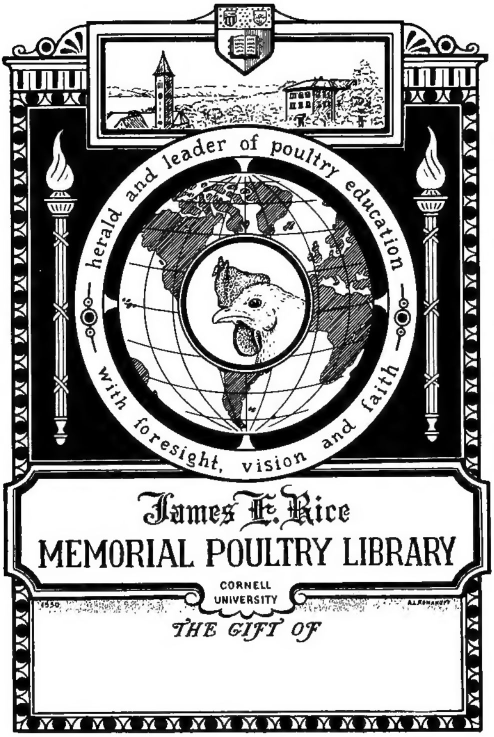
herald and leader of poultry education
with foresight, vision and faith
1930
A.L.ROMANOFF

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THE DEVELOPMENT OF THE OCULOMOTOR NERVE, THE CILIARY GANGLION, AND THE ABDUCENT NERVE IN THE CHICK.

BY FREDERICK WALTON CARPENTER.

WITH SEVEN PLATES.

CAMBRIDGE, MASS., U. S. A.:
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Reports on the Scientific Results of the Expedition to the Eastern Tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieutenant Commander L. M. Garrett, U. S. N., Commanding, published or in preparation: —

A. AGASSIZ. General Report on the Expedition.
A. AGASSIZ. I.[1] Three Letters to Geo. M. Bowers, U. S. Fish Com.
A. AGASSIZ and H. L. CLARK. The Echini.
F. E BEDDARD. The Earthworms.
H. B. BIGELOW. The Medusae.
R. P. BIGELOW. The Stomatopods.
S. F. CLARKE. The Hydroids.
W. R. COE. The Nemerteans.
L. J. COLE. The Pycnogonida.
W. H. DALL. The Mollusks.
C. R. EASTMAN. The Sharks' Teeth.
B. W. EVERMANN. The Fishes.
W. G. FARLOW. The Algae.
S. GARMAN. The Reptiles.
H. J. HANSEN. The Cirripeds.
H. J. HANSEN. The Schizopods.
S. HENSHAW. The Insects.
W. E. HOYLE. The Cephalopods.
C. A. KOFOID. III.[3] The Protozoa.
P. KRÜMBACH. The Sagittae.
R. VON LENDENFELD. The Sponges.
H. LUDWIG. The Holothurians.
H. LUDWIG. The Starfishes.
H. LUDWIG. The Ophiurans.
J. P. McMURRICH. The Actinaria.
G. W. MÜLLER. The Ostracods.
JOHN MURRAY. The Bottom Specimens.
MARY J. RATHBUN. The Crustacea.
HARRIET RICHARDSON. II.[2] The Isopods.
W. E. RITTER. The Tunicates.
ALICE ROBERTSON. The Bryozoa.
B. L. ROBINSON The Plants.
G. O. SARS. The Copepods.
H. R. SIMROTH. The Pteropods and Heteropods.
TH. STUDER. The Alcyonaria.
T W. VAUGHAN. The Corals.
R. WOLTERECK. The Amphipods.
W. McM. WOODWORTH. The Annelids.

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[1] Bull. M. C. Z., Vol. XLVI., No. 4, April, 1905, 22 pp.
[2] Bull. M. C. Z., Vol. XLVI., No. 6, July, 1905, 4 pp., 1 pl.
[3] Bull. M. C. Z., Vol. XLVI., No. 9, September, 1905, 5 pp., 1 pl.

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No. 2. — CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE, UNDER THE DIRECTION OF E. L. MARK, No. 172.

The Development of the Oculomotor Nerve, the Ciliary Ganglion, and the Abducent Nerve in the Chick.

By Frederic Walton Carpenter.

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Introduction.

"Von allen motorischen Nerven ist mit Ausnahme vielleicht des Hypoglossus kein anderer zum Gegenstand so widerspruchsvoller Angaben und Deutungen geworden, wie der Oculomotorius. Er ist als dorsaler, als ventraler und als gemischter Nerv in Anspruch genommen worden; man hat ihm metamerischen Werth zu- und abgesprochen; er ist als Theilstück des Trigeminus definirt, und ihm sind alle Beziehungen zum Trigeminus geleugnet worden. Man hat Ganglien an ihm entdeckt, deren Ursprungsort man in der Ganglienleiste sah; man hielt sie dann für eine Abspaltung des G. ciliare; man schrieb sie einem eigenen G. oculomotorii zu, das nichts mit dem G. ciliare zu thun habe; man leugnete die Ganglien ganz und gar — kurz es war nicht mit ihm fertig zu werden." — Dohrn (**'91**, p. 2).

Since Dohrn commented thus in 1891 upon the diversity of opinion which exists concerning the oculomotor nerve and the ciliary ganglion, three investigators have added still another to the already large number of conflicting statements. They have asserted that in selachians the oculomotor nerve grows from the mesocephalic ganglion to the ventral face of the mid-brain, and not in the opposite direction, as had previously been supposed. Dohrn himself, in the article from which the quotation is taken, described an entirely new mode of origin for the cells of the ciliary ganglion, namely, migration from the neural tube into the root of the oculomotor nerve.

This lack of agreement in regard to the developmental history of the oculomotor nerve, and particularly of the ciliary ganglion, seemed a sufficient justification for a renewed study of the subject. In the case of the abducent nerve, opinions of observers being more in accord, a study of its development might be expected to result in little more than a confirmation of generally accepted views. Though primarily concerned with the oculomotor nerve and ciliary ganglion, I have, nevertheless, included in this paper my observations on the histogenesis of the abducens. Its study has been made easy by its presence in the series of sections in which the later development of the oculomotor has been followed, and as a typical ventral cranial nerve with motor functions it has proved interesting for the purposes of comparison with the oculomotor. The remaining eye-muscle nerve, the trochlear, first appears at a comparatively late stage, and my observations have not been extended to it.

Several considerations led to the selection of the chick as the subject for investigation. First, closely connected stages in the development of the eye-muscle nerves have been studied in but few of the Amniota, the greater part of the observations having been confined to selachians. Secondly, no investigator has directly concerned himself with the genesis of these nerves in birds since Marshall published the first accounts of their development in 1877 and 1878. Marshall's descriptions are admittedly incomplete, and certain of his interpretations are questionable in the light of more recent studies in other classes of vertebrates. Since his time observations on the nerves in question have been fragmentary and incidental. Thirdly, in the case of the chick it is possible to control incubation, and obtain embryos in the required stages of development.

It is a pleasure to acknowledge here my sense of obligation to Professor E. L. Mark, under whose guidance the present work was carried on in the Zoölogical Laboratory of Harvard University. The constant interest, the helpful suggestions and the conservative judgments of Professor Mark have been of the greatest value to me. I am also indebted to Professor H. V. Neal, of Knox College, for advice as to the use of the vom Rath fluid in the early stages of the development of nerves.

PART I.—ANATOMY AND HISTOLOGY.

A. Historical Survey.

a. ANATOMY.

1. *Eye-Muscle Nerves.*

THE older anatomists (Muck, **'15**; Bonsdorff, **'52**; Budge, **'55**; and others) who first investigated the eye-muscle nerves of birds found them homologous with nerves of similar function in other classes of vertebrates. The third, or oculomotor, nerve arises from the ventral face of the mesencephalon, and is distributed to the dorsal, ventral and anterior rectus muscles and to the ventral oblique muscle. The fourth, or trochlear, nerve emerges from the dorsal aspect of the brain, at the posterior boundary of the mesencephalon, and innervates the dorsal oblique muscle. The sixth, or abducent, nerve takes its origin from the ventral side of the metencephalon, and passes to the posterior rectus muscle. A slender branch of this nerve is given off to the muscles of the nictitating membrane (quadratus and pyramidalis). In Bronn's Thierreich is mentioned on the authority of Bonsdorff an anastomosis between the sixth nerve and the ramus ciliaris trigemini in Corvus cornix. In this bird fibres are also said to pass to the ramus ciliaris externus of the ciliary ganglion; while in Grus cinerea a fine branch of the abducens passes partly to the ramus ciliaris internus of the ciliary ganglion, and partly to the ganglion itself. The distribution of abducent fibres to the eyeball in birds has also been recorded by Jegorow (**'86–87**), who considers it possible that these may be sympathetic fibres, which join with the sixth nerve as it passes through the cavernous sinus and proceed cephalad in its trunk.

2. *Ciliary Ganglion.*

A well-marked ganglion is always found in connection with the oculomotor nerve of birds. This ganglion corresponds to the ciliary ganglion of human anatomy, which was first described by Schacher in 1701 (Jegorow, **'86–87**). In man it occurs in the posterior region of the orbit as a small, laterally compressed, somewhat four-sided body, measuring about 2 mm. in an antero-posterior direction. From behind it receives branches from three different sources: a short or motor root (radix brevis) from the oculomotor nerve, a long or sensory root (radix longa) from the nasal branch of the ophthalmic division of the trigeminus, and a sympathetic root (radix sympathica) from the sympathetic plexus of the cavernous sinus. It gives off in front six to eight ciliary nerves, which proceed to the sclerotic and choroid coats, ciliary muscle, iris and cornea of the eyeball. These nerves are distinguished as the short ciliary nerves from the so-called long ciliary nerves, which emanate from the nasal branch of the trigeminus, and have the same distribution as the short ciliaries (Quain's Anatomy, Thane, **'95**).

The ganglion in question has received various names from different authors (ciliary, ophthalmic, lenticular, oculomotor, Schacher's). It is commonly described in the text-books of human anatomy in connection with the trigeminal nerve. It is almost invariably stated to be sympathetic in nature (as first suggested by Arnold, **'31**), although it differs from typical sympathetic ganglia in giving origin to medullated peripheral nerves (the short ciliaries) instead of non-medullated fibres.

