper one finds him following St. Remy's grouping of the cells and adding a few ideas upon the finer structure of the fibrillar substance. These ideas were doubtless founded more upon the general results obtained with the methylen blue and the Golgi methods, which by this time had become very generally known, than upon any observations of his own made by the aid of his methods of staining.

He describes and figures diagrammatically three kinds of fibers. One of these, of large size, originates from large cells and passes outside of the central nervous system after first giving off in the latter a few short and fine branches. These he calls motor fibers. Another kind, of much smaller size, enter from cells outside the central system and branching more or less profusely connect with the small branchlets of the first, forming thus the terminations and connections of sensory fibers.

The third kind are short, small fibers originating from the chromatin cells and, branching profusely, connect with the fine branchlets of the other two kinds of fibers. As will be seen in subsequent pages, this general idea is supported by facts, though, as indicated above, it was with Viallanes almost purely hypothetical.

The last of the three papers is one by Binet (94). This author so far as the structure of the dorso-cerebron is concerned seems to follow Viallanes without a question, and deals almost wholly with the ventral system, which he treats anatomically and physiologically. He seems to have added a few new facts to our knowledge of the subject treated, although he leaves very much still to be done. The points at which he seems to have erred or where his treatment is deficient will be noted, when they are closely related to the matter in hand, in subsequent pages. Here it may be noted that he seems to have obtained the beginning of a correct idea of the constitution of the arthropod nervous system based upon the work of Retzius and others employing similar methods; but, failing completely in his use of the Cajal-Golgi method and obtaining but litttle better results with methylen blue, he concludes that, since in any one preparation neither of these methods brings out the whole structure they are not to be depended upon, and then passes on to a dependence upon a modification of the old method of Weigert and becomes lost in the mass of detail that he so much desired to obtain.

The results of other writers will be noted in connection with the descriptions of the structures with which their works deal.

MATERIAL.

The material used has been almost exclusively the common honey bee (*Apis mellifica*), which was at hand in abundance, for which I owe many thanks to Dr. C. F. Hodge. Possibly a thousand or more brains were treated by several of the bichromate of silver methods, and of this number scarcely more than fifteen or twenty per cent. were found successfully impregnated.

METHODS.

Aside from impregnation with bichromate of silver, the methods that I have employed are various, and among these the one that has given the best results, brought details to light most beautifully, has been one using sulphate of copper and hæmatoxylin with brains hardened in from 10 to 20% formol for twenty four hours or longer. Such preparations show the axis-cylinders as purplish-brown fibers within their surrounding slightly bluish sheaths, the nuclei of the latter and of tracheæ, the tracts of nerve fibers and some of the association fibers, clearly marked off from the surrounding ground work of fine branchlets forming the *Punktsubstanz* of the older German writers and the medullary substance of Viallanes. The structure of the cell bodies and their nuclei is also well brought out.

In some cases the freshly excised brains were dropped into 10 to 20% formol, in others they were placed in the following mixture, which gave just about as good results:

10% Potassium bichromate,	40 parts.
5% Sulphate of copper,	40 parts.
Formol, . .	20 parts.

This might be improved by leaving out the bichromate, which is rather unnecessary since the formol likewise has the property of rendering the components of animal tissues insoluble in water and alcohol.

Brains hardened in this mixture were washed for from a little while to some hours in tap water, then for from a few to twenty four hours in 70% alcohol, after which they were dehydrated, imbedded in paraffin, sectioned and stained on the slide in the hæmatoxylin.

In the other cases the sections of the formol-hardened brains were treated with the sulphate of copper (5%). In a solution of this they were left for from a few to twenty four hours or in a warmed solution for from 20 to 30 minutes. They were then washed off in tap water and stained.

The hæmatoxylin mixture that gives the best results is one containing phosphomolybdic acid, though the plain alcohol-water hæmatoxylin used in the method of Weigert and its modifications gave good results for certain details in the roots of the mushroom bodies. The former mixture is that suggested by Mallory and is composed as follows:

10% Phosphomolybdic acid	1 c.c.
Hæmatoxylin crystals	1 grm.
Chloral hydrate .	6 to 10 grm.
Water . . .	100 c.c.

Enough of this was added to a dish of water to give the latter a black appearance, or it was diluted about 1 to 5. From a quarter of an hour to an hour is required for staining. The sections hardened in the potassium bichromate mixture require a longer time than the others.

After staining, the sections were washed off with 70% alcohol and dehydrated or, if too deeply stained, left in the 70% alcohol for some time. With the dilute solution, however, there is not much danger of overstaining, if the process is watched.

For impregnation with bichromate of silver the rapid method of Cajal was at first employed, but only later to be set aside when it was discovered that one in which the osmic acid is replaced by formol gives a much more transparent background for the darkened fibers and cells, thus allowing much thicker sections to be cut, while at the same time retaining the rapidity that has made the osmic acid mixture so excellent. At first the osmic acid was replaced by the same amount (one-fifth) of pure formol, later Strong's suggestion of equal parts of 10% potassium bichromate and formol was followed. This was then modified to 5% bichromate and a smaller amount of formol as follows:

5% bichromate,	80 cc.
Formol,	20 cc.

This gave impregnations as good as the stronger and a little better than the weaker combination while at the same time lessening the formation of a black precipitate that is always found in formol-bichromate mixtures after they have stood some hours. This precipitate was avoided as much as possible by changing to fresh fluid every twenty-four hours. Impregnations may be obtained in brains left unchanged in the mixture until ready for the silver solution. The precipitate must however weaken both the formol and the bichromate and hence operate disadvantageously. I think my failures were more numerous with brains left in the unchanged fluid, (though no experiments were undertaken to settle the matter definitely,) and hence I am not inclined to agree wholly with Kopsch (**96**) when he asserts that the precipitate makes no material difference.

Like this writer, I also found that twenty-four hours in the formol-bichromate is sufficient for hardening and that tissues may then be transferred to pure bichromate. He employed a 3½% solution, however, while I, since it seemed to act more quickly, used a 5% solution.

From three to four or five days immersion in formol-bichromate are necessary for obtaining impregnations of nerve fibers, and almost three for the cells, while the tracheæ may be incrusted almost to the exclusion of nerve fibers after one or two days.

The more or less inevitable precipitate and crystals were of course met with, but on the whole my preparations were comparatively free from them. In fact, judging from the printed experiences of others, I seem to have been more favored than is usual. Only a few cases occurred out of the hundreds of brains sectioned where the precipitate at all resembled the fine branching of the nerve fibers, and in these there was no ground for a deception of the practiced eye, for the angular contours of the precipitate readily distinguished it from the rounded ones of the fibers.

The precipitate gave the greatest annoyance in the layer of cell-bodies. This is so thin on the more exposed parts of the brain that it was usually completely obscured when the brains were brought into direct contact with the fluids. Attempts were made to obviate this difficulty. Formic acid was tried and discarded, as was also Berkeley's (95) suggestion of adding a few drops of phosphomolybdic acid to the silver solution just before using. The latter can, in fact, do nothing more than weaken the solution of silver nitrate, and one may therefore as well take a weaker solution to begin with. When this is done and the tissue, after first quickly washing off the bichromate with water, is carefully rinsed in the weak solution, or one that has been previously used, before it is allowed to stand, one will be much less troubled with the incrustation.

This method did not prove as good, however, as one in which the brain was left *in situ* in the head, enough only of the front, top, or side of which was cut away to allow the fluids to enter. In such cases the part most exposed would be incrusted, while that opposite would be entirely free. Other methods were thought of and tried. That of wrapping a brain in filter paper was considered too rough a treatment; covering a brain with celloidin failed. Had the one suggested by Retzius (**92** *b*), namely, of dipping a brain in warm gelatine, been thought of or known in time, it would doubtless have given excellent results.

The nitrate of silver was employed in strengths ranging from ½% to 2%. The stronger solutions, though giving stronger impregnations, less evidence of beading, or fuller fibers, have the disadvantage of being more inclined than the weaker solutions to form artifacts. A solution of 1% strength was finally adopted for leaving the specimens in over night or until I was ready to section them.

Generally only one or two immersions in the fluids was given the specimens, since it was desirable to have only a few fibers impregnated so that very thick sections could be cut and thus give the entire trajectory or as much as possible of a fiber unobscured by other details.

The impregnated brains were transferred to absolute alcohol and then to celloidin. Where they were entirely free from the head or from chitinous particles that would tend to prevent them from becoming fairly saturated or surrounded with the celloidin, sections wese cut within two hours from the removal from the silver solution. But where they were surrounded by the chitinous cephalic capsule from six to twenty-four hours were found necessary to form a celloidin block of a consistency sufficient to prevent tearing and breaking of the sections.

Sections were cut all the way from twenty to two hundred and ten microns thick, thus, in the thickest, making only three or four frontal sections to a brain.

General Description.

External appearance.

Under the general term "brain" I here understand the whole of the neural mass included within the head, excepting only the two small ganglia generally known as the stomatogastric ganglia. The optic lobes and the subœsophageal ganglion are part of it. There is no real ground for leaving the latter portion out as is generally done under the term subœsophageal. Even when it is widely separated from the larger mass and is to be found crowded back into the pro-thorax, there is abundant reason, as shown by the physiological experiments of Binet (94) and others, for retaining this portion under the general term brain. Hence in subsequent pages it will be referred to as the ventro-cerebron in contrast to the super-intestinal portion or dorso-cerebron.

The optic lobes will be omitted from this paper for consideration in a later one.

The bee's brain thus limited is, roughly speaking, when viewed from the front, a quadrilateral structure, with rounded angles. Setting aside the ventro-cerebron, which projects backward, it is considerably compressed antero-posteriorly (Pl. XX), and abuts closely against the middle upper portion of the posterior walls of the head, leaving a very considerable space in front filled with tracheal air-sacs and the whitish, often yellowish or orange racemose bunches of the salivary glands. These latter organs also fill in the smaller spaces behind the brain and are closely applied to it. On the dorsal side are three small protuberances (Pl. XVII, XX) with black tops, or the so-called ganglia of the ocelli. Below in the lower third the brain is pierced by a large oval opening, the œsophageal foramen, with its largest axis vertical. Near the roof of this is the longitudinal median nerve of the stomatogastric system. On either side and below the foramen are the rather conspicuous antennal lobes forming the greater portion of what has been described as the deuto-cerebron. The ventro-cerebron, as already mentioned, projects considerably backwards, but it is so closely united with the dorso-cerebron by extremely thick and short œsophageal commissures that it is very readily recognized as part of the brain. So compact is this deuto-trito-cerebral portion of the brain that were it not for the fact that the labral nerves are recognized as arising from it, indications of the trito-cerebral lobe would be recognizable only in sections. Even in these its boundaries are indefinable.

THE CEREBRAL NERVES.

From the lower side of the antennal lobe there is given off the large antennal nerve, which passes forward and slightly downward to the entrance of the antennæ. From the lower surface behind the origin of the large nerve there originates a small one that may be readily traced in sections to the antennal muscles within the head. This, which I will denominate the *antenno-motor internus*, in contradistinction to the other, or *antenno-motor externus*, was first discovered and traced to its termination in the muscles by Newton (79) in his study of the brain of the cockroach. It is described by Viallanes (87) in his paper on the brain of the wasp as the "nerf antennaire accessoire" and was correctly identified by him with the nerve described by Newton, although he was unable to trace it to its termination in the muscles. Doubtless it may be found as a separate nerve in all tracheate arthropods. One occupying the same position I have recognized in *Scalopendrella immaculata* and traced into muscles that I supposed to belong to the antennæ.

Behind this internal antenno-motor nerve and immediately behind the base of the antennal lobe there is a somewhat larger nerve that I have traced towards the mouth-parts of the bee and from its position take to be the labral nerve. This arises from the trito-cerebron and may be seen in fragment in the photograph (fig. 2, Pl. XIV), which is of a section slightly too far forward to show the lobe and the entering nerve root.

From the lower side of the ventro-cerebron (Pl. XX) there arise not far apart from each other three pairs of large nerves that like the one just described may be readily traced to the mouth parts. Since in most of my preparations these parts were cut away to allow a free access of the fixing fluids to the brain or to free the object as much as possible from chitinous parts to avoid tearing during the process of sectioning, I have not yet traced the nerves to their endings. From their position, however, I infer them to be the mandibular, maxillary, and labial nerves. From the posterior lower surface of the ventro-cerebron there arises a small seventh pair of nerves directed backwards and downward toward the region just below the foramen magnum. Just how they terminate or what their function may be I have not thus far been able to determine. They were seen by Viallanes (87) in the wasp, but were left as now still to be traced.

In his monograph on the brain of the Orthoptera, Viallanes (88) described under the name of "nerfes tegumentaires" a pair of nerves emerging from the surface of the brain and passing on to the roof of the head. These appear to be nothing more nor less than a pair of nerves that he found in the wasp the year before and described as nerves of unknown terminations.

This eighth pair of nerves is readily seen and traced in the bee and one may be recognized in section in the lower photograph in plate XVI. Both in bichromate of silver and in hæmatoxylin preparations I have been able to trace out its entire course and to show that Viallanes' denomination of tegumentary nerve is entirely a misnomer. It arises from the side of the ventro-cerebron where its root enters the latter, passes in, somewhat downwards and backwards, towards the median line of the latter, makes a turn backwards and becomes lost in the general mass of fibrillar substance. The nerve (Pl. XVII) closely adhering to the posterior surface of the brain and beneath the general envelope of the latter passes outwards and upwards until it reaches the upper portion of the posterior surface of the inner or third optic fibrillar mass or ganglion, where it branches. One branch continues almost perpendicularly upwards, passes out of the brain envelope and branches among the lobes of the salivary glands. In bichromate of silver preparations the branches may be followed into the lobes, but I have not yet seen the finer terminations. The other large branch continues outward along the supero-posterior surface of the optic lobe, branching and leaving the envelope from time to time, and may be followed to the basement membrane of the retina where it finally emerges to pass into the glandular lobes situated in proximity to that structure. The nerve, then, instead of having anything to do with the integument, is the nerve to the salivary glands, and is doubtless made up entirely of efferent fibres.

The small pair of nerves described by Newton (79) as arising from the anterior surface of the brain in *Blatta* and going to the small white spot near the base of each antenna, are not, so far as I have been able to discover, represented in the bee.

THE GENERAL INTERNAL STRUCTURE.

Internally the brain is composed of a mass of very fine fibrils scarcely recognizable as such in ordinary preparations, which is very well called fibrillar substance. The upper portions of the anterior surface of this below the mushroom bodies to be described later and the corresponding part of the posterior portion of each of the two lateral lobes are directly covered by the membrane forming the perineurium. But in the region of the mushroom bodies, laterally, in the posterior median furrow, and below, about the greater part of the antennal lobes, filling the space between these and the proto- cerebron, and the lower and lateral surface of the ventro-cerebron (the upper surface of the latter is bare) it is covered by heaps of cells which spread out into layers of only one or two cells deep. Processes from many of these cells are gathered into large bundles which, penetrating the fibrillar substance, give it—both the brain and the ventral system as seen in sections—a lobular appearance that has been the subject of no inconsiderable amount of painstaking and lengthy and as tedious description, notably by Viallanes, and later by Binet (94) in his paper on the sub-intestinal nervous system of insects. The fibers thus entering become lost in the fibrillar substance by repeated branching or continue first to more distant parts, thus forming connecting tracts. This relation of the fibrillar substance and the fibers may be readily seen in the accompanying photographs, and in most preparations by ordinary staining methods. The assistance of the method of impregnation with bichromate of silver or that of intra-vitam staining with methylen blue is necessary to determine the relations of cells, fibers and fibrillar substance completely.