Comparative studies of the anatomical connections of the ciliary ganglion have been made by Schwalbe ('79), Jegorow ('86–87), Holtzmann ('96) and Ónodi (:01).

Schwalbe, in his extensive and much-quoted work on "Das Ganglion oculomotorii," shows that the ciliary ganglion is represented in the lower vertebrates by groups of ganglion cells distributed along the course of the oculomotor nerve. Passing upward toward the higher forms, the cells become more closely associated into a compact body, this change being accompanied by a gradual withdrawal of the ganglion from the trunk of the oculomotor nerve through the formation of a radix brevis. However, not all the higher vertebrates possess short roots, since in many mammals (sheep, calf, dog, rabbit) none exists, the ganglion being placed directly on the trunk of the oculomotor. Schwalbe denies the existence of a connection between the ciliary ganglion and the trigeminal nerve in several species, and believes the sympathetic root to be confined to mammals. He, therefore, asserts that the ciliary ganglion belongs primarily to the oculomotor, which he considers entitled to the rank of an independent segmental nerve.

Jegorow's researches on "le ganglion ophthalmique" were, like those of Schwalbe, very comprehensive. As far as the anatomical relations of the ganglion are concerned, he differs from the latter writer chiefly in regard to the importance of the connection with the trigeminus. This he regards as constant, and necessary for the existence of the ganglion, throughout the vertebrate series.

Holtzmann found the ciliary ganglion in amphibians, birds and mammals more intimately connected with the oculomotor than with the trigeminus. Although he found neuraxons joining the ciliary ganglion with the fifth nerve where Schwalbe believed no connection existed, he does not regard these neuraxons, in certain cases, as constituting a physiological radix longa.

The examination of many selachians as well as several bony fishes and mammals convinced Ónodi that the connection between the ciliary ganglion and the trigeminus is more intimate than Schwalbe's researches show. In selachians he frequently found a macroscopic ciliary ganglion external to the trunk of the oculomotor. The ganglionic groups connected distally with the third and fifth nerves he considers sympathetic in nature, and in support of this view calls attention to nerve fibres extending from them to form a plexus about the wall of a neighboring blood vessel.

The observations which have already been made on the anatomical relations of the ciliary ganglion in the group of birds will now be summarized.

Connection with the Oculomotor Nerve. A radix brevis is present in Strix flammea, in various species of the genus Corvus, in Falco tinnunculus and Sterna hirundo. The ciliary ganglion is placed directly on the trunk of the third nerve in the goose, Falco palumbarius, Aquila leucocephala, Meleagris gallopavo, Ardea cinerea, Vanellus cristatus and Gallinula pusilla (Gadow und Selenka, '91). To this list should be added Gallus domesticus, the pigeon and the duck (Holtzmann, '96).

Connection with the Ophthalmic Branch of the Trigeminal Nerve. Schwalbe ('79) describes a large ciliary nerve passing cephalad from the distal extremity of the ciliary ganglion of the goose. This nerve receives, a short distance from its origin from the ganglion, a slender ramus from the ophthalmic branch of the trigeminus, but no direct fibrous connection appears to exist between the last-named nerve and the ganglion. The same conditions were observed by Holtzmann ('96) in the hen, duck and pigeon, as well as in the goose. Schwalbe concluded from the appearances that no long root could be said to be present in birds, but Holtzmann has ascertained by microscopical examination that in the hen and goose (the only forms examined in this way) about one-fourth of the neuraxons of the communicating branch from the fifth nerve turn centrad, and, running parallel with those of the ciliary nerve, enter the ganglion. This connection he believes to be a survival of an embryonic union between the fundaments of the ciliary and Gasserian ganglia, and to possess a developmental rather than a physiological significance.

A few cases of direct connection between the fifth nerve and the ciliary ganglion have been recorded. Jegorow ('86–87) asserts that such a condition obtains in the pigeon and vulture. In Bronn's Thierreich, Muck ('15) is cited as authority for the statement that in several birds the communicating branch enters the anterior part of the ganglion. Bonsdorff ('52) describes for the crane two rami from the trigeminus which have the typical relations of long roots of the ganglion.

Connection with the Sympathetic System. Neither Schwalbe ('79), Holtzmann ('96) nor the older investigators discovered any evidence of a connection between the sympathetic system and the ciliary ganglion in birds. Jegorow ('86–87), while admitting that the distribution of sympathetic fibres has not been proved anatomically, infers, nevertheless, the presence of sympathetic neuraxons in the ciliary ganglion from the occurrence of certain fibres which pass from the latter to the walls of neighboring arteries. He considers it possible that sympathetic neuraxons may enter the third nerve in the cavernous sinus, where it comes into close relation with the cephalic extension of the cervical sympathetic system.

The only description of a sympathetic root of the avian ciliary ganglion to be found in the literature is that of Rochas ('85), who detected in the goose several fine fibres extending to the ciliary ganglion from the sympathetic plexus about the ophthalmic artery (Weber's plexus).

Ciliary Nerves. There is much variation in the number of ciliary nerves given off by the ciliary ganglia of different species of birds. Variations may also occur among individuals of the same species. Schwalbe ('79) states that the number may vary from one in many birds, including the hen, owl and goose, to seven in parrots.

Schwalbe figures for the goose a ciliary nerve (ramus ciliaris trigemini) emerging from the ophthalmic branch of the trigeminus distal to the origin of the communicating branch passing to the ramus ciliaris oculomotorii. Holtzmann ('96) shows that in the hen the communicating branch gives off an independent ciliary nerve to the eyeball.

b. HISTOLOGY.

1. *Oculomotor Nerve.*

In birds, as well as in man (Barratt, :01) and in teleosts (Herrick, '99), both large and small medullated neuraxons are present in the oculomotor nerve. This has been shown to be the case in the pigeon by Langendorff (:00), who found the main portion of the nerve composed of neuraxons of large calibre, while smaller ones occurred near the periphery. In all forms the majority of the small neuraxons pass into the ciliary ganglion.

2. *Abducent Nerve.*

I have not been able to find any description of the finer structure of the abducent nerve in birds. In man it is made up of large and small medullated neuraxons (Barratt :01).

3. *Ciliary Ganglion and Short Ciliary Nerves.*

Anatomical Evidence. The character and connections of the cells of the ciliary ganglion of vertebrates have long been favorite topics of investigation among neurologists.

Before the silver impregnation process of Golgi had come into general use, Retzius ('81) had already demonstrated by other methods the multipolarity of the ciliary-ganglion cells of mammals. In a later paper (Retzius, '94, '94ª) he confirmed his former observations by the aid of the Golgi process. Using the latter method, Kölliker ('94) and Michel ('94) obtained like results, and showed, furthermore, that the ganglion cells are surrounded by pericellular baskets of nerve fibrils. These pericellular baskets have also been demonstrated, and proved to be intracapsular, by the methylen-blue *intra-vitam* stain (Huber, '97). Inasmuch as all these conditions are characteristic of the cells of sympathetic ganglia, the investigators cited above are unanimous in declaring the mammalian ciliary ganglion to be sympathetic in nature.

On the other hand, Schwalbe ('79), a "partisan ardent," to quote Jegorow, of the cerebro-spinal character of the ciliary ganglion, found in the ciliary ganglion of the sheep and calf unipolar cells, such as are characteristic of cerebro-spinal ganglia. The crudeness of Schwalbe's methods, however, leaves his results open to question. D'Erchia ('94) discovered among the numerous multipolar cells of the cat's ciliary ganglion a few bipolar cells. Such cells were seen in both the cat and dog by Holtzmann ('96), who, furthermore, found the comparatively small ciliary ganglion of the rabbit to be composed mainly, if not wholly, of cells of the cerebro-spinal type, many being bipolar. Jegbrow ('86-87) figures, in a colored plate, spinal, sympathetic and ciliary ganglion cells of the cat, prepared by Boukhaloff according to a special differential method. The cells from the spinal and ciliary ganglia present the same appearance, whereas the sympathetic cells differ in staining qualities from the others. It is interesting to compare with these figures those given by His, Jun. ('91) of the same three kinds of ganglion cells taken from an embryo cat. Cells from the ciliary and from a sympathetic ganglion closely resemble each other, being small and unipolar. Those from the vagus ganglion (which belongs to the cerebro-spinal series) are, on the contrary, larger and bipolar in character.

Haller ('98) believes that the conditions which obtain in the central nervous system of the dog-fish and trout point to the cerebro-spinal character of the representatives of ciliary-ganglion cells found in these fishes. Golgi preparations of the mid-brain show, in addition to oculomotor neuraxons proceeding centrifugally from ganglion cells in motor niduli, other oculomotor neuraxons, which have no direct connection with central ganglion cells. These neuraxons he regards as centripetal processes from ganglion cells on the oculomotor nerve (i. e., ciliary ganglion cells). Such cells are accordingly to be looked upon as homologous with spinal-ganglion cells.

A considerable amount of evidence as to the nature of the ciliary ganglion in mammals has been derived from the employment of degeneration methods. To appreciate the significance of the results obtained, it must be borne in mind that in a typical sympathetic ganglion (one of the gangliated sympathetic cord) the motor neuraxons of the white ramus ("pre-ganglionic fibres"), originating from cells within the central nervous system, pass into the sympathetic ganglia, and end in pericellular baskets of fine fibrils about the sympathetic cells. From the latter are given off, peripherally, non-medullated neuraxons ("post-ganglionic fibres"), which make up the pale sympathetic nerves. These neuraxons, together with the sympathetic ganglion cells with which they are connected, form, consequently, the terminal link in a chain of neurons.

The investigations of Bach (**'96**) on the rabbit show that removal of the iris and ciliary body, to which the short ciliary nerves are distributed, results in a modification of the cells of the ciliary ganglion, while those of the nidulus of the oculomotor nerve remain normal. Apolant (**'96, '96**^{a}) cut the oculomotor nerve of young cats near its root. The fine medullated neuraxons passing to the ciliary ganglion degenerated peripherally as far as the cells of that ganglion, while these cells, together with the short ciliary nerves, remained unaltered. Bumm (**:00**) confirmed Apolant's results. After injury of the intrinsic eye muscles and the nerves distributed to them, nearly all the cells of the ciliary ganglion undergo changes (Marina, **'98, '99**), but, as shown by the further experiments of Marina, and by those of Fritz (**'99**), destruction of the cornea is also followed by a slight degeneration of some of the cells of the ciliary ganglion (one-eighth of the entire number, according to Marina). From this, both writers conclude that the ganglion is a mixed one, being largely motor, but also to some extent sensory in function. Fritz (**'99**) infers that the ciliary ganglion is connected with the sympathetic system from the fact that changes in the cells of the ganglion occur upon extirpation of the cervical sympathetic. Bumm (**:00**) is also of this opinion, since the cutting of the ciliary nerves in the cat results in the atrophy of only four-fifths of the cells of the ciliary ganglion. He considers the cells affected to be those of peripheral neurons, while the cells which remain unaltered are probably connected with the sympathetic system.

The study of degeneration preparations shows, then, that at least the majority of the mammalian ciliary-ganglion cells and their processes, the short ciliary nerves, may be considered the terminal neuraxons of a motor chain, and consequently sympathetic in their relations. The muscles innervated are of the unstriped variety.

Stefani (:01) was led to the conclusion that the short ciliary nerves have their centres, i. e., their ganglion cells, in the ciliary ganglion, by observing the effect on the cells of that ganglion when atropin is applied to the eye.

Histologically, the ciliary ganglion of birds differs from that of mammals. In the hen certain of its cells, as was first shown by Retzius ('81), are bipolar in character, each sending out two processes, which arise close together, and run either in the same or in opposite directions. Near their origins from the cell the processes are pale, but soon acquire medullary sheaths. Holtzmann ('96) examined the elements of the ciliary ganglion in the hen, duck, goose, and pigeon, finding in each of the four species both large and small ganglion cells. These were usually bipolar, but an occasional unipolar cell was observed, the single process of which soon divided into two. Holtzmann is of the opinion that while in many animals (amphibians, mammals) the ciliary ganglion contains both sympathetic and spinal cells, in birds a one-sided development, that of spinal elements, takes place. These do not, as a rule, become fully differentiated into true unipolar spinal ganglion cells, but remain in an embryonic bipolar condition.

From the foregoing, it is apparent that those cells of the ciliary ganglion of birds which have been described by investigators do not resemble histologically the sympathetic cells found in the same group. The great majority of the latter are well known to be multipolar, and, in general, to resemble the sympathetic cells of mammals (Ramon y Cajal, '91, '94; Timofeew, '98; Huber, '99).

Physiological Evidence. From a physiological point of view the ciliary ganglion of mammals is undoubtedly sympathetic. The experimental researches of Langley and Dickinson ('89) have demonstrated the fact that a moderate dose of nicotin, which has little, if any, effect on spinal ganglia, prevents the passage of efferent nervous impulses through sympathetic ganglia. These authors considered this result due to a paralysis of the sympathetic cells, but Huber ('97) has shown that it is more probable that the nicotin paralyzes the pericellular baskets of the preganglionic neuraxons about the cells, rather than the cells themselves. The physiological effect of nicotin has afforded, therefore, a valuable criterion for determining the character of the cells of the ciliary ganglion. After an injection of nicotin, Langley and Anderson ('92) found that the ciliary ganglion of the rabbit no longer transmitted nervous impulses.

Direct stimulation of the short ciliary nerves, however, still caused contraction of the ciliary body and the iris. The results of Langley and Anderson were confirmed for the dog and monkey by Marina ('98, '99). These investigators consequently regard it as proved that the neuraxons which innervate the sphincter iridis and the ciliary muscle are connected with the cells of the ciliary ganglion. The physiological experiments of Langendorff ('94) and Bernheimer ('97) point to the same conclusion. The former found that some time after death, when stimulation of the third nerve proximal to the ciliary ganglion was without result, excitation of the short ciliary nerves produced contraction of the iris. Bernheimer demonstrated that lesion of the oculomotor nerve in the monkey leaves the iris still active.

The physiological behavior of the ciliary ganglion of birds affords additional proof of the lack of similarity between its cells and those of the ciliary ganglion of mammals. Langendorff (:00) states, on the authority of Consiglio (:00), that, after the ciliary ganglion of birds has been subjected to the action of nicotin, stimulation of the third nerve is still followed by constriction of the pupil. He himself found that, in birds which have been bled to death, the neuraxons of the third nerve, the stimulation of which causes closure of the pupil, retained their irritability considerably longer than did those of mammals subjected to the same treatment. For these reasons he regards it improbable that an intercalation of sympathetic cells occurs, as in mammals, within the ciliary ganglion.

The fact that fibres emanating from the cervical sympathetic ganglia have no effect on the movements of the pupil in birds was established by Jegorow ('87), and has recently been confirmed by Langley (:03). In mammals, several observers have shown that stimulation of the cervical sympathetic nerve causes dilatation of the pupil (Hensen und Völkers, '68; Nawrocki und Przybylski, '91; Anderson, :03). The radially placed dilator muscle of the iris of birds is exceptionally well developed (Geberg, '83; Koganeï, '85; and others).

B. Observations.

a. Methods.

For the purpose of examining the main trunks of the eye-muscle nerves and their larger branches, dissections of the heads of adult fowls were made. Soon after death, the orbital cavities were opened by cutting through the conjunctiva and connective tissue, and the whole head placed in the picro-aceto-platino-osmic mixture of von Rath, the formula for which is given on page 175. After immersion in this fluid for from three to five days, the material was carried through several changes of 70 per cent alcohol, in which the excess of picric acid was, to a large extent, removed. The head was then allowed to stand until needed in a mixture of alcohol and glycerin. It was found that this treatment, which was suggested to the writer by Mr. W. A. Willard, differentiates well the nervous from the muscular tissues, and, aided by the use of the dissecting microscope, makes possible the tracing out of the distribution of very slender bundles of neuraxons.

In preparation for the detailed study of the more important and complicated relations of the nerves under consideration another method was adopted. Certain portions of the contents of the orbit were removed entire, care being taken to avoid straining or breaking the parts, and placed for fixation in either Zenker's fluid, osmic acid or the vom Rath mixture mentioned above. After dehydrating in alcohol, and imbedding in paraffin, serial sections of suitable thickness were made. The sections were cut in planes either at right angles to, or parallel with, the axis of the main trunk of the oculomotor nerve (see Plate 1, Figs. 1 and 2). The sections of the material fixed in Zenker's fluid were stained in acid-fuchsin. The osmic acid and vom Rath preparations needed no subsequent treatment for the differentiation of the medullated neuraxons.

Cells of the ciliary, the Gasserian (cerebro-spinal) and sympathetic ganglia were studied in the following manner, with a view to determining the number and character of their processes. The ganglia were removed from a freshly killed fowl and immersed in a 0.05 per cent solution of chromic acid, in which they were allowed to stand and slightly macerate for two or three days. They were then carefully teased apart with fine needles, and stained in acid-fuchsin. In this way a certain number of cells, retaining longer or shorter portions of their processes, were isolated from the rest of the ganglion, and prepared for examination. Other ganglia were fixed in the vom Rath mixture and studied in the form of serial sections.

b. ANATOMY.

1. *Eye-Muscle Nerves and Ciliary Ganglion.*

Oculomotor Nerve and Ciliary Ganglion. The nidulus of the oculomotor nerve lies in the ventral portion of the mesencephalon, near the mesocoele or aqueduct of Sylvius, in relation to which it occupies a ventro-lateral position. The situation of the nidulus in the cerebrospinal axis corresponds to that of the somatic motor column of ganglion cells (Gaskell) of the spinal cord. The neuraxons of the cells pass ventrad to emerge from the ventral face of the mesencephalon as the third nerve, which runs ventrad and cephalad through the oculomotor foramen, and then horizontally forward (Plate **1**, Fig. 1, *n. oc'mot.*). Passing ventrad of the posterior rectus muscle, it sends a small branch (*rm. mu. rt. d.*) dorsad and cephalad to the posterior edge of the base of the dorsal rectus muscle. Just distal to this branch, a large ventral ramus (*rm. v.*) is given off, on the opposite or ventral side of the nerve trunk. This ventral ramus passes beneath the ventral rectus muscle, and runs cephalad along the floor of the orbit to terminate, as a brush of fine fibres, on the ocular face of the ventral oblique muscle, about midway of its length. A slender bundle of neuraxons (*rm. mu. rt. v.*) arises from the main trunk of the nerve in close connection with the ventral ramus, and innervates the lower face of the ventral rectus muscle, near the proximal end of the latter. From the ventral ramus, soon after it passes the anterior border of the ventral rectus muscle, a small branch (*rm. mu. rt. a.*) is given off to the adjacent edge of the anterior rectus muscle.

Immediately distal to the origin of the ventral ramus, the remainder of the neuraxons of the third nerve enter the spindle-shaped ciliary ganglion (*gn. cil.*), which measures approximately two mm. in length, and has a greatest diameter of a little less than one mm. No radix brevis can be said to exist in the hen, since it is possible, in serial sections, to trace the cells of the ciliary ganglion back as far as the level of the ventral ramus (Plate **2**, Fig. 3, *C*). From the distal end of the ciliary ganglion, a comparatively large ciliary nerve (Plate **1**, Fig. 1. *n. cil. oc'mot.*) is given off. This runs parallel with the optic nerve, and penetrates the sclerotic coat of the eyeball. On its way, the ciliary nerve gives rise to a variable number of branches of microscopical size (Plate **1**, Fig 2, *rm. n. cil. oc'mot.*), which accompany it to the eye. The ciliary nerve receives, about one mm. distal to the region of the cells of the ciliary ganglion, a slender communicating ramus (Figs. 1 and 2, *rm. comn.*) from the ophthalmic branch of the fifth nerve.