THE TYPES OF NERVE CELLS.

By the assistance of the bichromate of silver method we may imagine a cell with a nerve fiber dividing at some distance from the cell body into two branches that form with it a T or a Y as probably the most typical of the nerve cells of the bee, or probably of arthropods in general. The assertion does not hold good completely, for there are cells in the optic lobes and even in the central part of the brain in which all the branches given off appear as very small branches of large fibers.

To classify for convenience of description the various modifications met with in the brain one may divide them into:

1. *Afferent* or *sensory fibers* in which the cell body is situated somewhere in the neighborhood of the external (to the brain) organ of sense and sends its neurite into the brain and its dendrite into the sense organ. Such cells may be called bipolar, and in them, as in all other nerve cells, the only criterion of the difference between dendrite and neurite is in the direction of the passage of the neural impulse with reference to the cell body, or to the trunk of the fiber leading to the cell body. Such fibers do not penetrate far into the brain, where they may terminate in a mass of fine branchlets as in the case of the fibers from the antennæ. In other fibers the terminal branching is more or less loose or not massed together, as in the case of whatever sensory fibers there are entering through the labral, mandibular, maxillary and labial nerves or from the ventral cord.

In the accompanying diagrams this class of fibers and all others bearing sensory stimuli into the portion of the brain here considered, as from the optic lobes and the ventral cord, are colored blue.

2. *Connecting fibers* in which the cell body is situated to one side of the track of the passing stimulus—assuming that it does not necessarily go to the cell body—and in which the dichotomous T- or Y-shaped branching is most easily recognizable. The peripheral of the two branches connects with the

terminations of the sensory fibers of the first class and, since it bears the transferred impulse inward, may be called the dendrite. Usually it is shorter than the other branch that, with others of its kind, passes as a tract of fibers through the fibrillar substance to the mushroom bodies, in which it breaks up into a bushy or arborescent mass of branches, or to other parts of the brain, where the branching is of a more open kind.

The fibers connecting the sensory fibers of the antennal lobes with the mushroom bodies are most typical of this class. Others that must be classed along with them enter from the optic lobes and along with them are represented in violet in the diagrams. Others found connecting the central body, later to be described, are doubtless to be classed here, since this body seems to be in connection with the fibers of the ocelli; but owing to the unsatisfactory condition of my present understanding of this body have been left in black. The mode of branching at the ends of the dendrite is represented in fig. 15, Pl. XXI, while the branching terminals in the mushroom bodies are shown in figs. 17, 18, 21, of the same plate. Most of these fibers appear to be provided with a nucleated sheath.

The representation of fibers found in the central body in figs. 32, 37, Pl. XXII, by comparison with figs. 17 and 21 of the preceding plate, which beyond a doubt represent the receptive terminations, would seem to indicate that the former are dendritic. Fig. 18, Pl. XXI, shows the terminations of the neurite-branches in the mushroom bodies as seen under a magnification of 586 diameters.

3. *The cells of the mushroom bodies.* These fall under the head of Y-shaped cells and consequently follow the class just described, but will be left for consideration along with the bodies which they largely compose. They are represented in red.

4. *Efferent fibers* which originate from cell bodies situated within the brain and bear efferent stimuli to muscles, glands or to cells outside of the brain are represented in the diagrams in brown. The cells of this order seem to depart widely from the simple T-shaped general type as is shown in fig. 36, Pl.

XXII, which represents the best specimen of motor cell that my preparations offered. That it is motor in nature is assumed from its general appearance, resembling to a certain extent the motor fibers described and figured by Bethe (95), and the fact that it is cut off near the cut end of a large fiber not figured that passes into the antenno-motor nerve and with which it appears to have been continuous, but on account of a slight bend outside the plane of the razor was cut in two. This appeared in a nearly sagittal section. In a thick section cut in the frontal plane, or nearly transversely to the main axis of the animal's body, fibers were seen, such as one represented in Plates XVII and XX, sending a process into a tract of fibers that appeared to pass down behind the antennal lobe, apparently into the root of the antennal nerve, which were therefore thought to be motor fibers. Combining these two with what was seen of fibers in other sections in about the same locality as the motor cell mentioned it would appear that the large motor cells send a process into the fibrillar substance, which almost immediately gives off small branches that may end at a considerable distance from their point of origin. The process becomes very much enlarged for a considerable extent of its course and may even send off branches of considerable size before passing on into the root of a nerve as a small fiber.

5. *The commissural fibers*, which are doubtless of the general T-shaped form, though I have not been able to find their cells of origin. They pass from one side of the brain to the other and may be represented by the fibers composing the superior commissure. The fibers composing the so-called commissure of the optic lobes may possibly also be classed here. Other fibers there are in plenty than those gathered into tracts passing between the two halves of the brain, but they are better classed with the next group.

6. *Association fibers* seemingly serving the purpose of connecting the elements already described with one another. These are mostly large profusely and irregularly branching forms some of which are shown in plate XXII. In some cases I have been able to make out the cells of these, in others I have not.

They all form a promiscuous group that might be, but for lack of a better knowledge of them and their cells of origin, may as well not be, subdivided. Almost all of them are known only from fragments of which those shown in plates XXI and XXII are the best examples. Some of them may possibly even be fragments of motor-fibers.

To these groups may be appended two others, one represented by the enormous fibers from the ocelli and the other by the equally enormous fibers situated near the dorsal surface of the ventral system and of the ventro-cerebron. They will be considered in connection with the ocellar nerves.

THE CONNECTIONS BETWEEN NERVE FIBERS.

What facts I am able to bring forth bearing upon the "contact" idea and the old "mesh-work" idea of the fibrillar terminations, though more properly considered here, I will defer until I have described the mushroom bodies, in connection with which the facts mentioned occur.

TRACHEÆ.

Besides these neural elements and the sheaths surrounding some of them, there are to be found large numbers of tracheal fibers. In bichromate of silver preparations they are the first elements to become impregnated and then are brought plainly into view. The larger branches may be very readily recognized in hæmatoxylin preparations. Their general tapering form and the time of their taking up the bichromate of silver prevents their becoming confounded with nerve fibers.

To explain their origin it must first be noted that the brain of the bee is surrounded by a number of tracheal sacs, the inner walls of which closely cover it. Here and there tracheal outgrowths from the sacs especially in the neighborhood of the cell clusters pass into the brain. They branch more or less profusely among the cells and then send smaller branches into the fibrillar substance as shown in fig. 29, Pl. XXII, which represents a camera drawing of the tracheæ of one of the mushroom bodies. Tracheæ almost identical in appearance with these, are found on all sides of the brain. Others, however, of a larger size are also found that enter into the fibrillar substance more deeply, and gain their entrance along with some nerve fiber or bunch of fibers.

In no case have I been able to make out a tracheal network such as described by Emil Holmgren (95) for the spinning glands of lepidopterous larvæ. So far as bichromate of silver preparations thus far made show, the branchlets all terminate independently of one another. In some of my copper-hæmatoxylin preparations there are, however, certain details that recall Holmgren's figures which lead me to suppose that a tracheal network may exist.

Special Description—the Proto-cerebron.

THE MUSHROOM BODIES.

From this hasty general account of the brain and its constituent elements I pass to a more detailed consideration of its parts and choose for the first the mushroom bodies as being the most conspicuous and as the better serving for the orientation of other parts later to be described.

These organs were first noted by Dujardin (50) in a study of transparent preparations *in toto*. From their slightly lobular or folded appearance he compared them with the convolutions of the human brain and described them as "lobes à convolutions" probably associated with the intelligence of the insect. As will be seen in the sequel, this supposition has very much more in its support than the crude or undeveloped morphological technique of that time was capable of bringing to light. Later they were again found by Leydig (64) who mentions them under the term "Gestieltes Körper." They were again described by Rabl-Rückhard (75) who, according to Viallanes (87), first correctly described the calyx. But it was not until Dietl (76) had applied microtomy and stained his sections with osmic acid that a complete description of their whole structure was obtained. Since that time they have been so often re-described for insects representing the different orders of hexapods that they may be considered as fairly well known structures very characteristic of—especially the higher—hexapods. Special swellings found on the brains of certain of the crustacea have been compared with them, but it is to be seriously doubted, I think, whether such swellings or cellular heaps are properly to be homologized directly with them. In neither Retzius' (**90**) figure of the brain of *Astacus fluviatilis* nor in Bethe's figures of the brain of *Carcinus mænus* can I find cells having the relations and the appearance of those that I find in the bee. I have noticed nothing resembling the structures in isopods, or amphipods, nor I have found indications of them in the brains of *Pauropus*, *Polyxenus*, juloid diplopods, *Scolopendrella*, *Lithobius*, nor even in several forms of *Thysanura* that I have examined. If cells homologous with those filling the cup-like calyx of the mushroom bodies of the bee are at all present in these forms, they are so undifferentiated as to be indistinguishable from the general mass of cells about them.

The Calyx-Cup.

The four bodies that in the bee and the Hymenoptera in general constitute what may be called the calyx-cup form the upper portion of the proto-cerebron, and are arranged side by side, a pair to each lateral lobe. In section, as shown in the photographs of Plates XIV and XV and in optical section in transparent unsectioned preparations, they are very noticeable from the curved masses of fibrillar substance that form the base and walls or calyx of each making them resemble optical sections of so many cups. Each cup holds a mass of cells that fill it to the brim. The walls of each lateral pair are nearly or quite contiguous, except distally where they diverge from one another leaving a space filled with a mass of small cells, as is also the space between each outer cup and the inner fibrillar mass of each optic lobe. Viewed from above they would appear elongated antero-posteriorly or with their included cells as four folds along the top of the brain, each extending backwards and inwards toward the median line. The inner one of each pair is broadest anteriorly and somewhat overlaps its outer mate or appears to crowd it back. On the other hand the outer one is broadest and extends the farthest posteriorly. Other general details may be made out from the photographs. Below them antero-laterally, below their whole posterior extent, or occupying the spaces between them and the rest of the proto-cerebron are to be found ganglionic cells of various sizes, but mostly of the small kind to be described elsewhere. There is also a small mass of cells continuous with the mass between the upper portion of each pair of cups, but which in the sections photographed appear to be cut off from the larger mass. Each fibrillar mass is outwardly clothed by a thin nucleated membrane.

These are the bodies described by Dujardin as "lobes à convolutions." By later writers they are variously called. Leydig (64) described them as "Lappen mit Windungen;" Rabl-Rückhard (75) as "Rind Körper;" Dietl (76), Berger (78) and Cuccati (88) as "Pilzhutförmiger Körper;" while Newton (79) introduced the name calyx, which was adopted by Packard (80) and Viallanes (87 and 88).

The bodies reach their highest development in the Hymenoptera and are much larger in the social wasps than in the honey bee. In *Blatta* the lateral walls of the cups are much reduced, and in the Coleoptera the cup-like form is scarcely recognizable, while in *Forficula* and *Acridum* the fibrillar substance only forms a broad plate. Even this is scarcely, if at all, recognizable in *Dytiscus*. In *Tabanus* and *Somomya* the four folds are reduced to two and in the former of these genera are scarcely to be distinguished by a comparison of their cells with those surrounding them. In the Hemiptera they are not distinguishable at all.

The Stalks of the Mushroom Bodies.

From near the middle of the lower surface of each cup a column of fibrillar substance passes into the main mass of the proto-cerebron. In the bee these are much shorter than in other forms. The inner one descends almost perpendicularly downward for a short distance where it is joined by the one from the outer cup, which is somewhat longer and has an inward and somewhat forward course. In transverse sections the columns or stalks present a nearly circular outline and are distinctly delimited from the surrounding mass of fibrillar substance.

The Roots of the Mushroom Bodies.

At the place of union of the two stalks there are given off two masses of fibrillar substance of cylindrical shape, but with a diameter considerably greater than that of the stalks. One extends obliquely downwards towards the median plane of the brain where it nearly abuts against the one from the opposite side (fig. 2, Pl. XIV). Sometimes, as shown in the figure, the point of one may slightly overlap the other. Like the stalks, this structure is easily distinguishable from the surrounding mass of fibrillar substance even in ordinary preparations.

The other, which may be distinguished from the one just described, or inner root, by terming it the anterior root, extends straight forwards and abuts against the peri-cerebral membrane. It is longer than the inner root, but has nearly the same diameter. In section it is nearly circular (fig. 1, Pl. XIV), and in the transparent preparations *in toto* appears as a circular body in each proto-cerebral lobe, considerably above the antennal lobe. For most of its course it is well delimited from the surrounding mass, but anteriorly it becomes fused with the surrounding fibrillar substance on its lower inner side. In this region it may be seen to be entered by many irregularly branching fibers, even in preparations stained with hæmatoxylin (fig. 1, Pl. XIV).

THE MINUTE STRUCTURE OF THE MUSHROOM BODIES.

In sections cut in the frontal plane and treated with sulphate of copper and hæmatoxylin the cells filling the cups of the mushroom bodies appear to be of two kinds, both arranged one above the other so as to present the appearance of tiers arranged more or less radially with respect to the calyx as a circumference. Laterally they are much larger than those in the middle, which in such sections form a dark colored triangle (fig. 1). Those at the side are much lighter. In sections of brains fixed and colored in von Rath s platino-osmo-picric acid mixture the contrast between the two kinds is noticeable only upon close inspection and then only as a difference in size. After staining with fuchsin brings out no further difference. The chromatin elements then appear more distinct and more numerous, but both seem equally well supplied. Nor is there a difference in the presence or absence of a small dark colored nucleolus in preparations treated after the copper-hæmatoxylin method. The slight chemical difference indicated by the difference in depth of coloring shown by the latter method is, however, supported by a difference in the fibers given off from the cells, as will be seen a few lines further on.

In similar sections of the brain of a wasp I find but one size in the cells of this region. But two sizes occur in the cockroach according to Flögel (78) and are doubtless to be found in other forms. But one or two kinds, the cells of the mushroom bodies in the hexapods generally, and of the regions compared with them in crustacea, are strongly distinguished from nerve cells elsewhere in the brain, and in the whole nervous system for that matter, in being nearly devoid of extra-nuclear protoplasm. This fact led Dietl to term them ganglionary nuclei, a term that was later altered by St. Remy (90) to the equally characteristic one of chromatic cells.

Between the tiers of cells fine fibrils and tracheæ make their way to the inner surface of the cup, the tracheæ also branching among the cells as already described or figured in Plate XXII (fig. 29). The nerve fibers may be traced, with considerable difficulty, however, to the cells. In bichromate of silver preparations both cells and fibers easily impregnate and where the section is in the right place or where too many elements have not become darkened, the fibers are readily traced into the fibrillar substance forming the calyx-cup (fig. 18, Pl. XXI).