Trochlear Nerve. The nidulus of the trochlear nerve is found in the somatic motor column in the ventral part of the mesencephalon, posterior to the nidulus of the oculomotor. The nerve (Fig. 1, *n. trch.*) takes its superficial origin from the dorsal surface of the brain, between the optic lobes and the base of the epencephalon. Turning ventrad and cephalad, it passes through the orbit, running mediad and dorsad of the posterior and dorsal rectus muscles, and ends on the ocular face of the dorsal oblique muscle (Fig 1, *mu. ob. d.*).

Abducent Nerve. Like the other eye-muscle nerves, the abducens has its nidulus in the somatic motor column. It lies in the ventral part of the metencephalon, and from it the abducent neuraxons run ventrad to emerge from the ventral face of this division of the brain, not far from the median plane. The trunk of the nerve (Fig. 1, *n. abd.*) proceeds cephalad, and, crossing dorsad of the oculomotor nerve, divides into several terminal ramifications, which are distributed to the portion of the posterior rectus muscle lying laterad of the ophthalmic branch of the trigeminus (*rm. opth. trig.*), which passes through the proximal part of the muscle. Shortly before terminating in this way, the abducens sends cephalad a branch (Plate 1, Fig. 2, *rm. mu. qd.* + *pyr.*) to the muscles of the nictitating membrane. This branch soon bifurcates, and between its forks the communicating ramus connecting the trigeminal and oculomotor nerves often passes.

Ophthalmic Branch of the Trigeminal Nerve. The Gasserian ganglion presents two well-marked divisions, an ophthalmic portion (Fig. 1, *gn. Gas.*) extending cephalad, and a maxillo-mandibular portion directed ventrad. The first becomes gradually narrowed into the ophthalmic branch of the trigeminal nerve (*rm. opth. trig.*) which, running cephalad, usually penetrates the posterior rectus muscle, and then passes, ventrad of the proximal ends of the dorsal rectus and dorsal oblique muscles, to the anterior boundary of the orbit. Here it divides, one large nasal ramus (*rm. na.*) entering the nasal chamber, while several small branches (*rm. f.*) extend dorsally to a more superficial distribution, and, taken together, correspond to a frontal ramus.

From a point opposite the distal extremity of the ciliary ganglion, the ophthalmic branch sends out a communicating ramus (Figs. 1 and 2, *rm. comn.*), which unites with the oculomotor ciliary nerve about one mm. distad of the ciliary ganglion. However, not all the neuraxons which here leave the ophthalmic branch reach the oculomotor ciliary nerve, since a slender bundle of them emerges from the communicating ramus about midway in its course, and proceeds toward the eyeball as an independent trigeminal ciliary nerve (Fig. 2, *n. cil. trig.*′). In some cases, another trigeminal ciliary nerve (*n. cil. trig.*″) leaves the communicating ramus near its union with the oculomotor ciliary nerve, and likewise passes as a separate fibre to the eyeball.

c. HISTOLOGY.

1. *Oculomotor Nerve.*

The trunk of the oculomotor nerve is made up of both large and small medullated neuraxons. Some of the former may reach the size of 15 micra in diameter, while some of the latter may measure only 3 micra. Between these two extremes all intermediate sizes are to be found. The trunk of the nerve is composed mainly of comparatively large neuraxons, among which a few small ones are interspersed, but at its lateral periphery a zone of small neuraxons occurs (Plate 7, Fig. 21). This zone is represented by the shaded portions of the diagrams shown in Plate 2, Figure 3, which represent cross-sections of the oculomotor at various levels along its course. The unshaded portion of the nerve trunk is that in which large neuraxons predominate. At *A* is shown the conditions which obtain in the nerve proximal to its branches. Diagrams *B* and *C* represent, respectively, sections through the origin of the branch to the dorsal rectus, and through the origin of the ventral ramus. It will be noticed that both draw their neuraxons from the unshaded portion of the nerve trunk. A photomicrograph of a cross-section of the branch to the dorsal rectus muscle is given in Plate 7, Figure 22. While the branch is mainly made up of neuraxons of large size, a certain number of smaller ones is also present. It is probable that the differences in size of the neuraxons correspond with the differences in the degree of development of the muscle fibres to which they are distributed. It has been pointed out by C. J. Herrick ('99) that large neuraxons of the eye-muscle nerves of Menidia are connected with large muscle fibres, and those of lesser calibre with small muscle fibres. In the eye muscles of the hen, fibres of varying sizes also occur. In a later paper (C. J. Herrick, :02), the writer just cited has advanced the opinion that differences in the calibre and medullation of neuraxons frequently signify nothing more than a correlation with the degree of functional development of the peripheral end-organs.

The neuraxons which pass into the ciliary ganglion are those which form the peripheral zone, shown by the shading in the diagrams of Plate 2, Figure 3. They are of small calibre. Distal to the ganglion the ciliary nerve is likewise entirely made up of small neuraxons (*D*), the medullary sheaths of which are, however, well developed.

2. *Abducent Nerve.*

The elements of the abducent nerve, when seen in cross-section, appear, for the most part, as large medullated neuraxons. As in the oculomotor nerve, a few small neuraxons occur among the larger ones. The nerve trunk closely resembles in appearance that of the oculomotor, except that a peripheral zone of small neuraxons is not present.

The branch given off to the muscles of the nictitating membrane is composed almost entirely of neuraxons of large size.

3. *Ciliary Ganglion.*

The cells obtained from the ciliary ganglion by maceration and isolation answer to the description of the ciliary cells of the hen already given by Retzius ('81). They are large bipolar cells, the processes of which become heavily medullated a short distance from the cell body (Plate 2, Fig. 4). In a few instances the two neuraxons were seen to arise by a common stem, so that the ganglion cell may be said to be unipolar in character.

With the object of comparing the finer structure of the ciliary ganglion with that of cerebro-spinal and sympathetic ganglia, attempts were made to obtain an *intra-vitam* methylen-blue stain. Three trials were made, but in only one of these were the cells of the ciliary ganglion affected. The cells in this instance were not, however, deeply stained, and no pericellular baskets of fibrils were differentiated about them, such as have been demonstrated about the sympathetic cells of birds by Huber ('99) after injection of methylen-blue into the blood system.

Such evidence as I have been able to obtain as to the sympathetic or cerebro-spinal nature of the ciliary ganglion has resulted from the use of the vom Rath mixture. After fixation in this reagent, sections of spinal ganglia can with ease and certainty be distinguished from sections of sympathetic ganglia. Spinal cells average larger, some measuring as much as 60 micra in diameter. Cells of this size are never found in sympathetic ganglia. Large medullated neuraxons are given off by spinal cells, and portions of these occur in every section through the ganglia. The peripheral neuraxons of the sympathetic cells, though also medullated, are never of as large calibre as those of the spinal cells. But the most convincing, and characteristic peculiarity of the sympathetic ganglia is the mass of fine fibrils which occurs in them, filling in the interstices between the cells, and obscuring, to some extent, their boundaries and cytoplasm. Though their relations to the cells are not well brought out by the vom Rath stain, these fibrils undoubtedly form the pericellular baskets which are known to be present in sympathetic ganglia. Owing to the absence of such an abundance of fibrous elements the spinal ganglia present a quite different appearance. The cells of these are unobscured, and their boundaries are sharply defined.

When the ciliary ganglion of the hen is prepared according to the vom Rath process, and sectioned longitudinally, it is seen, under the microscope, to be divisible into two regions (compare *A* and *B*, text Figure). Approximately two-thirds of the ganglion (*B*) is composed mainly of large, well-defined cells, around which very few pericellular fibrils occur. Some of these cells reach the dimensions of the largest of the spinal-ganglion cells. In this portion of the ganglion are found small, but heavily medullated, neuraxons. Of these, a part are evidently continuous with the neuraxons entering the ganglion from the oculomotor nerve. Others are plainly seen to leave the ciliary ganglion by the ciliary nerve, the greater part of which arises from this portion of the ganglion, and is made up of small, well-medullated neuraxons.

In the dorsal region of the ciliary ganglion, on the side toward the ophthalmic branch of the fifth nerve, occurs an accumulation (*A*) of small cells, which makes up approximately one-third of the entire volume of the ganglion. Here are found fine neuraxons, showing little evidence of medullation, and a quantity of delicate fibrils resembling those of the pericellular baskets of sympathetic ganglia, although not present in such profusion as in the sympathetic ganglia. A communicating ramus between the ophthalmic branch of the trigeminus and the oculomotor ciliary nerve has been mentioned. Longitudinal sections of the ciliary nerves show that the slender, very slightly medullated neuraxons which compose the communicating ramus divide into two sets upon reaching the ciliary nerve. One of these bundles turns toward the eyeball, and accompanies the ciliary nerve to its peripheral distribution. The other bundle is recurrent, being deflected toward the ciliary ganglion. Its neuraxons run parallel with those of the ciliary nerve, and enter that portion of the ganglion which is characterized by small cells and pericellular fibrils. From this region there is given off to the eyeball a bundle (α) of fine neuraxons with but slight traces of medullation. These accompany the medullated neuraxons from the remaining two-thirds of the ganglion (β) as component elements of the ciliary nerve. In certain cases they may be found occurring in the form of a distinct, non-medullated bundle, running close beside the larger group of medullated neuraxons, but separated from the latter by perineurium.

The relations of the two parts of the ciliary ganglion are shown in a diagrammatic way in the accompanying figure.

In any attempt to assign the ciliary ganglion, on histological grounds, to either the cerebro-spinal or sympathetic systems, it is plain that the two regions described above must be separately considered. In respect to the first or ventral region (*B*), it can be said that the size of its cells, the heavy medullation of both its central and peripheral neuraxons, and the comparatively small volume of the pericellular fibrils, agree with the conditions found in cerebro-spinal ganglia. The central and peripheral neuraxons are, however, of smaller calibre. It is probable that the large bipolar ganglion cells obtained by maceration methods, as already described, were from this region. These resemble cerebro-spinal elements, except that two medullated processes instead of one are given off by each cell; and even where a tendency toward unipolarity occurs, the typical **T**-shaped condition of a cerebro-spinal neuron is not attained.

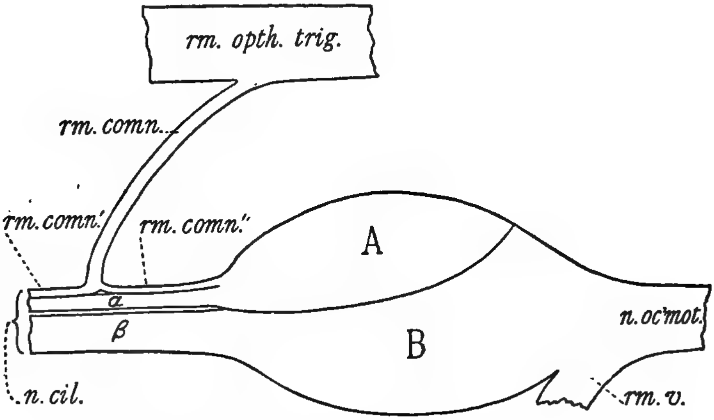

Diagram of a longitudinal section through the ciliary ganglion. *A*, region of small cells, non-medullated neuraxons, and pericellular fibrils; α, small, non-medullated ciliary neuraxons; *B*, region of large cells and small medullated neuraxons; β, small, medullated ciliary neuraxons; *n. cil.*, ciliary nerve; *n. oc'mot.*, oculomotor nerve (large and small medullated neuraxons); *rm. comn.*, communicating ramus (small non-medullated neuraxons); *rm. comn.'*, distal neuraxons of communicating ramus; *rm. comn.''*, recurrent neuraxons of communicating ramus; *rm. opth. trig.*, ophthalmic branch of trigeminal nerve; *rm. v.*, ventral ramus (large and small medullated neuraxons).

In the second or dorsal region (*A*) of the ciliary ganglion, the smallness of the cells, the absence of heavily medullated processes, and the comparative abundance of pericellular fibrils, suggest a sympathetic ganglion. Moreover, the resemblance is strengthened by the entrance into this region of fine, very slightly medullated neuraxons from a gangliated dorsal nerve, the ophthalmic branch of the trigeminus. These neuraxons are identical in appearance with those of a typical ramus communicans passing, in the thoracic region of the fowl, to a sympathetic ganglion. A lack of correspondence between this portion of the ciliary ganglion and a typical sympathetic ganglion is to be recognized, however, in the comparative absence of medullation around the fine ciliary neuraxons given off distally. The post-ganglionic neuraxons of a sympathetic ganglion are also of small calibre, but in the hen they are well medullated. This lack of correspondence, due merely to differences in the degree of medullation, seems comparatively unimportant. It should be remembered, too, that in other classes of vertebrates non-medullated neuraxons are characteristic of post-ganglionic sympathetic nerves.

PART II. — DEVELOPMENT.

A. Historical Survey.

In reviewing the literature which deals with the development of the ciliary ganglion, it must be kept in mind that the name "ciliary" has been applied by various authors to *two* entirely distinct ganglia. One of these is found at the base of the first or ophthalmic branch of the trigeminal nerve, while the other is connected with the oculomotor nerve, and is the true ciliary ganglion of the adult.

The first of these ganglia arises in the following manner. In early stages of development, at least in sharks and birds, the most anterior portion of the neural crest becomes differentiated, in the region of the eye muscles, into an enlargement resembling the fundament of a cerebrospinal ganglion. In sharks this has been observed to fuse later with the anterior part of the Gasserian ganglion, and the same fusion doubtless takes place in birds. From the ganglion originating thus, the first branch of the trigeminus proceeds forward (van Wijhe, **'82**; Beard, **'87**; Neal, **'98**). For this ganglion of the ophthalmicus profundus in sharks Beard, in 1887, proposed the name "mesocephalic." Following Dohrn and Neal, I have adopted this designation, since all names previously applied to the ganglion in question have been used as synonyms for the ciliary. Indeed, as already stated, the name ciliary itself has often been applied to it.

The separate development of the ganglion of the ophthalmic branch of the trigeminus, and its subsequent fusion with the rest of the

Gasserian ganglion, have been observed in mammals and amphibians, as well as in fishes. Chiarugi (**'94**, **'97**) makes such an assertion for the embryos of guinea-pigs, and Ewart (**'90**), mentions the discovery, in a five-months' human embryo, of vestiges of an "ophthalmicus profundus ganglion" lying under cover of the inner portion of the Gasserian. Brauer (**:04**) describes the development of the "ganglion ophthalmicum" and of the "ganglion maxillo-mandibulare" in the Gymnophiona as independent of each other. Hoffmann (**'85**) considers the Gasserian ganglion in both embryonic and adult reptiles as divisible into two parts. In some of the lower vertebrates, as cyclostomes (Dohrn, **'88**; von Kupffer, **'95**) and ganoids (Allis, **'97**), these two ganglia, the mesocephalic and the maxillo-mandibular, retain complete independence throughout life.

There is good evidence, then, that a distinct ganglion, the mesocephalic, is developed throughout the vertebrate series in connection with the ophthalmic division of the fifth nerve. This ganglion, except in the cases of certain low forms, soon becomes fused with the common ganglion of the maxillary and mandibular divisions to form the Gasserian ganglion of the adult.

The true ciliary ganglion appears much later than the mesocephalic, and is always more or less directly connected with the third cranial nerve. The various ways in which its development has been said to take place will be outlined in the following pages. It will be sufficient, at present, to say that all writers whose statements are based on actual observation agree that it does not arise, like the mesocephalic and other cerebro-spinal ganglia, through direct differentiation from the cells of the neural crest.

In the reviews which follow I shall summarize in chronological order the observations already made on the development of the oculomotor and abducent nerves and the ciliary ganglion in the five classes of vertebrates. As far as possible, I shall distinguish between the mesocephalic and the ciliary ganglia. Each author's nomenclature will first be given, and then, if the identities of the ganglia are clear from his description, the terminology adopted above will be substituted for the sake of clearness and uniformity.

1. Fishes.

The first investigations upon the development of the oculomotor and abducent nerves in fishes were made by Marshall in 1881. In the embryo shark (Scyllium canicula) Marshall (**'81**) found that, in Balfour's stage *K*, the third nerve arises from the ventral face of the mid-brain by a root triangular in shape, containing many "nerve cells." Running caudad and laterad, the nerve reaches the interval between the dorsal ends of the first and second head cavities, where it expands into a small ganglion. At this ganglion, the nerve divides into two main branches, one running cephalad along the top of the first head cavity to the extreme anterior end of the head, the other passing ventrad between the first and second cavities. A short branch, coming directly from the Gasserian ganglion, enters this small ganglion and later, uniting with the first branch of the oculomotor described above, forms the ramus ophthalmicus profundus of the adult; this ramus has, in most cases, the appearance of being a branch of the trigeminal nerve. From the posterior wall of the first head cavity are derived those muscles of the eyeball which later are innervated by the oculomotor. The author considers this small ganglion between the tops of the first two head cavities to be the ciliary ganglion of the adult, and agrees with Schwalbe that it belongs exclusively to the third nerve.

It is evident from later investigations by others that Marshall is here dealing with the mesocephalic ganglion, and that his first branch of the oculomotor has only an apparent connection with that nerve, being, as a matter of fact, the ramus ophthalmicus profundus of the trigeminus, with which the mesocephalic ganglion is primitively connected. The close contact into which the two nerves come in the region of the mesocephalic ganglion accounts for the author's failure to separate them. (Comp. van Wijhe, **'82**.)

The sixth or abducent nerve was first observed in stage *O*, some time after the oculomotor had made its appearance. It springs from the ventral face of the hind-brain by a large number of slender roots, and runs to the fundament of the posterior rectus muscle. The roots as well as the trunk of the nerve contain many more or less elongated, fusiform cells, but none of these are ganglion cells.

Marshall and Spencer (**'81**) confirm Marshall (**'81**) without adding anything of importance to the latter's account.

In 1882 van Wijhe published his excellent description of the development of cranial nerves in selachians. In Balfour's stage *I* he found the fundament of a ganglion connected with the ophthalmic branch of the trigeminus, and representing the anterior extremity of the neural crest. This ganglion — called the ciliary by van Wijhe, but evidently the mesocephalic of our nomenclature — at first lies immediately under the epidermis, but soon moves away from it in the direction of the ganglion of the second and third branches of the trigeminus. Not until the next stage *J*, does the oculomotor appear; it then arises by a broad proximal end from the mid-brain. Passing ventrad the third nerve crosses the ophthalmic branch of the fifth on its median side at the level of the mesocephalic ganglion, to which it becomes closely applied; but, according to van Wijhe's view, only a close contact, not an actual union, occurs. Later, the oculomotor nerve and the mesocephalic ganglion draw away from each other, although a slender communicating nerve continues to connect the two.

But van Wijhe's most important contribution to the subject was the discovery of a second ganglion, which, in stage *O*, appears as a dumb-bell-shaped mass of cells placed on the branch of the third nerve which supplies the ventral oblique muscle, in the position occupied by the ganglion oculomotorii described by Schwalbe (**'79**) in adult selachians. This ganglion oculomotorii (which is our ciliary) is comparatively remote from the mesocephalic ganglion, and the author emphasizes the lack of connection between the two. On account of its late appearance, and the presence of a small branch from it to the arteria ophthalmica, he considers the ganglion as belonging to the sympathetic system, but gives no account of its actual development. The mesocephalic ganglion he regards as homologous with a spinal ganglion. The origin of the oculomotor from the base of the brain, the time of its appearance, its histological structure, its lack of a true ganglion in early stages, and its crossing, if not union, with a dorsal root distal to the ganglion of the latter, seem to the author to prove that the nerve in question is a purely ventral one.

To Marshall's account of the comparatively simple development of the sixth nerve van Wijhe added practically nothing.

Beard (**'85**) describes the development in elasmobranchs of what he then called the ciliary ganglion, but later termed the mesocephalic. This account was repeated and supplemented in his notable paper of 1887, to which reference has been made. In this paper he clears up the existing confusion caused by the various names given to the ganglia developing in connection with the oculomotor nerve and the ophthalmic branch of the trigeminus. The first he shows to be the true ciliary ganglion of the adult, and, therefore, entitled to that name; and for the second he proposes, as already stated, the name mesocephalic. He describes the way in which, in elasmobranchs, the mesocephalic ganglion, deriving its cells partly from the neural crest and partly from the ectoderm in the region of a primitive branchial sense organ, gradually recedes from the skin, and fuses with the maxillo-mandibular ganglion.