Here the fibers from the larger or marginal cells break up into a series of fine branches that again subdivide and produce a bushy or arborescent formation that reaches to the outer wall of the calyx and of which the drawing (fig. 18, Pl. XXI), although made with a camera, can give but a poor conception. The preparation from which this drawing was made is one of the first that were fairly well impregnated, but not so well as later ones, and is far from showing the richness of branching seen in the latter. Further, the branches are delicate and the smaller ones covered with fine short processes that give the whole a more or less feathery appearance. The preparation is not black, but of a delicate reddish brown tint. The difficulty of representing them and the fact that the connections with the cell bodies are poorly represented in the other preparations caused me to be satisfied with the figure given.

The processes of the smaller cells forming the pyramidal central heap, as shown in the same figure (fig. 18, Pl. XXI), also pass into and branch in the fibrillar calyx-cup. These branches resemble those of the other fibers, but, as shown, are far less numerous. Moreover the processes from the cells may be slightly smaller.

As shown in the figure, the processes do not always follow the most direct line to the fibrillar substance, but seem often to bend about the intervening cell-bodies. Consequently little dependence can be placed upon even the best of preparations by ordinary methods for tracing fibers for any considerable distance from the cell body towards the fibrillar substance. Fibers may readily be seen, however, passing from the cellular mass into the calyx, for between the two there is a narrow space but loosely filled with fibers, which may be seen more or less indistinctly in the photographs.

In this space are to be seen small round deeply stained bodies, which upon close examination and by comparison with sections cut in a plane parallel to the inner walls or to the base of the calyx are seen to be composed of a large number of very fine fibers arranged parallel to one another and forming thus a closely crowded fiber tract. These radiate in all directions from the place of union of the calyx and the stalk from which they seem to come. Outwardly the fibers separate and gradually spread out over the whole inner surface of the cup. Such phenomena are best shown in bichromate of silver preparations, but may be seen in preparations by ordinary methods and have been figured by earlier writers (Viallanes, Cuccati).

A further study of bichromate of silver preparations will show that each fiber from one of these bundles after its separation from the rest becomes continuous with a fibrillar process entering the calyx-cup from one of the cells above. Thus there is formed a nerve cell of the general Y-type (fig. 18, Pl. XXI). No other nerve cells are found in the cups.

Before continuing the consideration of the fiber just noted it may be well to mention the form of the cell bodies here and of those elsewhere. The larger number of successful impregnations of the cell bodies of the cups present a perfectly smooth outline. Very many, however, have from one to five or six projecting processes, which may branch. In this respect the smaller cells of the pyramidal group are exactly like the larger border cells, though such a condition did not happen to be shown in the section from which figure 18 was drawn. To determine whether they differed in this respect the sections of several brains were examined, resulting in the conclusion just given. Many of the cells resembled those shown in figure 19, Pl. XXI. Whether these processes are protoplasmic continuations of the cells to which they are attached or whether they represent merely filled up adjacent inter-cellular spaces, is a rather difficult question to answer. Here is one of the most serious difficulties presented by the bichromate of silver method. A few such cells I have seen in the optic lobes, but there as elsewhere cells with smooth contours seem to be the rule, and the rule might be taken to indicate an artifact nature for the processes in question. Further than this I find no reason for believing them to be artifacts. On the other hand, the fact that there was no evidence of undoubted artifacts in the immediate neighborhood of the cells described, together with the peculiar circumstance of the extremely small amount of extra-nuclear protoplasm in the cells filling the cups and their generally crowded appearance, would indicate that probably the processes are really parts of the cells with which they are connected.

Returning to the fibers of these cells, it may be noted that it is the bichromate of silver method alone that is able to show their course and termination. Fortunately there is no difficulty, such as there is with the fibers of other regions, in determining their immediate relationships completely. The bundles of fibers already mentioned as radiating from the place of union of the calyx and stalk as though coming from the latter do so, or rather, to start from the parent cell, pass down into the stalk. At the junction of the stalk and the two roots each fiber divides into two branches one of which passes obliquely downward towards the median line, the other straight forward to the anterior surface of the brain. Both terminate without further branching, and the inner group form the inner root, and that directed forward the anterior root of the mushroom bodies. Throughout their whole course from the entrance into the stalk to their termination in the inner and the anterior roots the fibers remain parallel, the only deviation from a straight line being a slight waving. They neither decrease nor increase in size but in the stalk they sometimes, though not always, appear to be covered by fine short processes that can neither be described as thread-like nor tooth-like. These may be artifacts, but I am inclined to think that their non-appearance might as well be accounted for by defective impregnation.

There is found, then, in the mushroom bodies a nerve cell with a smooth or irregular body sending a process into the fibrillar substance forming the calyx, branching there profusely aud sending a second process from the first down through the stalk and forming an inner and an outer branch. As will be seen beyond all doubt a little farther on, the branching process in the calyx is the dendrite and the second process is the neurite. In the relation of its neurite to other fibers it recalls to some extent the relation between the neurites of the cells of the granular layer and the dendrites of the cells of Purkinje in the mammalian cerebellum, but as a whole the cell seems to be unique among all known nerve cells.

Fibers Ending in the Calyx.

In bichromate of silver preparations, besides the branching dendrites of the cells just described, there may also be seen a large number of other fibers all somewhat coarser than the fibers of these cells and permeating and branching in the calyx in all directions (figs. 23, 26, 27, Pl. XXI). Often they are impregnated almost to the exclusion of the fibers from the cells above. At other times both appear, but then they most often obscure one another, making it necessary to section a large number of brains in order to find cases sufficiently free from a repetition of details to enable one to determine the form and relationships of the various fibers correctly. When such cases occur it is found that the fibers terminating in the calyx all make their entrance in the neighborhood of the junction of the calyx and stalk, or from the under surface of the cups. All appear to send a main fiber in a circle about the head of the stalk and from this to radiate numerous branches to the more distant parts.

The difference in size and mode of branching of these entering fibers allows two kinds to be distinguished. In the smaller kind of branches radiated from the region of the stalk, one slender kind branch more or less irregularly and repeatedly, terminating finally in an irregular swelling such as shown in fig. 27, which represents a magnification of about 583 diameters.

The larger kind (fig. 23) radiate off from the portion encircling the head of the stalk a number of stocky branches that after penetrating the surrounding mass of fibers for a relatively short distance branch out into a cymose head. Other portions aparently of this same fiber pass out into more distant parts of the calyx. The figure given was drawn with as much care as possible and well represents what was seen, but appearances are often deceptive, and I am inclined to think there are two kinds of fibers here instead of one as represented. It may happen that fibers overlie one another in such a way as to appear as one continuous fiber, a deception that, especially in thick sections, the most careful focusing will not always avoid. The fibers shown in the figure as immediately surrounding the junction of the stalk and calyx appear to be restricted to the region covered by the median group of small cells. The others appear to have gained an entrance to one side of the stalk and take in a larger region, besides appearing to have a different mode of branching.

The difference in size between figs. 23 and 26 is mostly a difference of magnification, which in the former is 121 and in the latter a 102 diameters, yet the fibers represented in fig. 23 are actually the coarser.

Just where either of these two kinds, the fine and the coarse fibers originate, or what other parts of the brain are connected with the mushroom bodies by them is yet to be determined. Almost all that can be said is that six different tracts of fibers terminate here, two from the optic lobe, one from the ventral region, and three from the antennal lobes. To these may probably be added a seventh of a commissural nature. These tracts will be described further on.

The Fibers Ending in the Stalk and the Roots.

In certain places (fig. 1, Pl. XIV), as already pointed out, fibers entering the anterior roots of the mushroom bodies may be very readily seen in sections treated after the copper-hæmatoxylin method. In preparations by the bichromate of silver method others may be distinguished. One large tract traced to its cells of origin behind and between the stalks of the mushroom bodies by Viallanes (87) in his study of the wasp spreads out on the side of the anterior half of the anterior root and branching sends one branch into it. The fibers of this pass nearly horizontally across or obliquely downwards to the opposite side giving off from their upper side several sub-branches (fig. 21, Pl. XXI) that after passing a greater or less distance upward break up into a thickly bushy head. These all occupy almost the same level so that often in specimens treated with osmic acid or with hæmatoxylin, especially the latter, the appearance is presented of several bands crossing transverse sections of the roots. Figures 3 and 4 show these bands excellently, and represent the two roots as seen in a slightly oblique section treated with copper sulphate and a solution of hæmatoxylin made according to one of Weigert's formulæ. Bands of this sort occur throughout the whole extent of the root. In the inner root also similar bands, though less conspicuous, are found, but there instead of being transverse, they are longitudinal.

The fibers just described are more or less coarse, considerably more so than fibers entering the lower outer side of the root behind them (fig. 28). The sub-branches of the second kind of entering fiber also take an upward course and break up into a series of branchlets, which do not, however, form a compact bushy head. Where their cells of origin are situated I am unable to say further than that subsequent studies will probably show them to be situated somewhere beneath the calyx-cups, either to one side of or behind the stalks. Their outward-going branches seem to penetrate into the lower lateral depths of the brain. A third fiber enters this same region at a lower level and appears to come from the lower lateral side (fig. 28).

Behind these fibers near the junction of the roots, or in the plane shown in fig. 1, Pl. XIV, on the left, fibers are found entering on the lower inner side which present a more delicate appearance and are otherwise different from those first described (fig. 28). They branch more or less dichotomously and end in a tuft of branchlets which in preparations with osmic acid or hæmatoxylin give rise to the broken appearance shown in the section of the left root in fig. 1, a comparison with which will show that fig. 28 is not properly oriented and that it should be viewed from the corner of the plate so as to make the branches crossing the dotted ring take a nearly horizontal course.

In the region of the junction of the two roots and the two stalks rather coarse fibers are found (fig. 17) considerably resembling those first described, whose more or less bushy terminals along with those last described produced the knotted appearance described by Rabl-Rückhard (75) for the ant as "2-3 small clefts rounded off above," and the lenticular spots only faintly shown in fig. 2. The same appearance as that described by Rabl-Rückhard is found in the bases of the stalks in the bee, but the section represented in fig. 2 is too far back to show it. To imagine the figure, however, all that is necessary is to suppose the lenticular spots to be larger and united at their bases.

The lighter places between the spots are filled by the fibers of the mushroom body cells alone (fig. 17).

In the stalk my preparations show the existence of incoming fibers resembling the upper ones represented in fig. 28 more than any of the others. But details are not sufficient to enable one to determine their origin or the destination of their outer branches any better than, in fact not so well as, those entering the anterior root.

Very nearly the same thing may be said with respect to the fibers entering the inner root. Some of these appear to be connected with the central body later to be described, others seem to come from the opposite lower side of the brain. Their branches in the root are of the same general type as those represented in fig. 21, but the sub-branches are much shorter, more uniform, and end in a very much more compact head of branchlets. These of course cause the longitudinal banded appearance already mentioned.

Besides these six or seven groups of entering branches there are to be found numerous fibers irregularly branching over the surface or near the surface of the roots, which may also send small branches into them (fig. 22, Pl. XXI), and here may be noted a fiber seen in one section only that is of no little interest. Whether it belongs to any of the regular groups I am unable to say definitely, but think from its appearance that it must be a branch of one of the irregular fibers just mentioned. It is figured on plate XXI (fig. 25). It enters the right anterior root near its terminus from some little distance in the lateral part of the brain and is there of considerable size. But almost immediately upon entering it decreases in volume and after branching becomes connected with the neurites of the mushroom body cells. The junction appears as complete as though there existed here a veritable fusion. So fine are the fibers that the preparation also seems to show that the parallel fibers from the mushroom body cells have branches in this place. The latter condition cannot, however, be the true one, for in all other preparations, which are numerous, no such branching is shown. With Lenhossék (95) I agree that in general the bichromate of silver method, usually showing only silhouettes, is defective and very apt to mislead in the matter of fibrillar connections. But in the specimen in question viewed with a Leitz ocular No. 2, and objective No. 5, there is no more reason for doubting the continuity of the lines shown than there is in fibrils shown in preparations stained with hæmatoxylin or any other histological coloring matter. They are not superimposed, nor is there any reason for thinking them to be of tracheal nature.

When we consider the nature of the method used, it should not appear strange that fibrils in very close contact should be so impregnated with bichromate of silver as to cover up all evidences of separation. In fact it seems to me that such apparent evidences of continuity are to be expected, without, however, even raising a doubt as to the complete validity of the evidence obtained from the generality of terminations shown and from histo-ontogeny.

Before leaving the matter it must be noted that, although the figure given is a camera drawing made with the aid of careful focussing, it does not correspond with what appears when the camera is removed. Then the fibres *a*, *b* and *c* are seen to belong to the parallel fibres which are continued upwards beyond their junction with the fibrillar branches of the incoming fiber.

THE FUNCTION OF THE NERVE-CELLS OF THE MUSHROOM BODIES.

Ever since Dujardin (50) discovered the mushroom bodies and pointed out the relation between their size and the development of insect intelligence, nearly every writer on the subject of the hexapod brain who has referred to the matter of intelligence has recognized the fact. Leydig (64) thought them connected with the intelligence of the animal, but added that they also seemed to bear some relation to sight, or to the ocelli. Rabl-Rückhard (75) thought the same, except that he pointed out that Leydig's second supposition is incorrect, since in blind ants the bodies are found to be well developed, while the optic lobes and the nerves of the ocelli are absent. Forel (74) pointed out the same facts and added that the mushroom bodies are much the largest in the worker ant, and that those in the female are larger than those in the male. Two years later Brandt (76) affirmed the same condition to be true for the Hymenoptera generally. Berger (78) agreed with Dujardin and the rest. Dietl (76) was inclined to dissent, and Flögel (78) seemed to consider the roots and stalks as a framework (*Gerüst*) for the rest of the cerebral substance. Nevertheless the tabular summary of his study on the different orders that he gives at the end of his paper is of no inconsiderable value in showing the truth of Dujardin's inference, so far as comparative anatomy is able to do so. The physiological experiments of Faivre (57) and others, which have lately been repeated and perfected in the excellent work of Binet (94), are of great value in showing that the seat of intelligent control of an insect's movements is in the dorso-cerebron. Thus far, however, no attempts seem to have been made to determine experimentally the function of the mushroom bodies as parts distinct from the rest of the dorso-cerebron. Experiments are badly needed to complete our knowledge of the structures.

All that I am able at present to offer is the evidence from the minute structure and the relationships of the fibers of these bodies. This seems to be of no inconsiderable weight in support of the general idea started by Dujardin. For in connection with what was made known by Flögel and those before him and has since been confirmed and extended by other writers, one is able to see that the cells of the bodies in question are much more specialized in structure and isolated from the general mass of nerve fibers in those insects where it is generally admitted complexity of action or intelligence is greatest. Considering the calyx and the cells above it alone, one finds that according to Flögel neither are recognizable in the Hemiptera, that in Diptera (*Tabanus*) and Odonata (*Aeschna*) the bodies are recognizable from those in the neighborhood only by a slight difference in the size of the cells representing them ; that in Lepidoptera the calyx-cup is very small or entirely absent, that in the Coleoptera (*Tenthrido, Cynips*) the calyx is not so extended as to be very well recognized as a cup, and that in the Orthoptera the lateral walls of the cup are either very small

(*Blatta*) or entirely absent (*Forficula, Acridium*, etc.); while in the Hymenoptera the calyx is folded upwards so as to give room for many more neural elements and connections.