As this change of position takes place, a nerve — the ophthalmicus profundus — is developed, connecting the mesocephalic ganglion with the branchial sense organ. The oculomotor appears later than the ophthalmicus profundus, and never has any direct connection with the mesocephalic ganglion, although, during development, it is for a time closely applied to the latter. The true ciliary ganglion is not present until much later. When it does appear, the mesocephalic ganglion and the oculomotor nerve are connected by a small communicating branch, probably corresponding to the radix longa of higher animals; and it is near the entrance of this branch into the third nerve that the ciliary ganglion is first to be seen. Beard did not follow the development of the ganglion step by step, but calls attention to the assertion of Hoffmann (**'85**), that it arises in reptiles as an outgrowth of the ophthalmic (mesocephalic) ganglion. He favors the view that it belongs to the sympathetic system.

Phisalix (**'88**, **'88^a**), mistaking the mesocephalic for the ciliary ganglion in skate embryos, asserts that at first the oculomotor nerve and its ganglion are independent of each other. The ganglion is said to result from the dividing into two of the ganglion of the trigeminal nerve before the oculomotor has appeared.

Ewart (**'90**) gives us the first account of actual observations on the development of the ciliary ganglion in fishes. He finds that, at a certain stage in skate embryos, a slender outgrowth from the inferior border of the ophthalmicus profundus (mesocephalic) ganglion meets and blends with the descending (ventral) branch of the oculomotor. This outgrowth is crowded with cells, while the fibres of the descending branch of the oculomotor, as well as its root and trunk, are "absolutely destitute of cells." Later, cells accumulate at the junction between the outgrowth and the oculomotor, as if the intermingling of the two sets of fibres formed a network which resisted the further migration of cells from the mesocephalic ganglion. At a still later stage, in typical cases, all the ganglion cells are seen to have left the outgrowth, and to have accumulated on the oculomotor as a rounded mass, from which ciliary nerves take their origin. The ganglion thus arising, plainly the ciliary, stands, therefore, in the relation of a sympathetic ganglion to a dorsal cranial nerve, the ophthalmicus profundus.

Dohrn (**'91**) takes up the matter of the histogenesis of the oculomotor more fully than previous writers on the eye-muscle nerves, and also offers an entirely new explanation of the origin of the ciliary ganglion. He observed (p. 3) that in the embryos of selachians the third nerve first makes its appearance as a number of crowded pale cells in the marginal veil of the mid-brain. The plasma of these cells emerges from the ventral side of the neural tube as fine processes, which unite to form an irregular network. The meshes of this network are extended by the fusion of the processes of large cells, the nuclei of which lie in the plasma mass. The network stretches out through the mesenchyme, and gives rise, in the vicinity of the front end of the chorda dorsalis, to the small trunk of the oculomotor nerve. Dohrn's view of the structure of the growing nerve is in general accordance with the opinions of Balfour, Marshall, Beard, von Kupffer, and others, who support the "chain theory" of nerve formation. To prove that the medullary tube is the source of these cells whose processes make up the nerve trunk, Dohrn devotes much space and many figures. He shows that cells may be observed in the root of the oculomotor nerve, half in and half out of the medullary tube. Although he is obliged to admit that with present staining methods it is not possible, in early embryonic stages, to distinguish emigrating medullary cells from the surrounding mesodermal cells, he calls attention to the fact that the nuclei of the nervous network are larger than the nuclei of nearly all the neighboring mesodermal cells. Numbers of rounded and oval nuclei are to be seen in the course of the oculomotor before this grows down and connects with the mesocephalic ganglion, the long axes of these nuclei being perpendicular to those of the nuclei of the ganglion. The nuclei lying along the third nerve cannot, therefore, be considered derivatives of the mesocephalic ganglion.

In older embryos there occur, in the course of the third nerve, groups of differentiating ganglion cells, corresponding in position to the ganglia found along the oculomotor in the fully grown animal; and the development of these cells can be followed with certainty until the adult condition is reached. The ganglion cells arising in this way Dohrn believes to have been originally migrant medullary cells.

After considering the definitions which have been given to cerebrospinal and sympathetic ganglia, Dohrn reaches the conclusion that in the diffuse ciliary ganglion of selachians we have a ganglion which, because of its unique origin from emigrant medullary cells, belongs neither to the cerebro-spinal nor to the sympathetic systems.

In its histogenesis, the abducent nerve was found to resemble closely the oculomotor. Cells were discovered, wandering out into its roots from the ventral wall of the hind-brain, but in the case of this nerve none of these become ganglion cells in the adult.

Following the article of Dohrn just cited, three investigators published in rapid succession accounts of the development of the oculomotor nerve in selachians. These accounts were remarkable for the fact that they agreed in ascribing to the third nerve an extraordinary origin, the possibility of which had apparently never occurred to other investigators.

Platt (**'91**) describes, in embryos of Acanthias vulgaris, a line of nerve cells extending cephalad from the trigeminal ganglion, and soon enlarging into the fundament of a ganglion, which she terms the ciliary. This ganglionic fundament, first meeting an anterior prolongation from the neural crest (which develops into the transitory "thalamic nerve"), finally ends in a mass of cells connected with the primary nasal epithelium. This line of cells is later represented by the ramus ophthalmicus profundus trigemini. (From the foregoing description I consider it probable that Platt's "ciliary" ganglion is the same as Beard's mesocephalic.) From the inner (median) cells of this ganglion, the oculomotor nerve takes its origin as a cellular proliferation, which grows from the ganglion toward the brain, with which it becomes united in the floor of the midbrain. Two figures are given showing the oculomotor when it consists of but a single cell. The author concludes that the third nerve is, therefore, primarily sensory, the mesocephalic ganglion being at this time connected with a patch of thickened epithelium, and no muscle cells having as yet appeared in the walls of the premandibular cavity.

Mitrophanow (**'93**) followed with a confirmation of Platt's account of the origin of the oculomotor. He observed this peculiar development of the nerve in embryos of Raja, Torpedo, and Pristiurus. The ganglion from which the third nerve grows, as a cordon of cells, to the brain is plainly the mesocephalic, but the author prefers to call it the ciliary, although he indicates his familiarity with the name mesocephalic by mentioning it several times as a synonym for ciliary.

Finally, Sedgwick (**'94**) maintains that nerves do not develop as processes from central cells, according to the view of His, but arise through the differentiation of a reticular substance already in position. The oculomotor is formed in elasmobranchs as a differentiation of this reticulum, resulting from the breaking up of the neural crest, and first appears as a forward projection of nuclei from the ciliary (mesocephalic) ganglion. In the author's words (p. 96), "The third nerve, therefore, presents this interesting and remarkable peculiarity in Scyllium and Acanthias; it grows or is differentiated from the ciliary ganglion to the floor of the mid-brain and not in the opposite direction, as has hitherto been supposed." Sedgwick publishes no figures in support of his contention.

In his study of the development of the cranial nerves of Ammocoetes, von Kupffer ('91) assigned to the nerve he believed homologous with the oculomotor of higher vertebrates both dorsal and ventral roots and spinal as well as sympathetic ganglia. In a later paper (von Kupffer, '95) he states that the oculomotor in Ammocoetes appears to be a ventral nerve with which is related dorsally the anterior half of the first trigeminal ganglion.

The third nerve and the ciliary ganglion in embryos of Amia calva are described by Allis ('97). This writer has, however, no positive information to offer as to the early stages of their development.

Hoffmann ('97) states that the oculomotor, when first detected in Acanthias vulgaris, appears as a fibrous ventral root. At this time there is no ganglion at the proximal end of the nerve. His observations on the abducens confirm those of Marshall and van Wijhe.

Chiarugi ('97) declares, in opposition to Mitrophanow, that the third nerve in selachians grows centrifugally from the base of the mid-brain.

By the use of his modification of the vom Rath method, Neal ('98) demonstrated in so convincing a manner the neuroblasts of the oculomotor and their processes in Squalus acanthias that he removed all doubt as to the origin of the nerve from the ventral wall of the mid-brain. The neuroblasts showed the characteristics of those described by His in the spinal cord, and their darkly staining processes could be followed partly into the mesenchyme, where they were grouped to form the nerve trunk, and partly in a posterior direction within and parallel to the medullary wall, where they took part in the formation of the ventral fibre tract. The nerve growing out in this fashion from the mid-brain exhibits many nuclei lying peripherally along its fibres. It soon connects with the cells of the mesocephalic ganglion. Whereas the nerve is several cells in thickness near the ganglion, its calibre grows less toward the brain wall, a condition which, if one were unacquainted with its earlier history, might lead to the supposition that the growth of the nerve takes place from the ganglion toward the brain. Cells were observed migrating out from the mesocephalic ganglion and adhering closely to the oculomotor fibres. The fate of these cells was not determined, nor was the development of the ciliary ganglion followed. No entirely satisfactory evidence of migration of medullary elements was observed.

The abducent nerve was found by Neal to arise in the form of a slender bundle of neuraxons from neuroblasts situated in the ventral horn of the medulla. The number of its roots increases during development from one to three or four. The nuclei seen along its course are distinctly peripheral in relation to its fibres. There were no convincing indications of the migration of cells from the neural tube.

The development of the third nerve in selachians was described by Hoffmann (**'99**), but he added nothing new to the subject. The nerve in question grows down from the mid-brain and anastomoses with the ganglion ophthalmicus. This is the mesocephalic ganglion of Beard (**'87**), with whose article the author in the main agrees; but he considers the name ophthalmicus preferable to mesocephalic. Later, the oculomotor nerve and the mesocephalic ganglion draw apart, remaining connected, however, by a ramus anastomoticus. Presently, two ganglia appear on the third nerve, corresponding in position to those described by Schwalbe (**'79**) for adult selachians. Although the author was not able to work out the development of the ganglionic groups appearing on the oculomotor, he believes the account of Ewart (**'90**) to be correct, and considers the ciliary the most anterior sympathetic ganglion of the head.