If one considers the little that has thus far been made known by means of the bichromate of silver and the methylen-blue methods concerning the cerebral nerve fibers in other invertebrates, one finds that sensory stimuli are transferred to a number of irregular cells or fibers distinguished roughly by the term association fibers and from these transferred to motor or other fibers bearing efferent neural impulses. And from such a comparison it appears that in the groups of insects certain of these association fibers have gradually been set apart from the rest so as to render it possible for an entering stimulus to become an efferent impulse by taking a direct or an indirect course. In the former case the course is to be compared with the course of a stimulus producing reflex action in man. Later on it will be seen that the present assumption of the existence of fibers permitting such a course is fairly well founded. Thus a sensory impulse from an optic lobe or from an antenna may reach the fibers going to the mouth parts through possibly but one association fiber.

In the other case it may take a special or somewhat indirect course to and through the fibers of the cells of the mushroom bodies and from them reach the efferent fibers through the processes of one or more association cells. From those facts it seems far within the bounds of reason to suppose that the nerve cells of the mushroom bodies rendered so prominent by their specialization of form and position are the elements that control or produce actions that one distinguishes by the term intelligent.

An analysis of these actions is needed, but that is beyond the limits of this paper. Suffice it to point out that the experiments of Binet (94) and others show that when the connections between the dorso- and ventro-cerebron are destroyed the phenomena afterwards observed are similar to those seen in a pigeon or mammal when its cerebral hemispheres are removed. One difference is notable, namely, that the operation of eating in the case of the insect appears to be reflex ; for when one, vivisected as just indicated, is placed upon its food it begins and continues to eat. In the other case the animal must be fed. The various bodily movements of the insect, however, after a time take it away from the food, and once away it is wholly unable to return. Such insects when passing food even almost within touch of their palpi are wholly unable to change their course so as to secure it, although the movements of their palpi plainly show that its presence has affected them. Whether this would still remain the case when the vivisection is of such a nature as to allow sensory stimuli from the antennæ or visual stimuli to act through the reflex channels already mentioned is as yet unknown. From a consideration of the facts that I have pointed out and the facts demonstrated by comparative anatomy and embryology relative to the homologies of the antennæ one is warranted in expecting that the animal would still lack the power of *directing* its movements.

THE CENTRAL BODY.

This peculiar body was first made known by Dietl (76) as "the fan-shaped structure," and was two years later described by Flögel (78) as the central body, a term that has since been generally employed. It lies above and behind the ends of the inner roots of the mushroom bodies and is wholly composed of large nerve fibers and fibrillar substance, plus, doubtless some tracheal elements (figs. 2, 5, 6, 7, 8, 9, *c.b.*). A few of its connections I have been able to ascertain, but very much yet remains to be learned, so much in fact that any assertion as to its functions can be but little better than a mere guess. Viallanes (87) describes it as connected with all the surrounding parts of the brain, but that is an assertion too sweeping for the facts known to me after an application of the bichromate of silver, the copper-hæmatoxylin and platino-osmo-picric acid methods, and was much too sweeping for the actual facts known to Viallanes. Berger (78) recognized the body in *Dytiscus* as a lenticular body receiving a bundle of fibers from each side which entering broke up into its individual fibers, some going out anteriorly, some posteriorly, or, in short, as a center of disassociation.

The body throughout my diagrams and figures is distinguished by the letters *c.b.*

In the honey bee this body as a whole has a very much distorted spherical shape. In frontal sections the fan-shape described by Dietl and Berger is apparent (fig. 5), though the outline presented might be better described as reniform. Viewed from above or in horizontal sections it has a somewhat trapezoidal outline.

Internally, as shown by sections in the frontal plane, it is divided by a space filled with nerve fibers and tracheæ, into an upper and larger portion covering a lower and smaller portion. Both are seen in preparations by ordinary methods to be composed of fibrillar substance, but in frontal sections the lower usually stains more deeply (fig. 5). Antero-posteriorly the upper portion is also much the larger and considerably overhangs the other, partly covering two masses of fibrillar substance a little farther on to be described as tubercles.

Taken as a whole, fibers seem to reach it from or leave it in nearly all directions ; but the two parts seem to be supplied somewhat differently. Those entering the lower are seen to originate from cells above the antennal lobes and upon reaching the lower lateral edges to take a transverse course below the body and send several branches upwards that subdivide arborescently producing a compact mass of branchlets that recall the arborescent and bushy terminations of the association fibers in the roots of the mushroom bodies (figs. 32 and 37). As in the case of these latter fibers, it is to the compact branching mass of fibrills that is due the depth of color so noticeable in preparations stained with osmic acid or with hæmatoxylin. Other fibers either pass out or enter from the fibrillar substance of the brain immediately in front, while branches from association fibers in the anterior region seem to enter the anterior end and the posterior lower end of this portion of the body (fig. 40, Pl. XXII).

In the upper portion the same arborescent method of branching also occurs, and gives rise to the wavy upper contour shown in figs. 5 and 6. But here the fibers originate from cells above the body in the median plane or from cells behind it and after passing behind the body enter the cleft separating the two portions, where many of them are gathered into bundles with an antero-posterior course. These recall the radiating bundles seen in the cups of the mushroom bodies. Other fibers also send their branches into it from its outer surface (Pl. XVIII).

Just behind the inner roots of the mushroom bodies large numbers of fibers seem to be given off, some of which pass downwards to the neighborhood of the œsophageal foramen, while others take a more lateral course (fig. 5). It is this appearance, which is very noticeable in preparations by ordinary methods, that doubtless led Viallanes to make the assertion referred to. When impregnated with bichromate of silver these fibers seem to originate from cells situated somewhere behind the central body and, after passing over its surface and sending branches in to it, to take the course described and shown so well in fig. 5. Some of them are probably the neurites of a group of cells whose dendritic branches form a commissure immedidiately behind the central body (fig. 9, Pl. XVI) and send their sub-branches into its posterior surface (Pls. XVII and XVIII, cells 5 and 6).

Another group of cells lying above the body in the median plane send their processes backwards over its surface and after sending a branch to what will soon be described as the fibrillar arch pass down behind and enter the space separating the upper and lower portions of the body and branch in the former portion (cell 2, Pl. XVIII). Fibers from cells situated behind the body and above the fibrillar arch also make the same connections. Another group of fibers originating from cells above the antennal lobes pass obliquely inwards to the space just behind the lower half of the body and passing upward in front of the glomerules end in the upper half. What connections are made by them I have not thus far been able to ascertain. No fibers passing between any portion of the central body and the calices of the mushroom bodies have been seen, and whatever indications have been noticed of connections with the inner roots of these bodies are of such a fragmentary and otherwise imperfect nature as to render their existence very doubtful. All that may be safely said is that it is connected with the fibrillar arch, possibly the ocellar glomerule, with the mass of association fibers immediately in front, with the lower lateral regions of the proto-cerebron, and with the trito-cerebral region forming the œsophageal commissure, where its fibers may possibly connect with others entering from the ventral cord, or with those belonging to the ventro-cerebron.

THE TUBERCLES OF THE CENTRAL BODY.

Behind the lower portion of the central body and partly covered by the overhanging upper portion (fig. 6, Pl. XV) are two small round, deeply staining masses of fibrillar substance to which Viallanes (87) applied the term of "tubercules du corps central." Just what their relations are to the central body, or what may be the origin of the fibrils forming them I have not been able to determine definitely. But from the fact that in thick unstained sections one can distinguish in the immediate neighborhood behind them masses of fibrillar substance of a similar globular appearance I am inclined to think them globules of the same kind and having the same or similar relationships as the latter. My preparations do not satisfactorily show fibers leading into or going from them. But there are indications that the mass of smaller glomerules is formed by terminations of the nerves from the ocelli very much as the so-called olfactory glomerules later to be described are produced by the terminations of the fibers from the antennae, and for that reason I choose to call them ocellar glomerulæ. This particular region of the brain along with the central body needs considerably more light than I am at present able to throw upon it.

THE FIBRILLAR ARCH.

This peculiar structure may as well be considered here, since it is connected with the central body, behind which and somewhat below the level of whose upper surface it lies. It is a rod-like mass of fibrillar substance that upon either side rises from but is scarcely connected with, the mass of fibrillar substance behind the union of the roots and stalks of the mushroom bodies and passes directly across the median line through the large mass of cells filling the posterior median furrow, thus forming a sort of commissure described by Viallanes (87) as "le pont du lobes cerebraux." It does not form a commissure, such as is ordinarily understood by the term, even though it connects the two lateral halves of the brain, and seems much better denominated by the term "gabelförmiger Körper" employed by Cuccati (88) or better still by the one that I have used. The central portion of the arch may be seen in figure 8, while in figure 9, several sections below, the pillars upon which it rises appear as two dark spots, one on either side of the enormous nerves from the ocelli.

In preparations treated with copper-sulphate and hæmatoxylin or by the platino-osmo-picric acid method of von Rath, large nerve fibers may be distinguished passing irregularly along its outer surface, and seemed to originate from cells situated on both sides of the brain near its ends. Viallanes (87) mentions fibers passing from it to the central body, a connection that as already intimated my preparations with bichromate of silver show to actually exist. A group of fibres from cells in the median plane above the central body send each a short branch that ends here in a tuft of branchlets (fig. 2, Pl. XVIII) and then continues on down into the central body as described when speaking of that structure. This short branch and its tuft-like ending without doubt represents the dendrite and the larger branch to the central body the neurite of the cells of this group. Other groups situated above and both before and behind reach the central body after branching in exactly the same manner. Viallanes (87) supposed that possibly the structure received branches from the ocellar nerves, but was far from being sure. Whether his supposition is true my preparations thus far made do not enable me to decide definitely, but from the fact that the nerves in question seem to begin to break up or become less numerous in this region and from a few indications in bichromate of silver preparations I am inclined to think that possibly his supposition will sometime be found to be true. What connections are made by the fibers mentioned as covering the outer surface of the structure, I am not prepared to say.

THE ASSOCIATION FIBERS OF THE PROTO-CEREBRON.

The fibrillar substance of the regions surrounding the bodies already described, or the rest of the central proto-cerebron, is composed of the association fibers coming from, and the tracts of fibers going to, these bodies, together with bundles of fibers entering it from various groups of cells and giving rise to a great number of irregular fibers to be classed under the general term of association fibers. In only a few cases have the cells from which these fibers originate been impregnated along with their fibers so as to make their relationships perfectly clear. What little has been learned I have endeavored to bring out in the diagrams that follow as well as in the camera sketches in the last two plates.

The fibers, as may be readily seen in fig. 1, take various courses, binding the upper, the lower and the lateral parts together. Fibers originating from cells above the antennal lobes pass up on the inner side of the anterior roots of the mushroom bodies and branch arborescently in the region just above them (fig. 31 and fiber 10 in the diagrams). Just below the root a small branch is given off that passes outward horizontally. Other fibers seen in preparations by the copper-hæmatoxylin method in front of the plane of fig. 1 seem to originate from cells above the antennal lobes, and, after passing upwards near the median line as rather large fibers, bend over the anterior roots of the same side and become lost in the fibrillar substance (Pl. XVII). The fibers of the cells in the median line under the edges of the calyx-cup and in front of the central body also seem to branch in this region, for I find no indications of their forming a chiasma and passing into the lower regions of the brain as described by Viallanes (84) for the Orthoptera, and by Cuccati (88) for *Somomya*. Other fibers of unknown origin (fig. 40, Pl. XXII), but of a very conspicuous appearance branch rather profusely in this region of the fibrillar substance and send branches back into the central body. Others bend over the inner roots and send branches upwards and across to the region immediately above the base of the anterior root of the opposite side (fig. 32, and fiber 50, Pl. XVIII). Another seems to arrive, (whether from over the top of the central body or from somewhere beneath the calyx-cup, is difficult to decide,) and branches near the junction of the two roots, one branch going toward the central body, the other straight downward (fiber 21, Pl. XVII). A similarly perpendicular fiber is also found on the outer side of the root (fiber 20, Pl. XVII). Still another (fig. 32) seems to arise as a small fiber from over the central body, passes downward to the opposite side, where it becomes much enlarged, and gives off numerous branches, these even passing out under the anterior root. It may possibly be one of a group of fibers (fiber 49, Pl. XVIII) originating from a group of cells near the fibrillar arch and passing directly forwards over the central body.

A horizontal fiber (fig. 22, Pl. XXI) originates somewhere at the side of the brain and after giving off several branches that spread out over the top of the anterior root ends in an arborescent system of fine branchlets in the upper part of the middle portion of the cerebron just across the root.

The fibers connecting the anterior and posterior region are most striking in appearance and are of considerable extent. One (fig. 30) apparently originates from cells in the region above and behind the antennal lobe and passes backward to one side of the median plane giving off a branch that subdivides and passes to the median anterior root, one passing up close to it and the other to a lower level. After giving off this branch it becomes very much smaller and passes on backwards, giving off several small branches meanwhile. Near the posterior wall it divides into two branches of small size, but of considerable length, the one going directly upward and branching among the ocellar glomerulæ, the other directly downward into the œsophageal commissure and the ventro-cerebron.

Another fibre (48) equally, if not more peculiar, is shown in figure 34. This appears to originate from a cell situated behind the inner root of the mushroom bodies (providing one may judge from the appearance of the fiber and the direction of its branches). Just behind the inner root and to one side of the base of the central body it becomes very much enlarged, gives off two relatively short branches and then one long one that passes up over the inner root and over the anterior root just in front of the junction of the two with the stalks, as shown by the dotted lines in the figure. Another branch a little further forward passes up to and branches in the fibrillar region to one side of the central body, while in front of this a number of short branches are given off that branch very profusely in the region to one side of the base of the central body. The main fiber continues forward to the neighborhood of the antennal lobes giving evidence of further branching, but on account of being either unimpregnated or cut off can not be traced farther.

The fiber shown in figure 35 is nearer the median plane and appears to come from the œsophageal commissure, passing upward and then directly forward under the central body, giving off along its course several branches that run back into or towards the commissure and then four very long though small branches that pass upwards in front of the central body ending, so far as can be traced, above the level of the top of the latter. One of the four passes farther forward and gives off a branch that turns back into the neighboring region to one side.

In figure 33 a more peculiarly twisted fiber (35) is shown, which was found in the lateral region of the proto-cerebron below and to one side of the anterior root and behind the optic body, near which it may possibly originate. Its base is at the right of the figure. It passes outwards for a short distance then backwards, gives off a branch that turns upon itself, divides again several times, some of the branches going upwards, the rest downwards and forward. There it passes downward for a short distance and divides into two large branches of almost equal size, one going backward, so far as traceable, apparently to the posterior region of the brain, the other forward, twisting above the parent stem and finally breaking up into a number of branches that terminate behind the central body.

The Deuto-cerebron.

THE ANTENNAL LOBE.

The antennal lobes comprise by far the larger portion of this division of the insect brain, especially so in the honey bee, and the rest of the Hymenoptera for that matter, where the remaining small portion is so fused with the proto- and the trito-cerebron as to leave little or no trace of separating boundaries.

Considering first the antennal lobes, one may say that sections cut in various planes show that each lobe is composed internally of a nearly spherical mass of fibrillar substance connected with the rest of the brain by a small neck of the same substance and surrounded on all sides by a large number of cells, some of which belong to it and some to the proto- and the trito-cerebron, and fill in the deep spaces between it and these two parts. Inside of this sphere and near or composing its periphery one finds small globular masses that by any of the ordinary methods of staining take a much greater depth of color than the more internal part, and in them one recognizes the great non-nucleated cells of Leydig (64) and Rabl-Rückhard (75), which were first more correctly described by Dietl (76) as olfactory bodies. Flögel (78) claims the honor of pointing out their true significance, for, he says, he called attention in an unpublished communication to the Kieler Physiologische Vereins, July 30, 1874, to the fact that they are not cells. Fig. 1 shows the bodies or glomerulæ very plainly.

Between them even in ordinary preparations processes from the bordering cells may be traced to the inner fibrillar substance, but it is doubtful whether branches entering them may be seen in such preparations. Cuccati (88) regarded them along with the rest of the mass as made up for the most part of branches of these processes that by subdividing formed with whatever other fibers that might be there a sort of net work. The only difference that he supposed to exist between them and the central portion of the mass was in the greater fineness of the meshes of the net. But while his supposition with respect to the relation of the glomerulæ to the surrounding cells is correct and even though some of my preparation are so strongly impregnated with bichromate of silver as to present considerable resemblance to a meshwork, I am inclined to believe other preparations showing a tuft-like system of branching illustrate the true condition (fig. 10 and 16, Pl. XXI), and that the idea of connection by contact holds as well here as elsewhere. As already pointed out cases might occur in such preparations in which the darkened fibers might appear perfectly continuous, so as not even to be explained by Lenhossék's suggestion of a silhouette of superimposed fibers, and still not be fused or continuous. Happily such deceptive appearaces seem to be rare except in too heavily impregnated preparations.

When impregnated with bichromate of silver the glomerules strongly recall the appearance of the olfactory glomerulæ figured by Retzius (92) for the vertebrates, and may perhaps be very well called olfactory glomerulæ. But exactly what their relations may be with the surrounding cells and the incoming fibers I am not able to say definitely. In none of my preparations is an unbroken connection shown between them and the cells clothing the lobes, the fragmentary appearances, however, amply warrant the supposition that the processes of the cells make their way between the bodies and after passing some distance in the middle mass of fibers send a branch into one of the glomerulæ and another one into the proto-cerebron (fig. 10, 16 and 24, Pl. XXI). Whether the process from a single cell sends branches to more than one body does not appear, but if one may judge from the form of the cells of the mushroom body, probably it does not.

THE ROOT OF THE ANTENNO-SENSORY NERVE.

Besides the fibers just described there are to be distinguished two other kinds. One of these composes the root of the antenno-sensory nerve, which in preparations with osmic acid or by the copper-hæmatoxylin method may be traced from its entrance into the lobe on the lower anterior surface nearly to the posterior upper surface. Throughout its course it gives off numerous fibers and branches. My preparations by the better neural method that are favorable for tracing it are not numerous. Fig. 16 represents one in which the fibers shown are all that are impregnated in this region. Here a fiber is seen coming in from the nerve and at some distance from its entrance bending aside to a glomerula from which another fiber passes out and then on towards the proto-cerebron. The other fiber soon after entering breaks up into three branches one of which terminates in a glomerula. The tuft-like termination was not seen when the drawing was made, but after the latter was fixed to the plate a re-examination of the specimen brought it to light, but with scarcely sufficient distinctness to be drawn with a camera.

If one is to credit, as one must, the long list of writers since the time of Newport dealing with the antennæ anatomically and physiologically, one must conclude that these organs have at least two, and in many cases, if not always, three different functions. That they are both tactile and olfactory has long been known, and recently Child (94) has brought forth very good anatomical reasons for their being also auditory. Such being the case one might expect to find as many different kinds of terminations in the antennal morula.

There is a striking resemblance between the tufts forming the glomerulæ and those forming the olfactory glomerulæ in mammals as described and figured by Retzius (92 *a*); and, since in the ventro-cerebron where sensory fibers from the oral nerves undoubtedly terminate no such glomerulæ are found, one may be very easily led to the conclusion that the glomerulæ are for olfactory terminations. But I am unable to produce evidence of other terminations and must for the present conclude that the glomerulæ are formed by the terminations of all kinds of fibers from the antennæ. This conclusion is supported by the fact that the tubercles of the central body, in which fibers from the ocellar nerves apparently terminate, and the ocellar glomerulæ have a very similar appearance.

Another kind of fiber is shown along with its cell in fig. 15. This was found in the posterior ventral regions and bears a slight resemblance to cells and fibers that are undoubtedly of efferent nature. It may be a portion of such a one that by branching among the olfactory glomerulæ as indicated in the figure makes a reflex course from the afferent antennal fibers to the antennal muscles. Still it may be only an association fiber of which there may be many in the antennal lobe, though their appearance does not distinguish them as such as readily as in the case of the association fibers of the rest of the brain. Whatever other fibers there are that might be classed as such are of small size. Some of them appear to pass into the neck already spoken of as connecting the lobe to the rest of the brain.

THE ROOT OF THE ANTENNO-MOTOR NERVES.

The small internal antenno-motor nerve supplying the antennal muscles within the head appears to be but a branch of the larger one passing on to the antenna and with it has a common root. In sagittal sections treated by ordinary methods this may be readily followed on the lower side of the antennal lobe and somewhat to one side of its median line as a bundle of medullated fibers that passes through the group of cells filling the lower space between the œsophageal commissure and the globular mass of fibrillar substance of the lobe. It penetrates the fibrillar substance here and may still be followed through an inward, backward, and upward course for a considerable distance. Gradually it decreases somewhat in size or loses its fibers, and is finally untraceable. In such sections of brains impregnated with bichromate of silver the fibers are frequently found impregnated and then form a large bunch of branching fibers spreading out in the commissure taking in the trito-cerebron and to a slight extent the ventro-cerebron. Branches also pass upwards into the proto-cerebral region. In one case of a thick frontal section embracing the posterior part of the antennal lobe and nearly all of the proto-cerebron behind its plane a single fiber considerably smaller for a portion of its length can be seen above the level of the lobe, as shown in Plate XVII on the right where an attempt was made to reproduce it. Below it decreases in size and joins several other fibers, the whole of which were not impregnated, and forms with them a band of fibers traceable down behind the lobe until hidden by the intervening strongly impregnated glomerulæ. As this band occupies the same position as the antenno-motor root seen in ordinary preparations I take it for granted that the fiber is motor and belongs to this nerve. The large part of the fiber inclines posteriorly in passing upward, terminating, so far as traceable, very close to the inner root of the mushroom body at some little distance from the median line. Three of its branches are impregnated. The lower one passes forwards towards the inner side of the antennal lobe and does not subdivide. From this fact and its apparent destination I have supposed that its cell of origin is situated among the cells filling this space between the lobe and the commissure. Higher up two branches are given off nearly together, one passing internally towards the median line, and the other, which is much longer, passing outward and downward in the trito-cerebral region and branching. But here it is obscured by other details. A short distance above this another long branch is given off. This goes diagonally backwards to the posterior-lateral angle of the proto-cerebron ending in several small branches.

In other sections made in the horizontal plane fibers of a similar appearance were found taking a horizontal course and passing apparently beneath the antennal morula (Pl. XIX). These branch, as shown in the diagram, much more profusely than the other one just described, a fact that is doubtless due to their better impregnation. One sends a long slender process, or rather continues as such, backwards to the layer of cells clothing this part of the brain. But whether it actually arises from any of them I am unable to say. It is not impossible, and, if one considers the fiber shown on the opposite side of the plate, which after branching profusely and irregularly sends off a slender process in the direction of the antenno-motor nerve, it may not seem improbable. The details are not sufficient to settle the matter, however, and until they are shown to exist, I shall be inclined to believe that probably all the cells giving rise to the antenno-motor nerve are situated close to or in the lobe on the anterior side of the brain. Fig. 39 represents a camera drawing of the two fibers just described and also another from the next section above them.

The Dorso-Cerebral Fiber Tracts.

THE CONNECTIONS WITH THE OPTIC LOBES.

Tracts of fibers passing from the optic lobes into the central part of the proto-cerebron were early recognized by Berger (78) and Bellonci (82), but the interpretations of these authors are very largely incorrect. Viallanes (87,88) seems to have described most of them much more correctly, and the same may be said of Cuccati (88), so far as I am able, without an actual study of sections of *Somomya*, to homologize his results with my own. Certain peculiarities are figured and described by him that render a comparison difficult.

Before describing the connections it should be noted that the masses of fibrillar substance forming what are usually known as the optic ganglia, but which are much more properly denominated fibrillar masses, are seen in frontal or horizontal sections treated by ordinary methods to be composed of two outer layers of densely staining masses, and very much resemble in form two meniscus lenses placed one within the other. The space between them is filled with a loose mass of fibers, and the whole is so placed as to have its convex surface directed outward and its concave surface inward.

The inner of these masses lies in hexapods close against the central proto-cerebron, being separated from it by a layer of cells and a few bands of fibers. In other words there is no optic nerve such as is found in the Crustacea. The attempts by the earlier writers to distinguish an optic nerve were long ago shown by Viallanes (87) to be more or less unsuccessful, since there is not one but several connecting tracts. These with the optic lobe sufficiently removed from the rest of the brain, might, however, produce the homologue of the crustacean optic nerve.

The Anterior Optic Tract.

Even in ordinary preparations there are indications of fibers passing radially or nearly perpendicularly to its two surfaces, through the inner fibrillar mass. Emerging from the inner surface these are gathered into two bundles, the larger of which passes forward, and slightly downward along the outer surface of the central proto-cerebron and finally terminates in a small oval body called by Viallanes (87) the optic tubercle, situated immediately above the antennal lobe and to one side and below the terminus of the anterior root of the mushroom bodies of that side. In preparations with bichromate of silver the bundle is often very prominently shown, and in addition also the arborescent terminations of its fibers in the optic body, as shown in the diagrams that follow. This body in the bee is divided into a large inner mass and a very small outer mass, and into the latter some of the fibers of the tract send each a small branch before passing on to the larger body.

Other fibers apparently arising from cells in the immediate neighborhood also branch in the body and connect it with other parts of the brain. One group passes to the opposite side and appears to terminate in the opposite optic body. Others pass backward, but no tracts appear to connect it with the mushroom bodies, although individual fibers are often found going in that direction.

The Postero-superior Optic Tract.

As just indicated, the fibers emerging from the convex surface of the inner fibrillar mass divide into a large and a small bundle. The latter may be considered the postero-superior optic tract, which seems to have escaped the notice of Viallanes (87, 88). It may be easily traced in preparations either by the copper-hæmatoxylin method or by the platino-osmo-aceto-picric acid method of von Rath, and after leaving its larger companion, which is almost immediately, it passes upward along the outer surface of the central proto-cerebral mass, and joining the antero-superior tract, to be described a few lines further on, takes an inward course until, arrived close to the stalk of the outer mushroom body, it leaves this other tract and passes behind the stalk close to the junction of the latter with the calyx. Whether any of its branches pass into the calyx here I am not able to say definitely, but apparently they do. In preparations with bichromate of silver some at least of its fibers may be followed across the intervening space to the opposite side of the stalk of the inner mushroom body. Whether any of them continue on into the superior commissural tract my preparations thus far made do not show.

The Antero-superior Optic Tract.

This as described by Viallanes (87) and Cuccati (88) starts from the outer fibrillar mass. Instead of originating like the two tracts just described from the radiating fibers of the mass, it arises from the fibers filling the space between its two lenticular portions. These fibers are gathered into a bundle and leave the mass at its antero-superior edge. Passing backward and inward through the intervening layer of cells, the bundle reaches the outer surface of the central proto-cerebral mass, then turning upward joins the postero-superior bundle. Just before reaching the stalk of the outer mushroom body it leaves its companion and passes in front of the stalk, close to its junction with the calyx, to the space between the two stalks where its fibers branch, one group passing into the outer, the other into the inner calyx. In one preparation I was able to determine the cells of origin of this tract and to follow it through several sections to its connection with the optic mass. According to the facts shown in this brain impregnated with bichromate of silver the description should be reversed and the union of the tract with the optic mass be spoken of as its terminus, for the cells from which it originates comprise a small group on the supero-anterior-lateral surface of the central proto-cerebral mass and send their processes as a bundle of fibers almost directly backward to the space between the two stalks, whence a branch passes into the calices and another to the fibrillar optic mass, as described.

The Antero-posterior Optic Tract.

This has been well described by Viallanes (87) in his memoirs on the hexapod brain and also by Cuccati (88) in his paper on *Somomya erythrocephala.* Like the tract last described it is formed from the fibers coming from the central portion of the outer optic fibrillar mass, which it leaves at the same point. Leaving the antero-superior tract at the optic mass it takes a backward and somewhat inward and downward course through the intervening mass of cells, passing over the anterior optic tract and between the inner optic mass and the central portion of the proto-cerebron and turns into the latter at its postero-lateral lower angle. After entering here the fibers separate from one another and branch, but may be followed for some distance towards the median line. Where its cells of origin are to be found I cannot say definitely. But in certain of my bichromate of silver preparations I have seen processes from cells in a group near the starting point of the tract entering the fibrillar mass, and it is not improbable that they are the cells of origin of the fibers of this tract.

*The Posterior Optic Tracts.**

Of the remaining tracts connecting the optic lobe with the central proto-cerebral mass, there are several; but before pro-

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*The following shows to what extent my results correspond with those of Viallanes (87) who found four and I five tracts connecting the optic lobe with the central cerebral mass:

A. Connections with the outer optic mass.
   1 Faisceau supéro-antereur =
   Antero-superior tract *mihi.*
   2. Faisceau supéro-postereur =
   Antero-posterior optic tract *mihi*.
B. Connections with the inner optic mass.
   3. Faisceau inféro-antereur =
   Anterior optic tract *mihi.*
   4. Faisceau inféro-postéreur, 2 tracts =
   2 of my posterior tracts.

In his work on the grasshopper (88) he was unable to find the two tracts from the outer mass, while from the inner mass he found arising two tracts, one corresponding to my anterior optic tract, the other—his cordon commissural—to my lower optic commissure.

ceeding with their description it should be noted that the inner optic mass is so turned as to bring its posterior edge much closer to the central brain mass than its anterior margin. It is at this posterior margin that the entrance to the space between its two lenticular portions is situated.

From this opening emerge a large number of fibers gathered into several bundles, the most of which terminate in the adjacent posterior lower portion of the central proto-cerebron.

Of these bundles Viallanes (87) distinguished four, and Cuccati (88) seems to have found some of them in *Somomya*. The inner optic region of this genus, as shown by the latter author, differs so much from what I find in the bee or have seen figured or described elsewhere that comparisons are very uncertain. What he calls the ovoid body (eiförmige Körper) doubtless corresponds to the inner optic mass as generally met with, but what may be the homologue of his S-form body I am at a loss to know unless it may possibly be the outer lenticular portion considerably separated from the inner one. But in case that were true, there would be an anomalous condition of fibers from the concave face of the outer optic mass passing through the space, a condition of affairs that is not true in the case of the bee nor probably in any other hexapod. He also figures and describes several tracts of fibers that apparently correspond to some of those to be described here a few lines ahead, but as originating from the outer surface of the S-form or of the ovoid body, which, I take it, is equivalent to describing them in the bee as arising from the outer surface of the inner optic mass, and this is not true.