Allis (**:01**, p. 131) mentions the presence of small and large cells in the ciliary ganglion of an embryo of Mustelus lævis. The large cells resemble cerebro-spinal ganglion cells, and the author suggests the probability that both spinal and sympathetic elements enter into the composition of the ciliary ganglion. Long and short roots were distinguished, but no extra-cranial sympathetic root could be made out.

2. Amphibians.

Almost nothing is known of the development of the third and sixth cranial nerves and the ciliary ganglion in amphibians. Johnson and Sheldon (**'86**, p. 94) state that in the embryo newt the oculomotor arises, like certain other of the cranial nerves, as an outgrowth of the neural crest, but no details of the process are given. According to Marshall (**'93**, p. 133) the oculomotor is present as a slender nerve in tadpoles of the frog at the time of the opening of the mouth. It arises from the lower part of the side of the mid-brain, not far from the median plane, and has already the course and relations of the nerve in the adult. Its early development has not been ascertained.

3. Reptiles.

Our knowledge of the development of the eye-muscle nerves and the ciliary ganglion in reptiles is derived almost entirely from the extended accounts of the two investigators, Béraneck and Hoffmann, both of whom studied embryos of Lacerta agilis.

Béraneck ('84) found the oculomotor, in an early stage of development, arising from the ventral face of the mid-brain by a triangular root crowded with cells possessing round nuclei, "et par touts leurs caractères se rapprochent beaucoup des cellules médullaires." Whether this cellular accumulation at the root of the nerve is really ganglionic, or whether its cells, like those distributed along the nerve, later form the sheaths of the fibres, could not be determined. At the proximal termination of the oculomotor occurs a little cellular mass, which the author believes to represent the ciliary ganglion. At this stage no communicating branch exists between this or any other part of the third nerve and the ophthalmic branch of the fifth.

In later stages, numerous cells are to be seen distributed along the whole nerve, those at the broad root being rounded and closely resembling the medullary cells, while those more distally situated are fusiform, with their long axes parallel to the nerve fibres. These differences in shape among the cells of the oculomotor are more apparent the older the embryo. The cells are more abundant in the proximal than in the distal part of the nerve trunk. The approximately spherical ciliary ganglion incloses round cells with distinct nuclei and fine granules. It is now connected by a slender ramus with the ophthalmic division of the trigeminal nerve. From the anterior face of the ciliary ganglion there runs cephalad, for an undetermined distance, a fine bundle of fibres, which the author believes to represent the ophthalmic branch of the oculomotor described in sharks by Marshall ('81). In old embryos, the ciliary ganglion shows the relations to the third nerve found in the adult: it is situated a little on one side of the nerve trunk, to which it is attached by a very short and thick bundle of nerve fibres.

Nowhere in his account does Béraneck advance the theory that the cells along the third nerve may have been derived through migration from the neural tube, nor does he express an opinion as to the source of the cells which differentiate *in situ*, in the oculomotor, into the cells of the ciliary ganglion.

The abducens appears somewhat later than the oculomotor, springing as a slender nerve from the ventral face of the hind-brain. During its development it presents but a single root, fibrillar in character, and destitute of cells, except for a few mesodermal elements which surround it externally. The same conditions are found along the course of the nerve trunk, the only cells connected with it being of mesodermal origin, arranged in a single layer about its periphery.

The account of the development of the ciliary ganglion given by Hoffmann ('85) is at variance with that of Béraneck, although both authors used as material the same species of lizard, namely, Lacerta agilis. While Hoffmann saw the younger stages of the development of the ganglion in snake embryos, the entire process was worked out in lizards only. According to his observations, the anterior part of the neural crest gives rise to two ganglia, that of the first branch of the trigeminus — the ophthalmic (mesocephalic) — and the ganglion common to the second and third branches — the Gasserian. The oculomotor develops later than the trigeminus, springing by a broad base from the ventral surface of the mid-brain. It is composed of a small amount of finely striated protoplasm, containing many nuclei closely crowded together. Passing on the median side of the mesocephalic ganglion, the nerve sends out to the anterior face of the latter a communicating ramus. By the aid of several drawings and a series of diagrams, the author shows that a large mass of cells is proliferated from the distal end of the mesocephalic ganglion, that this mass separates from the parent ganglion, and, guided by the communicating ramus, makes its way to a point close to the third nerve, with which it becomes united by a very short and thick bundle of fibres. This mass of cells becomes the ciliary ganglion of the adult, and the bundle of fibres binding it to the third nerve, the radix brevis. The ganglion retains connection with the fifth nerve through a slender radix longa, which, however, does not end in the mesocephalic ganglion, but in the ramus nasalis, a branch of the ophthalmic nerve, which grows out from the distal extremity of the mesocephalic ganglion while the ciliary ganglion is undergoing development. Hoffmann is convinced of the sympathetic nature of the ciliary ganglion, basing his opinion on the late appearance of the ganglion, its origin from the homologue of a spinal ganglion, and its development through the participation of both sensory and motor nerves, one, the ophthalmic, arising by a true dorsal root, the other, the oculomotor, by a true ventral root.

C. L. Herrick ('93) gives a figure of the developing oculomotor nerve in a snake embryo, showing migration of nuclei from the mid-brain into the root of the nerve. These nuclei he holds to be those of cells which, outside the neural tube, produce the nerve fibres.

4. Birds.

Remak ('51) and His ('68, '79) describe and figure in chick embryos, between the third and fifth days, a cellular prolongation extending cephalad from the Gasserian ganglion, and swelling into a crescentic enlargement near the eye vesicle. This structure is regarded by His as the persistent neural crest in the anterior head region. Both authors, without tracing its fate, assume that the crescentic terminal enlargement is the ciliary ganglion. Kölliker ('79) expresses himself as also of this opinion, although he acknowledges the insufficiency of the evidence on which the assumption is based. That the ganglion in question is the mesocephalic, and not the ciliary of the adult, is beyond doubt.

The first study of the development of the eye-muscle nerves of vertebrates was made by Marshall ('77, '78) on chick embryos. He found that the neural crest forms, at the twenty-ninth hour of incubation, a prominent outgrowth above the mid-brain. At forty-three hours this outgrowth is directed ventrad and lies in close contact with the walls of the mid-brain; and at fifty-three hours a large mass of cells is to be found connected with the mid-brain, and about half-way down its side. In a sixty-hours' chick, the oculomotor nerve arises from the ventral surface of the mid-brain, but is farther from the median plane than at later stages. From this evidence the author is "led to the belief that the third nerve is developed directly out of the outgrowth from the top of the mid-brain" seen at the twenty-ninth hour, and "that, at some period between the forty-third and sixtieth hours, its attachment shifts down from the top of the mid-brain to the lower part of its sides" (p. 25). Rabl ('89) accepts, on theoretical grounds, this view of the origin of the third nerve.

Longitudinal sections of a ninety-six-hours' chick show the oculomotor as a large nerve, arising from the ventral face of the mid-brain. Its base is "ganglionic," and it terminates a little posterior to the optic nerve, in a "ganglionic" swelling. From its enlarged distal end two branches are given off, one passing cephalad and dorsad to the fundament of the posterior rectus muscle, the other continuing the course of the main trunk, crossing the ophthalmic nerve nearly at right angles, and passing caudad and ventrad of the optic nerve. No mention is made of a connection between any part of the third nerve and the ophthalmic division of the fifth.

In a subsequent paper (Marshall, '81) the author accepts the view advanced by Schwalbe ('79) that this terminal swelling of the trunk of the oculomotor represents the ciliary ganglion of the adult. He advances no opinion as to the source of the cells of the ganglion.

Marshall's observations on the sixth nerve were incomplete. It was first detected in an embryo of ninety-three hours. Unlike the oculomotor, it arises by a series of slender roots instead of a single, large "ganglionic" root. It is a very slender, cellular nerve and does not branch.

Foster and Balfour (**'83**, p. 128) make brief mention of a connection between the ophthalmic branch of the trigeminus and the oculomotor in the chick, soon after the third day of incubation. They merely state that, near the eye, the ophthalmic branch of the fifth nerve "meets and unites with the third nerve, where the ciliary ganglion is developed."

The view of Remak and His in regard to the development of the ciliary ganglion from the neural crest is shared by Goldberg (**'91**). Like them, he mistakes the mesocephalic ganglion for the ciliary.

Gọronowitsch (**'93**), on the other hand, declares that the primary neural crest completely disappears in bird embryos during an early period of development. The ciliary ganglion arises later, and quite independently of the neural crest. The writer did not observe the actual process by which it is developed, but is inclined to accept the explanation given by Dohrn of its origin in selachians. He states that he himself has observed in teleosts abundant evidence of the migration of cells from the medullary tube into the root of the third nerve.

D'Erchia (**'95**) gives a description and a figure of a communicating nerve between the ophthalmic branch of the trigeminus and the ciliary ganglion in an embryo chick of twelve days' incubation. He, therefore, denies Schwalbe's assertion that no sensory root of the ciliary ganglion exists in birds. This difference of opinion is easily explained by the fact that D'Erchia made his observations on embryonic, and Schwalbe on adult material. While present in the embryo, this *direct* connection between the trigeminal nerve and the ciliary ganglion does not persist in the adult. (See Plate **1**, Figs. 1 and 2.)

Rex (**:00**) observed that in embryos of the duck the ciliary ganglion first makes its appearance as a distinct thickening in the course of the oculomotor nerve, due to the presence of an accumulation of ganglion cells. He did not follow the development of the ganglion.

5. MAMMALS.

The observations on the genesis of the eye-muscle nerves and the ciliary ganglion in mammals have been fragmentary.

In sections of rabbit embryos, Kölliker (**'79**) discovered the oculomotor arising at the earliest stage observed from the lateral, not the ventral, face of the brain. It showed no evidence of a ganglionic swelling at its base, and no cells were intermingled with its fibres. About its periphery was a thin envelope, formed by a single layer of mesodermal cells. Later, the nerve was observed to have descended to the ventral face of the brain.