But to proceed with the optic tracts, there may first be described one, noted by both Viallanes (87) and Cuccati (88), leaving the inner margin of the inner lenticular body and passing into the central proto-cerebral mass a little above the point of entrance of the antero-posterior tract and continuing thence as a loose band of fibers across the posterior region of the brain and below the fibrillar arch to the inner optic mass of the opposite side, thus forming what may be termed the upper optic commissure. It does not pass directly across but is arched slightly upward. It may be followed with little difficulty in ordinary preparations, and I have several times found its fibers impregnated in brains treated by the bichromate of silver method. Whether its fibers branch in the central brain I cannot say definitely. There are indications, however, that they do, and further, that their cells of origin may be situated among those forming the mass of cells behind the central body.

Below this, in a plane taking in the anterior optic tracts and the optic body, and a little below the lower level of the inner roots of the mushroom bodies, there are three tracts, which may be seen in figure 10, Pl. XVI. These differ considerably according to the direction of the plane in which the section is cut, and also seem to differ somewhat in different individuals. In another brain from that from which the figure was taken there is a bundle that is not shown in the figure. This is described by Viallanes (87) as divided into a thicker and a thinner bundle, which is the case here. Both emerge from the inner edge of the inner lenticular body and terminate in the neighboring central region after penetrating no further than do the posterior two of those shown in the figure. The anterior of the two is considerably the larger and from its manner of staining may readily be considered as composed of many very fine fibrils. The other is composed of fewer and coarser fibers and seems to arise more directly from the space between the two lenticular bodies.

Below these are two more bundles, or the posterior two shown in the figure. These resemble the one just described and arise and terminate similarly.

At a slightly lower level is the last of the series, which arises from near the margin of the inner lenticular body and passing directly into the central mass, bends slightly downward and then upward again to its former level and passes on as the lower optic commissure to the lobe of the opposite side. This is a much more compact and well marked bundle than the upper optic commissure and seemingly gives off no branches, although further study will probably show that it does. In one preparation by the copper-hæmatoxylin method in which the sections are in the horizontal plane I find fibers above it on each side of the brain that seem to run down to and join it in its middle portion. But in bichromate of silver preparations, although I have several times found some of its fibers impregnated I have not found sufficient evidence to warrant my saying that it branches. Just where its cells of origin are I have not been able to determine.

THE DORSO-CEREBRAL COMMISSURES.

Of the bands of fibers connecting the two lateral halves of the dorso-cerebron there are at least six, and of these two have already been noted in connection with the optic tracts. Some of them have long been known, but on account mostly of a lack of proper neurological methods have seldom been correctly understood. Viallanes (87,88) seems to have made fewer mistakes than any other writer who has considered them.

The Superior Dorso-cerebral Commissure.

This band of fibers crossing the median line of the brain above the central body and between the two inner stalks of the mushroom bodies (fig. 2) was noted by Dietl (76) and Berger (78) and considered as connecting the two optic lobes, a mistake perpetuated by Bellonci in his study of *Grylotalpa.* The fibers are brought out very prominently by most of the ordinary methods and I have repeatedly found them impregnated in brains treated by the bichromate of silver method. They are all of small size and non-medullated. By a comparison of frontal and horizontal sections (figs. 2 and 7) they are seen to form a band whose broadest extent is in the antero-posterior direction, and to be divided at either end into two parts—a division that can sometimes be distinguished throughout the length of the commissure—one of which passes behind and the other in front of the stalk. There does not seem to be a crossing of the fibers, but those passing in front of one stalk also pass in front of the other. In preparations with hæmatoxylin or with osmic acid the halves may be traced in horizontal sections around the inner stalks to the space between these and the outer ones and apparently into the calices. Since the tracts from the optic and antennal lobes also enter this region, very much care is necessary in distinguishing the different tracts, but since they fuse to some extent upon entering the calices, it is impossible to follow any one of them singly. Viallanes probably correctly interpreted this bundle as a commissure between the two pairs of mushroom bodies. There is apparently very little probability of any of its fibers reaching the optic lobes, though none of the methods employed by me have thus far demonstrated conclusively that they do not, nor have I been able to determine their exact terminations in the calices nor the location of their cells of origin. In preparations with hæmatoxylin and with osmic acid processes from the cells behind the inner side of the inner stalks have been traced upwards and forwards, apparently passing into the commissure as it passes around the stalks, but no such fibers have been found impregnated in brains prepared according to the bichromate of silver method. This negative evidence is not, however, at all conclusive since a sufficiently large number of brains have not been treated.

The Anterior Commissure.

The small band of fibers composing this commissure was first discovered by Viallanes (87) as connecting the two optic bodies. It may be followed in ordinary preparations without much difficulty from the posterior margin of one optic body across the anterior region of the brain and below the roots of the mushroom bodies to the optic body of the opposite side. Apparently its fibers originate from the group of cells immediately inside of and below the body. The processes from the cells seem to pass upward, and after sending a short process into the body where as seen in bichromate of silver preparations, it branches very profusely, and then passes across the median line. I have not been able to determine exactly its termination on the opposite side or whether it or any of its branches penetrate the optic body here. One bichromate of silver preparation where the fibers of the tract are most completely impregnated is inconclusive from the very fact of the extent of the impregnation. From it one might conclude that branches pass into the optic body, but the greater number into the region immediately behind it.

The Optic Commissures.

The two tracts of fibers forming the one the upper and the other the lower optic commissure have already been described in connection with the optic tracts. As noted there, I am unable to say definitely whether either give off branches to the brain in passing, and it may be added here that I have no evidence to show that a single nerve cell makes the entire connection between the lobes, if such be actually the function of the tracts. The question needs much further study.

The Inferior Dorso-cerebral Commissures.

The two groups of fibers connecting the lateral halves of the dorso-cerebron immediately above the œsophageal foramen have been variously misunderstood. They are shown in fig. 10 where they appear as two short tracts in front of the larger lower optic commissure. The anterior of the two was supposed by the earlier writers to connect the antennal lobes, and even the olfactory glomerulæ of one side with those of the other. Of such a direct connection I find no evidence whatever, though without doubt the two commissures may be considered as connecting the two deuto-cerebral lobes. In ordinary preparations sectioned in the horizontal plane both commissures are found immediately above the foramen, in fact almost bordering upon it, and may be traced for a short distance into the fibrillar substance of either side where the fibers curve slightly downward and separating from the tract branch and disappear. In frontal sections the fibers may be followed a little farther than in those cut in a horizontal plane. In fig. 5 one of the tracts may be seen though somewhat indistinctly.

In bichromate of silver preparations, although I have frequently found commissural fibers impregnated, I have not found sufficient details to warrant a definite assertion as to the exact relation of the tracts to the rest of the brain, nor as to the situation of the cells giving rise to their fibers. What details there are, however, indicate that the anterior tract connects the two regions, which may be called deuto-cerebral, immediately behind the antennal lobes. If it in any way connects the two lobes or their glomerulæ, it is only by means of intervening association fibers. But such a connection is doubtful from physiological reasons. It seems much more probable that the commissural fibers by the aid of association fibers of one side, should connect the glomerulæ of that side with motor fibers of the other. Still the other supposition is not impossible, and one should rather follow the maxim of Hunter, "do not think, but go and see", and wait until facts, physiological or otherwise, are obtained to decide the matter.

The fibers of the posterior tract, which is separated from the other by the ascending tracts from the antennal lobes to the mushroom bodies, connect more posterior parts of the brain. The fibers shown in fig. 38, apparently belong to this tract since at the median line they occupy the same position. Here they are obscured by a mass of precipitate filling the roof of the foramen, but since there are no other fibers impregnated here, there can be little doubt that the fibers of the opposite side are a continuation of them. The branching and larger portion of them is found in the posterior lateral lower angle of the brain, and it is possible that they may originate from cells in this neighborhood. One of them, it may be noted, sends a slender branch forwards toward the antennal lobe.

THE ANTENNO-CEREBRAL TRACTS.

The existence of tracts of fibers passing upwards from the antennal lobes into the proto-cerebron has been known ever since Bellonci (82) published his account of them in *Gryllotalpa*. But of the three pairs of such tracts he seems to have distinguished but two, and certainly misunderstood the relationships of these. For he describes them as antenno-optic connections passing from the antennal lobe upwards into the proto-cerebron and to the optic lobes by way of the superior commissure, which he recognized with Dietl and Berger as connecting the optic lobes. The same error was committed by Cuccati (88) who found in *Somomya* what is unquestionably the homologue of the inner tract to be described a little farther on, and which is also the main tract discovered by Bellonci. Viallanes (87) found the tract in the wasp and for the first time described it correctly.

In certain of my preparations of the brain of the bee by the copper-hæmatoxylin method these antenno-cerebral tracts are very distinct and very easily followed. This is the case in sections cut in any of the three planes.

The Inner Antenno-cerebral Tract.

The one first to be described is the largest and also the one first discovered. It arises in the neck of fibrillar substance connecting the antennal morula with the rest of the brain and ascending upwards, inwards and backwards (fig. 2) it passes between the two ventral commissures of the dorso-cerebron (fig. 10). Thence curving backwards somewhat it passes behind the root of the mushroom bodies and the outer hinder margin of the central body and in front of the fibrillar arch (figs. 8 and 9) to the level of the superior commissure, behind which it may be seen in section in fig. 7. From here it bends forward and passing around in front of the inner stalk of the mushroom body enters the inner calyx at its junction with the stalk and on the antero-lateral side of the latter.

In bichromate of silver preparations I have several times found the fibers of the tract impregnated for nearly their entire length. And in many cases different portions of the tract in successive sections were so well impregnated that their superimposition was a very easy matter. Fig. 24 represents the superimposition of three such sections and shows the tract from the calyx above to the inside of the antennal morula below. In no case have I found fibers from a glomerula passing into the tract, but the arrangement of the many fiber-fragments that have been seen almost conclusively demonstrated that they enter it (fig. 24). The fiber from the glomerula shown in the figure offers a very good example.

Nor have I found the fibers in cennection with cells, but, considering their connection with the glomerulæ as practically demonstrated, it may be remembered that very good reasons appear for considering the glomerulæ as connected with the cells clothing the morula, and from this it is fairly evident that the same cells give rise to the fibers of the tract. A little further evidence will appear in connection with the outer tract.

The Middle Antenno-cerebral Tract.

The next tract to be considered is the smallest of the three and arises as a branch of the one just described at a point just above the level of the ventral commissures. It takes an outward course behind the mushroom body (fig. 6) and continues upward to the region behind and between the stalks and then bending forward somewhat passes into the outer calyx.

This seems to be the branch figured by Bellonci as passing outward into the supposed tract between the optic lobes. In several of my bichromate of silver preparations it is very readily followed.

The Outer Antenno-cerebral Tract.

This tract is of considerable size and originates, as shown in bichromate of silver preparations (fig. 24), from cells above the antennal morula. From the morula it passes backward and outward towards the side of the central brain mass and gradually turning upwards passes behind, but in contact with, the lower optic commissure (fig. 6) and finally reaches the outer dorsal surface of the fibrillar substance and there, joining the antero-superior optic tract, passes in front of the outer stalk into the calyx above. Whether any of its fibers continue to the other calyx or not, I cannot say.

In some frontal sections there appears to be given off from this tract below the lower optic commissure a small bundle of fibers that curves outward and apparently joins the commissure. But in horizontal sections it seems to follow the commissure to a point near the outer surface of the fibrillar substance, where it turns abruptly forward and enters the mass forming the antero-lateral lower angle of the central cerebral mass.

THE DORSO-VENTRAL TRACT.

Five tracts of fibers have thus far been described as entering the calices of the mushroom bodies and there still remains another. This was first brought to my notice in a frontal section of a brain impregnated with bichromate of silver, and was subsequently recognized in a similar section of a pupal brain treated by the copper-hæmatoxylin method. It begins as a small band of fibers in the region between the two stalks, where branches of it enter both calices, and passes downward beneath the cells clothing the posterior surface of the brain to the œsophageal foramen, then continues anteriorly along the roof of this so as to reach the opposite side of the brain near the anterior surface. In its passage along the roof of the foramen its fibers send branches into the side from which the main fibers came, and these form an arborescent termination among branches of fibers coming from the ventro-cerebron and the ventral cord. Since these latter fibers cross the median line above the foramen anteriorly, the passage of the tract to the opposite side brings it into close relation with them along their whole extent along the roof of the foramen. This relation is best shown in plate XX, which shows two fibers of the tract as seen in a single section. The cells of origin of the tract have not been seen. But sufficient has been determined to show in what close relationship the cells of the mushroom bodies stand with the ventral nervous system.

The Ocellar Nerves.

In the bee the ocelli are situated close together, and as a consequence their so-called ganglia are contiguous and their nerves to a large extent fused. The nerve from the median ocellus passes downward and backward between the two inner calices and fusing with the nerves from the lateral ocelli forms with them a single mass that divides to pass around a large trachea piercing the brain in the median line between the calyx cups. Immediately below this the fibers again come into close contact, but at a little lower level some of those coming originally from the median ocellus separate from the rest and follow a course that takes them down in front of the fibrillar arch to terminate finally, as apparently shown in copper-hæmatoxylin preparations cut sagittally, in the tubercles of the central body.

The others form a broad band of fibers passing down behind the fibrillar arch to which, as suggested by Cuccati (88), some of them may give off branches. Certainly some of the smaller fibers cannot be traced below this level (Pl. XVI).

Both the anterior and the posterior groups are composed of two kinds of fibers, one enormously large and the other of ordinary size. The large fibers are very noticeable in preparations by the copper-hæmatoxylin method from the fact that they stain but slightly and thus appear as light colored spots in a deeply colored surrounding mass of cells (fig. 7-9). Similar results are obtained with von Rath's platino-osmo-aceto-picric acid mixture. The unstained fibers look very much like sections of tubes. But in preparations treated with Weigert's hæmatoxylin, or in those after-stained with fuchsin the fibers stain more or less deeply and thus demonstrate that they are at least not empty tubes. Even in preparations by my copper-hæmatoxylin method staining sometimes takes place. In such cases the inner mass appears in section to be shrunken away from the surrounding fibrillar wall, but remaining connected with it by slender filaments. This would seem to show that they are not formed upon exactly the same plan as other nerve fibers. A careful histological study of their structure is necessary.

The nerves thus constituted may be followed for some distance below the fibrillar arch, but seem to branch and gradually decrease in size. This is noticeable in the figures, where in fig. 7, the anterior nerve appears with three large fibers and at a considerably lower level (fig. 9) there is but one. The fibers of this nerve soon become untraceable and appear to pass into the fibrillar arch and the ocellar glomerule beneath.

Some of the fibers of the other two nerves seem to terminate in the same way, but a large number of the larger fibers continue downward, as seen in both horizontal and frontal sections, until they reach the neighborhood above the œsophageal foramen, where they separate. Some seem to terminate in this region. The others come into close contact with the hinder surface of the brain and pass on downward in the upper surface of the œsophageal commissures to the ventro-cerebron, whence they pass on backward along the dorsal surface of the ventral cord, thus effectually disproving Binet's (94) assertion that there are no large fibers in the dorsal region of the cord comparable to those found in crustacea. In many cases I have found these large fibers of the cord in bichromate of silver preparations passing along the dorsal surface of the ventro-cerebron on into the region just below the level of the central body as shown in Pl. XX. What their significance may be I do not at present undertake to say. Had Binet persevered longer in his trial of either of the two methods preeminent in the study of the nervous system, he probably would have found them. But while the existence of the large fibers is beyond question, there is still a chance that my description of them as coming from the ocelli is erroneous, for the reason that I have not been able, in specimens prepared by the bichromate of silver method or by any other, to follow a fiber through an unbroken or unsectioned course from the ocellar ganglion or the upper portion of an ocellar nerve to the ventral cord. Yet impregnated fibers have been followed without interruption from the copper-the level indicated above, and ∧ the large fibers have been carefully traced through sections treated according to my copper-hæmatoxylin method. It should be noted that Cuccati (88) also traced them in *Samomya*, as I have done here, into the ventral cord. Viallanes (87, 88) did not succeed in following them below the fibrillar mass behind the inner root of the mushroom bodies.

THE FIBERS FROM THE BRAIN TO THE OCELLAR GANGLIA.

Besides the fibers just described as constituting the ocellar nerves there may, in preparations by the bichromate of silver method, be distinguished others of an efferent nature (fig. 42, Pl. XXII). These may be traced from below the level of the calices into the ocellar ganglia where they branch arborescently. None are large. Where they originate or what may be their fibrillar connections within the brain, I have not as yet been able to learn. Not many preparations were obtained showing them passing out of the ganglia, and in fact only one in which they could be traced from below the calices, and from this the two fibers of the figures were taken.

As there are no muscular structures in the ganglia, their function is doubless to control the action of the pigment of the pigment cells.

The Commissural and Ventro-cerebral Region.

Since in the case of the bee they are so closely bound to it, the parts composing the œsophageal commissures may be considered along with the ventro-cerebron.

As already pointed out, the trito-cerebral lobe is very much reduced and is mainly distinguishable externally by the labral nerve. This is not far behind the internal antenno-motor nerve and its root may be traced for a short distance into a small lobe just inside the neck of the antennal morula. Fig. 2 is just a little too far forward to show it, but a section of the nerve may be seen on the left at its point of entrance. In bichromate of silver preparations the fibers entering from it very quickly form a bushy tuft of branches just beneath the root of the antenno-motor nerve. Some of these reach back into the ventro-cerebron.

The roots of the other oral nerves may be followed in ordinary preparatious each as a light band of fibers that passes upward above the point of entrance of the nerve and then bends inward towards the median line and ends in a roll of fibers that is apparently much more easily distinguishable in other forms than in the bee, and which Binet (94) calls the ventral column. This passes backward into the ventral cord. The two roots that Binet describes for each crural and each ventro-cerebral nerve in *Cerambyx* and other beetles I do not find in my sections of the bee's ventro-cerebron. This may be due to their being fused, but the attention that I have given this portion of the brain is as yet small in comparison to that given the dorso-cerebron.

In bichromate of silver preparations some of the fibers entering from the nerves very quickly break up into branches, but reach a little above the lower half of the ganglion. In a few cases the roots were found impregnated for nearly their whole extent and did not appear to give off many branches to the ventral region. In one case two cells in front of the mandibular nerve were each found connected with a fiber that passed out through the nerve, but whatever inner branches they may have had were not impregnated (Pl. XX). In another case a large cell was found on the lower lateral side of the brain sending a process into the region above, where it gave off a very extensive small branch (fig. 36). Near the broken end of the fiber another that is not shown in the figure began. This was apparently a continuation of it. The appearances of the section indicated that the fiber had been cut on account of its forming a slight bend outside the plane of the razor. The second fiber turning forwards gradually became swollen distally and then decreasing passed as a smaller fiber into the root of the antenno-motor nerve. The latter cell then is certainly motor, and taking for granted what has already been fairly well demonstrated by other observers; namely, that cells in the brain sending their neurites out of it are motor or bearers of efferent neural impulses, and the fibers entering from external cells are sensory, it is just as surely true that the other cell is of a motor nature.

This ventral position of motor cells here tends to indicate that the dorsal motor and ventral sensory area of ventral ganglia, as distinguished by physiologal experiments, is considerably independent of the position of the cell. It may be pointed out that in dorsal lesions it is the connection of the dendrites of motor cells with fibers bearing stimuli to them from other parts of the nervous system that is broken; while in ventral lesions it may be the terminations of sensory fibers or of association cells and their fibers or both that are destroyed. From this it may be seen how indefinite are apt to be results obtained by the physiological vivisection methods. Should experiments be repeated with a thorough knowledge of the location of the cells about a ganglion so as to render it possible to rupture individual cells and not fibrillar connections, and sufficient time is allowed to elapse for the degeneration of the dendrites and neurite of the ruptured cell, it will doubtless be found that ventral and lateral portions of the ganglion are motor.

Such careful experiments are needed and, performed upon the ventro-cerebron, they may, by the aid of either the methylin blue intra-vitam or the bichromate of silver method, be able to demonstrate which of the large number of cells located there perform the function of co-ordinating the movements of the body.

The association fibers of this ventral region of the brain are numerous, and of the many fragments of them seen one of the best is shown in fig. 24. This, as is evident from the figure, occupies the upper portion of the commissural region and sends the greater part of its branches and branchlets dorsally into the lateral region of the proto-cerebron in the dorso-ventral plane of the anterior root of the mushroom bodies. One branch passes forward inside the inner antenno-cerebral tract.

Numerous fibers may be found connecting the antennal morula through its neck of fibrillar substance with the commissure. A single fragment shown in plate XX (fiber 37) sends a process upward in the posterior region that branches below the level of the ocellar glomerulæ, while another is sent forward apparently to the antennal lobe. Just before reaching this it sends a secondary branch downward into the ventro-cerebron. The fibers seen entering the ventro-cerebron from the ventral cord are in some cases remarkable for their size. These large fibers occupy the dorsal region and have already been spoken of in connection with the nerves of the ocelli. Fragments of them have been seen as far back as the first thoracic ganglion, and anteriorly, as before noted, they have been traced in bichromate of silver preparations into the proto-cerebron behind the ocellar glomerulæ. Branches are given off in this region that pass among the glomerulæ to the commissural region as shown in the plate. Much shorter ones are given off in the ventro-cerebron. Another large fiber (fiber 38) apparently ends in the ventro-cerebral and commissural region. Lower down in the ventro-cerebron another fiber is shown (fiber 41) that branches among the fibers from the oral nerves and thence apparently passes backward into the ventral cord. A smaller fiber (40) makes the same connections.

In some of my preparations there may be distinguished what may be described as a roll of fine fibers, the individual fibers of which cannot be traced, that passes through the ventro-cerebron and thence upward through each commissure; whence it crosses to the opposite lower side of the dorso-cerebron or over the anterior part of the roof of the œsophageal foramen. I do not know what this can be unless it is a continuation of the ventral column described by Binet (94). Its passage into the dorso-cerebron is directly contradictory of this author's assertion that "il n'existe dans le ganglion sous œsophagien aucun croisement des connectifs qui prennent leur origine dans le cerveau." But Viallanes (87,88) speaks of a fibrillar tract that passes from the cord to the opposite side of the dorso-cerebron. In close connection with this roll individual fibers may be followed from the cord to the same destination.

What is apparently a branch of this roll continues upward towards the central body in the commissure of the same side, or without crossing the median line.

It is this roll of fibers that has already been mentioned in connection with the dorso-ventral tract, with the fibers of which it seems to come into contact. Assuming that, which is doubtless true, it is the continuation of the ventral columns described by Binet (94) and that the root of the crural and the alary nerves terminating in it are sensory, which is also probably true, there is then seen to be a direct sensory tract for external stimuli from all parts of the body to the calices of the mushroom bodies, a fact of no little importance in completing the chain of evidence demonstrating that the cells of these bodies are the ones that enable the animal to adapt itself to the varying conditions of life.

A similar group of fibers may be followed in copper-hæmatoxylin preparations from the ventral cord through the ventro-cerebron to the antennal lobe within the region of the inner terminations of the motor-fibers to the oral and ventral nerves. In such preparations fibers leaving the tract may be readily seen and it is not a connection between the antenno-motor nerves and the ventral cord such as Cuccati (88) seems to imply in his description of the same tract in *Somomya.* Connecting the pair of tracts in the ventro-cerebral region are four transverse bands of fibers. These have been noted several times in bichromate of silver preparations, but the longitudinal tracts to the antennal lobe were found impregnated but once.

The transverse œsophageal commissure seems to have become completely fused with the ventro-cerebron in the bee, and is apparently represented by a few transverse fibers found in the lower floor of the œsophageal foramen.

The Cell Groups.

Having finished the description, incomplete though it be, of the central fibrillar substance of the bee brain, there still remain the groups of cells clothing the mass to be discussed. The location of these, after recognizing the general form of a hexapod nerve cell, is of little physiological importance compared with the extent and connections of their fibers, but morphologically they may have considerable significance.

As before mentioned, the cells of the brain are gathered into masses that completely cover the fibrillar substance in certain regions and fill in the spaces between its lobes. Thus the spaces between the optic lobes, the antennal morula and the central cerebral mass are completely filled by them, as is also the deep furrow between the two lateral proto-cerebral lobes on the posterior side of the brain.

These masses are, with certain exceptions, subdivided into small groups the fibers of which form a bundle in penetrating the central mass. These groups so far as I have been able to distinguish them may be designated by numbers as follows below. The most prominent of the exceptions to the rule of the formation of small bundles are the cells about the calices of the mushroom bodies. These are very similar in appearance to the small cells filling the central portion of the calyx-cups and their general mass is in some places continuous with that filling the latter, their relation to which may be compared to the overflowing contents of a cup. They are found in the space between each pair of calices and in that between the latter and the fibrillar mass below, anteriorly and posteriorly, and grade into the mass of cells between the central mass and the fibrillar masses of the optic lobes. No processes from any of them to the portion of the brain beneath them have been seen in any of my preparations, but in all they seem to be in some way closely related to the calices. In one instance a process was traced into a calyx from a cell in the space between the pair of cups, and this, branching there, exactly resembled the dendrites of the cells inside. Since this was one of the earlier of my discoveries, and since the boundaries of the cup are not always distinct in non-stained, or bichromate of silver preparations, and since at this moment I am unable to verify the matter, there is here a possibility of a mistake. If not, and the cells are of the same order as those inside the cup, their neurites must be looked for as passing inside to the radiating bundles of fibers.

Between the posterior margins of the stalks and immediately below the calices I have several times found larger cells impregnated, whose processes passed in between the stalks and up between the calices. Perhaps these may be the cells giving rise to the fibers of the superior commissure, but the details to be seen are too poor to warrant a conclusion.

THE CELLS OF THE DORSO-CEREBRON.

I. To proceed with the enumeration of the groups of cells, there may first be noted a small group of medium sized cells, situated dorso-antero-laterally beneath the outer calyx, the processes of which pass almost directly backwards to the neighborhood of the inner surface of the outer stalk and form the processes giving rise to the fibers of the antero-superior optic tract.

II. Behind and below these, but in close proximity, is another group of similar appearance, the processes of which form a tract passing into the fibrillar substance towards the median line of the brain.

III. Below the anterior optic tract nearly half way between the inner optic mass and the optic body is a group of moderately large cells, the tract of fibers from which passes under the optic tract and upwards towards the middle superior surface of the anterior root of the mushroom body, above which they seem to branch. In all preparations where seen there is considerable difficulty in distinguishing the fibers of this tract from the outer branches of the tract from the posterior region of the calices to the root.

IV. Immediately outside of and below the optic body is a similar group whose processes pass beneath the optic tract upward and inward, apparently, along the lower surface of the anterior root.

V. Inside of and below the optic body is a group of cells of median size whose fibers pass upward along the outer side of the anterior root.

VI. Below these and above the antennal morula is a group that sends a tract of fibers upwards across the inner side of the root (figs. 24 and 31, fiber 10 of the diagrams).

VII. Outside of these and above the morula are three small groups that send as many tracts of fibers inward to the central body (fiber 30). They pass below the latter structure and, turning upwards in front of the tubercles of the central body, enter the space separating its dorsal and ventral portions. Apparently they form the tract that is figured by Bellonci (82) as connecting the inner antenno-cerebral tract with the superior commissure on the opposite side of the brain, or as forming a chiasma with its companion from the opposite side.

VIII. Near the latter group is another whose processes form the outer antenno-cerebral tract (fig. 24).

IX. Beneath the calices and in the median plane is a group of cells recognizable in fig. 1, the processes of which pass directly downward, and according to Viallanes (88) enter the œsophageal commissure of the brain, thus forming a chiasma. In the wasp (Viallanes 87) and in *Somomya* (Cuccati 88) their relationships seem to be the same as in the bee, in which I find no evidence of crossing.

X. Immediately behind the latter group is another composed of cells of the same large size, the fibers of which pass backward over the central body and connect it with the fibrillar arch (fiber 2).

XI. Considering the posterior region of the brain there may first be noted a small group situated below the outer calyx at a point where the outer antenno-cerebral tract reaches the dorsal surface of the fibrillar substance. Its processes pass downwards into conjunction with the tract and might be taken for its processes of origin were it not for the fact that bichromate of silver preparations show that its cells are situated in the antennal lobe. Where the fibers of this group go to I have not been able to determine.

XII. Behind the stalks of the mushroom bodies is a small group of large cells whose processes pass between the stalks to the anterior root (fiber 7) giving rise to some of the association fibers in that structure.

XIII. Behind the inner stalk there is a group of medium sized cells whose processes pass inward behind the inner antenno-cerebral tract and behind the central body into which each fiber sends several branches (fiber 5).

XIV. Behind the lateral margin of the central body and beneath the fibrillar arch is a companion group whose fibers pass directly forward and turning about in front of the inner anteno-cerebral tract pass behind and send branches into the central body (fiber 6). The two groups thus form a commissure behind this structure. As before mentioned it is possible that their neurites may be the fibers seen leaving the central body and passing into the lower lateral portions of the protocerebron and towards the commissural region (fig. 5).

XV. Above these groups and between the central body and the fibrillar arch and below the latter is a small group whose processes form a bundle (figs. 2, 5, 6, 8) passing just inside of the inner antenno-cerebral tract over the top of the central body to the median anterior mass of fibrillar substance (fiber 49).

XVI. Above these and in front of the arch is a small group of cells, often staining more deeply than those surrounding them, whose processes pass directly downwards outside of the tract just described and appear to enter the inner antenno-cerebral tract (fiber 3),

XVII. Above the ends of the fibrillar arch is a large group of cells of large size whose fibers form a dorso-ventrally flattened band that passes forwards outside of the inner antenno-cerebral tract and above the superior commissure (figs. 2, 7, 8) and bending about the inner stalk distribute themselves in the fibrillar substance above and outside of the anterior root of the mushroom bodies (fiber 23).

XVIII. Below the fibrillar arch and a little below the commissure of the central body is a loose group of cells whose processes in some cases appear to pass into the superior optic commissure. In others they pass across to the fibrillar mass behind the base of the junction of the roots and stalks of the mushroom bodies (fiber 4).

XIX. Behind group XVI and separated from it by the fibrillar arch is one that appears to send its processes downward into the inner antenno-cerebral tract, but probably they are sent into the central body.

XX. Another group below these and the fibrillar arch sends its processes downward and inward apparently under the superior optic commissure, in front of which they bend upwards and apparently pass to the calices along with the fibers of the superior commissure and those of the inner antenno-cerebral tract.

XXI. The cells about the antennal morula are most numerous in the space between it and the rest of the brain, although they cover almost its entire surface, and are perhaps gathered into as many groups as there are inter-glomerular spaces. One group that should have been noted before is situated in the inner superior side of the neck of the morula and sends its fibers upward through the anterior portion of the central mass of fibrillar substance and near the median line. Near the lower surface of the inner calyx they turn outward over the anterior root.

XXII. Three groups that may be considered as one on account of their situation below the neck of the morula have their processes directed upwards toward the neck.

XXIII. In the lateral lower side of the central cerebral mass are several groups. One large one at the posterior lower edge of the inner optic mass sends its processes straight forward into the fibrillar mass forming the anterior lateral angle of the brain below the anterior optic tract.

XXIV. Another group inside the last sends its fibers into the adjacent posterior angle.

XXV. A little above the group just noted is another that sends its fibers in among the terminations of the posterior optic tracts.

THE CELLS OF THE VENTRO-CEREBRON.

Excepting the dorsal surface the whole of the ventro-cerebron is covered with a mass of cells all of which are of considerable size, but largest ventrally. Among them may be distinguished seven principal groups.

XXVI. A ventro-median group between the origin of the maxillary nerves sends a band of fibers directly through the mass above, passing behind a group of commissural fibers among which may be those of the transverse œsophageal commissure to the dorsal surface.

XXVII. A second ventro-median group also occurs between the origins of the labial nerves. Its fibers after reaching the neighborhood of the dorsal surface separate and apparently reach the latter.

XXVIII. Between this group and the origin of the nerve is another of large cells whose processes form a distinct tract passing upward and outward just outside of the ventral column at the level of which it branches, one half continuing upward and forward towards the commissural region, the other turning outward and becoming lost in the surrounding fibrillar substance.

XXIX. A group outside of the last and behind the origin of the labial nerve sends a band of fibers nearly half way through the mass behind the root of the nerve.

XXX. Between the origins of the labial and the maxillary nerves and outside of them on the lower lateral surface is a large group whose fibers forming a well marked band pass inward and then upward near the root of the maxillary nerve and then upward and inward and apparently forward towards the commissural region.

XXXI. Considerably above the last, or on the upper lateral surface and below the origin of the salivary nerve, is a group whose fibers pass directly inwards and join those of the last group near where these turn forwards.

XXXII. Just above the one just described and in front of the plane of the origin of the maxillary nerves is a group that sends a band of fibers upwards into the commissural region.

Conclusion.

From the facts detailed in the preceeding pages it is evident that even though there are more difficulties in the way of obtaining good results than with the vertebrates, a patient application of the bichromate of silver method will throw as much light upon the organization of the hexapod nervous system as it has upon that of the higher animals. By its aid during the past winter the minute structure of the so-called mushroom bodies has been brought to light and several links added that almost complete the chain of evidence demonstrating the function of these peculiar bodies to be that of enabling the insect to intelligently adapt itself to its surroundings. They are shown to be connected at their calices with two pairs of sensory tracts of fibers from the optic lobes, with three from the antennal lobes and with one, that is probably also sensory, from the ventral nervous system. Their roots are shown by fragmentary evidence, sufficient to warrant the conclusion, to be very probably connected with the inner terminals of motor, or possibly of other efferent fibers, but the exact course of the connection and the number of cellular elements composing it remains to be demonstrated.

The central body is plainly shown to be connected with the fibrillar arch, and possibly the ocellar glomerulæ, and probably through these also with the nerves of the ocelli. Further it is connected with the fibrillar mass in front, and with that below it, but it does not appear to be connected with the mushroom bodies unless it be with their roots. It receives its fibers from cells situated above and behind it, and from some above the antennal lobes.

The olfactory glomerulæ so-called, are shown to be formed by the tuft-like terminals of the fibers composing the antennal morulæ, and in these the terminals of the fibers of the antenno-cerebral tracts seem to play the most prominent rôle.

Several tracts of fibers from the optic lobes connect the latter with other parts of the brain than the mushroom bodies, and some of them doubtless form a part of an optic reflex tract with fibers from the ventro-cerebron and the ventral cord.

Such reflex tracts are not evident in connection with the antennal lobes, but the positions of fiber fragments seen indicate the possibility of reflex connections here also.

Some of the fibers from the ocellar nerves terminate in the tubercles of the central body, others in the ocellar glomerulæ. Some also may connect with the fibrillar arch. Some of the large fibers pass downward and become the enormous fibers of the dorsal surface of the ventral cord.

A tract of fibers, probably a continuation of what Binet calls the ventral column of the ventral cord, passes upward through the commissures and comes into connection above the œsophageal foramen with a dorso-ventral tract to the calices of the mushroom bodies.

A tract from the cord that is probably a branch of the ventral column passes forward to the posterior part of the antennal lobes giving off fibers on their branches along the way among the terminations of the fibers passing into the oral and the antenno-motor nerves.

In the ventro-cerebron of the bee there is recognizable but one root to each of the oral nerves. Of these that of the maxillary nerve is most prominently, and that of the mandibular nerve the most meagerly, developed. The roots connect with the ventral column as described by Binet (94) for one of the branches of the double root recognizable in the Coleoptera.

Motor cells have been found in a ventral position in the ventro-cerebron, which does not accord with the distinction, based upon physiological experiments by Faivre (57) and Binet (94) of a dorsal motor and a ventral sensory area for each ganglion of the ventral cord. This is reconciled by pointing out that it is the fibrillar connections that are destroyed in the lesions produced dorsally, and the association cells and fibres and the terminations of sensory fibers in ventral lesions. If experiments be performed destroying individual cells and thus producing a consequent degeneration of their individual fibers, it will probably be found that the ventral surface of a ganglion may be described as a motor area.

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EXPLANATION OF PLATES.

EXPLANATION OF COLORS.

Red. Cells and fibers of the mushroom bodies.

Blue. Sensory fibers from cells outside of the central cerebral mass.

Violet. Tracts connecting the calices of the mushroom bodies with other parts of the nervous system.

Green. The superior dorso-cerebral commissure.

Brown. Motor and other efferent fibers.

Black. Association and miscellaneous fibers and cells.

EXPLANATION OF ABBREVIATIONS.

a. c.—Anterior commissure.

a h.—Anteror roots of the mushroom bodies.

a. i. c.—Antero-inferior dorso-cerebral commissure.

A. L.—Antennal lobe.

a m.—External antenno-motor nerve.

a. m^1.—Internal antenno-motor nerve.

a. s.—Antenno-sensory fibers.

c. b.—Central body.

c. c.—Fibrillar arch.

c. cb.—Commissure of the central body.

clx.—Calices of the mushroom bodies.

d. v.—Dorso-ventral tract.

e. clx.—Calices of the outer mushroom bodies.

F.—Oesophageal foramen.

g. cb.—Tubercles of the central body.

i. clx.—Calices of the inner mushroom bodies.

i. h.—Inner roots of the mushroom bodies.

i. o. c.—Inferior optic commissure.

l.—Labial nerve.

l. cb.—Lower portion of the central body.

l. t. 2g.—The antero-posterior optic tract.

md.—Mandibular nerve.

mx.—Maxillary nerve.

o^1 o^2 and o^3—Antenno-cerebral tracts. o^1 inner, o^2 middle, o^3 outer.

o. b.—Olfactory bodies or glomerulæ.

o. c.—Ocelli, $oc.^1$ median; $oc.^2$ right, $oc.^3$ left.

oc. n.—Posterior group of fibers from the ocelli.

op. b.—Optic body.

p.—Posterior nerve.

p. i. c.—Postero-inferior dorso-cerebral commissure.

p. o. t.—A posterior optic tract.

r. o. g.—Region of the ocellar glomerulæ.

s.—Stomatogastric nerve.

s. n.—Nerve of the salivary glands.

s. o. c.—Superior optic commissure.

s.æ. g.—Ventro-cerebron or subœsophageal ganglion.

t. op. b.—Anterior optic tract (to the optic body).

st.—Stalks of the mushroom bodies.

n. c.—The superior dorso-cerebral commissure.

u. c. b.—Upper portion of the central body.

u. t. 2*g.*—Antero-superior optic tract.

u. t. 3*g.*—Postero-superior optic tract.

v. c.—Ventral column.

z.—Small cells of mushroom body.

PLATE XIV.

Fig. 1. Frontal section several sections in front of the junction of the roots and stalks of the mushroom bodies, showing association fibers in the median region, and the antennal morula. *7.* Tract of fibers from cells behind the stalks to the anterior root of the mushroom bodies ; *tr.*, large trachea piercing the ocellar nerves and the dorsal region of the brain. *s.* Median nerve of the stomatogastric system ; *z*, pyramid of small cells of the mushroom body. Prepared by the formol-copper-hæmatoxylin method.

Fig. 2. Frontal section through the stalks and inner roots of the mushroom bodies, embracing the superior and the antero-inferior dorso-cerebral commissures. Same method as fig. 1.

Figs. 3 and 4. Frontal section. The two anterior roots of the mushroom bodies, showing the bands produced by the bushy terminations of the association fibers. By a modified Weigert method.

PLATE XV.

Fig. 5. Frontal section just behind the inner roots of the mushroom bodies, showing the fibers radiating from the central body. By the formol-copper-hæmatoxylin method.

Fig. 6. A frontal section further back, embracing the inferior optic commissure and the middle and the outer antenno-cerebral tracts. Same method.

PLATE XVI.

Horizontal sections, all by the formol-copper-hæmatoxylin method.

Fig. 7. Section cutting off the inner calices of the mushroom bodies and embracing the superior dorso-cerebral commissure and the top of the central body. *c. cb.* commissure of the central body.

Fig. 8. A section at a lower level embracing the top of the fibrillar arch.

Fig. 9. A section embracing the posterior commissure of the central body and passing just through the top of the lower portion of this. The "pillars" of the fibrillar arch appear on either side of the light tract formed by the large fibers of the ocellar nerves.

Fig. 10. A section embracing the two inferior dorso-cerebral and the lower optic commissures, and two of the posterior optic tracts. The salivary nerve appears in the upper right hand corner as a light spot.

PLATE XVII.

Fig. 11. A frontal view of the brain exclusive of the outer portion of the optic lobes as a transparent object, showing the different bodies in dotted black outline and the fiber tracts in colors. For an explanation of the latter see explanation of colors. General outline and the outlines of the calices taken from a camera drawing of a brain mounted *in toto* in balsam. The outlines of the other bodies and the fiber tracts taken from sections prepared by the formol-copper-hæmatoxylin method and reconstructed by the aid of millimeter paper and by the superimposition of camera drawings.

PLATE XVIII.

Fig. 12. A thick horizontal section embracing the region from the base of the inner mushroom bodies to the middle of the optic bodies. Outlines from formol-copper-hæmatoxylin sections as in fig. 11.

PLATE XIX.

Fig. 13. The remainder of the brain below that represented in fig. 12. Outlines from sections as in fig. 12.

PLATE XX.

Fig. 14. The lateral half of the brain viewed in optical sagittal section from the median plane outward. Outlines from thick sections prepared by the Golgi method.

PLATE XXI.

Cells and fibers from camera drawings of bichromate of silver preparations.

Fig. 15. Cells and fibers from the antennal lobe. x 121.

Fig. 16. Fibers from the antennal nerve and an olfactory body. In the section the right hand branch of the upper fiber was found, after the drawing here was made, to end in a small tuft of branches forming a portion of a glomerula. x 121.

Fig. 17. Terminations of an association fiber in the junction of the stalks and roots of the mushroom bodies. x 121.

Fig. 18. Cells and fibers of the mushroom bodies. x 102.

Fig. 19. Cell bodies of the same. x 121.

Fig. 20. An olfactory glomerula formed by the termination of a fiber of one of the antenno-cerebral tracts.

Fig. 21. The terminations of association fibers in the anterior root of the mushroom bodies.

Fig. 22. A fiber passing across the top of one of the anterior roots and branching profusely in the region just inside of it. Some of the branches seem to penetrate the root.

Fig. 23. Fibers terminating in the calices entering about the origin of the stalk.

Fig. 24. A drawing from three superimposed sagittal sections embracing the region from near the median line to the outer side of the anterior root. *g*, cells on the outside of the antennal lobe; above them and obscuring their fibers is a mass that may be composed of several over impregnated cells just above the antennal morula. For the rest see the diagrams in plates XVII to XX.

Fig. 25. Fiber entering an anterior root and apparently fusing with the parallel fibers. See text, p. 161.

Fig. 26. The smaller kind of fibers terminating in the calices. x 102. See text, p. 157.

Fig. 27. The terminations of the same magnified about 586 diameters.

Fig. 28. Association fibers terminating in the anterior roots. This figure should be viewed from the adjacent corner of the plate. See text, p. 160.

PLATE XXII.

Fig. 29. Tracheal terminations in the calyx of the mushroom bodies, x 102. Frontal section.

Fig. 30. Fiber 36 of diagrams. x 121. Sagittal section.

Fig. 31. Fibre 10 of the diagrams. x 102. It originates from a cell situated above the antennal morula. Sagittal section.

Fig. 32. Fibers from an oblique horizontal section. One with arborescent terminations in the central body Two passing from one inner root to the region above the anterior root of the opposite side. One passing forwards over the central body and branching in the region in front of it.

Fig. 33. A twisted fiber from the region below and behind the optic body. Sagittal section.

Fig. 34. Fiber from a sagittal section. x 121. It passes below an inner root and sends a branch up over the union of the same with the stalks.

Fig. 35. Fiber passing antero-posteriorly below the central body and sending several branches up in front of the latter. x 121.

Fig. 36. A portion of a motor fiber with its cell-body. See text, p. 174.

Fig. 37. Fiber from the antennal region terminating arborescently in the central body. From a frontal section. x 121.

Fig. 38. Fibers of the posterior inferior dorso-cerebral commissure. x 102.

Fig 39. Fibers apparently belonging to the antenno-motor nerve, and one commissural fiber of the ventro cerebron.

Fig. 40. Three fibers from two consecutive median sagittal sections. All three are seen to send a process each into the central body. A fragment in the lower part of the figure may be a portion of the outer or right hand fiber of the upper part of the figure. x 121.

Fig. 41. A fiber from the base of the central body sending long branches down into the ventro-cerebron and to the anterior portion of the ventral cord. x 121.

Fig. 42. Two fibers terminating in a so-called ocellar ganglion. x 121.

NOTE.—On page 174, line 8, for "(p.)" read "(p. 161)."

ERRATA.

Page 133, line 5, add 1895-6.
" 184, " 21, for Grylotalpa read Gryllotalpa.
" 192, " 22, delete the copper-.
" 192, " 23, " and A.
" 192, " 26, for Samomya read Somomya.
" 210, delete the note at the foot of the page.