His ('80, '88, '88ᵃ) maintains that the ciliary ganglion develops in man from the anterior portion of the first ganglionic or trigeminal complex of the head, which is a direct descendant of the neural crest. He does not accept the distinction made by Beard ('87) between a mesocephalic and a ciliary ganglion, but asserts that the ganglion which Remak, himself, and so many others have seen at the anterior extremity of the neural crest, is identical with the long-known ciliary ganglion. In opposition to Schwalbe, he assigns this ganglion to the fifth rather than to the third nerve, since it develops over the fore-brain, while the third nerve grows out from the ventral face of the mid-brain. Furthermore, the oculomotor arises as a purely motor nerve, and, as such, is not entitled to a ganglion.

Both the third and sixth nerves arise in human embryos as fibrous outgrowths of neuroblasts situated in the ventral zone of the medullary wall, not far from the median plane.

It is stated in Quain's Anatomy ('95, Thane, p. 388) that Martin ('90) found a dorsal root of the oculomotor nerve in an embryo cat. The original article has not been accessible.

His, Jun. ('91) compared, in an embryo cat, the cells of a cerebro-spinal, a sympathetic and the ciliary ganglion. In the first, he found large, bipolar cells, and in the sympathetic and ciliary ganglia, small, unipolar cells.

Chiarugi ('94, '97) observed the oculomotor nerve, in the youngest guinea-pig embryos in which it was present, springing from the ventral side of the mid-brain, near the median plane. On the trunk of the nerve, close to the root, he discovered a rudimentary ganglion. Since no ganglion cells were to be seen along the further course of the nerve, between the ganglion and the place of connection with the ophthalmic branch of the trigeminus, he considers it improbable that the ganglion owes its origin to nervous elements which have passed from the trigeminus to the oculomotor. In the wall of the brain there were to be seen, however, several neuroblasts, lying along the root fibres of the third nerve, and, apparently, advancing to the free surface. This leads him to the supposition that the cells of the ganglion are derived through migration from the brain wall. He believes that this ganglion has no connection with the ciliary ganglion, which develops later in close relation with both the inferior branch of the third nerve and a communicating ramus passing to it from the ophthalmic branch of the fifth. He states that he found the origin of the ciliary ganglion difficult to trace, but is inclined to think that its cells come from the ophthalmic branch of the trigeminus. At the origin of the communicating branch from the latter nerve, a small cluster of ganglion cells was found.

Throughout the whole length of the third nerve, there could be seen, disseminated among the nerve fibres, nuclei of cells, the interpretation of which the writer found very difficult.

The ciliary ganglion was recognized by Dixon (**'95**) as a distinct cellular mass in a human embryo of the sixth week. It appears at first to be more closely connected with the frontal and fourth nerves than with the nasal and third nerves. It later shifts its position, and, by the eighth week, has established connections as in the adult. (Comp. Reuter, **'97.**)

Reuter (**'97**), though concerned chiefly with the development of the eye muscles in the pig, furnishes some interesting information in regard to the early stages of the ciliary ganglion. He discovered, in an embryo measuring 14 mm. from nape to rump, differentiating ganglion cells lying in the oculomotor nerve, both at the place where it divides into its terminal branches and in the course of its long branch to the ventral oblique muscle. In a later stage these cells are accumulated in one mass in the form of a distinct ciliary ganglion. At the time of the first appearance of the cells, no connection exists between the oculomotor and the first branch of the trigeminus. Later, a radix longa is developed. The writer obtained no clew as to the source of the cells of the ciliary ganglion, but, in view of the latter's late development, he considers it very unlikely that its cells have any genetic connection with the neural crest or the Gasserian ganglion. He is of the opinion that His (**'88^a**) and Dixon (**'95**) have mistaken for the ciliary ganglion the fundament of the dorsal oblique muscle during the period between the disintegration of the neural crest and the first appearance of the ganglion.

It is evident from the foregoing reviews that, while observers agree in the main as to the development of the abducent nerve, there is a wide diversity of opinion in the cases of the oculomotor nerve and the ciliary ganglion. Consequently, as far as the latter structures are concerned, it is difficult to draw from the existing literature satisfactorily supported generalizations. Especially is this true of the ciliary ganglion, which appears to vary in its manner of development not only among animals belonging to different classes of vertebrates, but also among animals belonging to the same class. Even in the same species the accounts of its origin, in one instance, disagree (comp. Béraneck, '84, and Hoffmann, '85). The weight of the evidence, however, seems to justify the following general statements: —

1. The oculomotor nerve develops after the manner of a ventral spinal nerve from the floor of the mid-brain. Its histogenesis has been described both in accordance with the "process theory," i. e., formation by neuraxons growing out from centrally situated neuroblasts (Neal); and in accordance with the "chain theory," i. e., formation by chains of cells which anastomose in the mesenchyme (Dohrn).

Marshall's theory of a primary connection between the third nerve and the neural crest is not supported by the facts, he himself being unable to trace satisfactorily the intermediate steps in the shifting of the nerve from a dorsal to a ventral position. Kölliker, it is true, finds the nerve in rabbit embryos at first half-way up the side of the neural tube, but his observation in this respect stands alone. Other investigators have so convincingly disproved the statements of Platt, Mitrophanow and Sedgwick, who hold that the third nerve grows from the mesocephalic ganglion toward the brain, that their erroneous conclusions must be set down to inadequate methods and mistaken interpretations.

2. The developing oculomotor nerve exhibits throughout its course numerous cells distributed among its fibres. Its proximal extremity is enlarged and crowded with cells.

With these statements all writers except Ewart and Kölliker agree. Ewart ('90) asserts that in skates at the time of the formation of the ciliary ganglion the oculomotor fibres are free from cells; and Kölliker ('79) finds no cells connected with the oculomotor in rabbit embryos, except a single peripheral layer which is of mesodermal origin.

3. The abducent nerve develops after the manner of a ventral spinal nerve, usually by several roots, from the ventral wall of the hind-brain. Numerous cells are associated with the nerve fibres in fishes and birds, but not in reptiles (Béraneck), and probably not in mammals.

The comparatively few observations on the genesis of the sixth nerve are all in general agreement.

4. The ciliary ganglion may originate either (*a*, sympathetic type of development) by the migration of ganglion cells from the mesocephalic ganglion into the oculomotor nerve, either directly or by way of the ophthalmic branch of the trigeminus (Ewart, Hoffmann, Chiarugi); or

(*b*, unclassifiable type of development) by the development of ganglion cells *in situ* in the third nerve (Dohrn, Béraneck, Rex, Reuter).

None of the investigators who have observed the formation of the ganglion *in situ* have advanced an opinion as to the source of its cells with the exception of Dohrn, who gives evidence of their derivation through migration from the wall of the neural tube.

5. In all vertebrates, at an early stage in the development of the of the ciliary ganglion, a connection, in the form of a communicating ramus, is established between it and the ophthalmic branch of the trigeminus.

B. Observations.

1. Methods.

The two most satisfactory staining methods for the purposes of my study proved to be the mixture devised by vom Rath for fixing tissues and the Heidenhain iron haematoxylin stain. The vom Rath fluid used according to Neal's procedure (see Neal, **:03**) has the very desirable effect of differentiating neuroblasts and their growing processes. It colors but slightly other cells of the neural tube (ependymal cells, spongioblasts and indifferent cells), and the same is true of its effect on the cells of the mesenchyme. In preparing the fluid the formula used was that given in 1895 by vom Rath ('**95**, p. 283) :—

200 c.c. saturated solution of picric acid.
1 grm. platinic chloride, dissolved in 10 c.c. water.
2 c.c. glacial acetic acid.
25 c.c. 2 per cent osmic acid.

In this mixture, embryo chicks were allowed to remain for three days or more, during which time the fluid was once changed. They were then washed for a minute in two changes of methyl alcohol, and placed for from twenty-four to forty-eight hours in a 0.5 per cent solution of pyrogallic acid, which intensified the stain. From this reagent the embryos were brought up slowly through the different strengths of alcohol to absolute, then cleared in xylol, and embedded in paraffin. This treatment rendered the material very brittle, and careful handling was necessary in all operations subsequent to immersion in the fixing fluid. After serial sectioning and fixation to the slides, no treatment for the further staining of the tissues followed. The paraffin was dissolved in xylol, and the sections were immediately mounted in xylol-balsam. The preparations were allowed to dry uncovered, since the use of cover glasses is likely to be followed by an alteration in the stain, resulting in a faded or yellowish appearance, and loss of good differentiation.

Heidenhain's iron haematoxylin stain was employed in the usual way after fixation either in Zenker's fluid, or in a saturated aqueous solution of corrosive sublimate to which had been added 1 per cent glacial acetic acid. Besides giving its well-known sharp nuclear stain, iron haematoxylin differentiates clearly the primitive fibrils as soon as these begin to appear in developing nerves. It is less favorable than vom Rath's mixture for the earliest stages of nerve formation, as it is not a selective stain for the processes of the neuroblasts. After fixation in Zenker's fluid or the corrosive-acetic mixture, it is seen that these early neuraxons appear frequently to approach, and to unite longitudinally with one another, thus giving to the nerve the structure of a coarse reticulum.

Among the other general stains tried Brazilin and Delafield's haematoxylin gave the most satisfactory results. Golgi impregnation and *intra-vitam* staining with methylen-blue were attempted, but repeated trials failed to produce the desired effect on the eye-muscle nerves of the embryos.

The method of van Gieson was used in advanced embryos for the purpose of studying the first stages in the formation of the sheaths of Schwann. By following Heidenhain's iron haematoxylin with the van Gieson mixture of acid fuchsin and picric acid, a good plasma stain was obtained, which brought out distinctly the cytoplasmic processes of the cells accompanying the nerve fibres, as well as those of the mesodermal cells.

Serial sections of embryos of various ages were made in the following planes: —

1. Parasagittal. Such series gave nearly longitudinal sections of the third and sixth nerves, and were best adapted to the study of their roots and the cell migration from the neural tube, since the roots of these nerves are spread out in a longitudinal but not in a transverse direction. Obliquely longitudinal sections of the ophthalmic branch of the fifth nerve were obtained in the series cut in parasagittal planes.

2. Transverse to the longitudinal axis of the mid-brain. Owing to the cephalic flexure, cutting in this plane gave longitudinal sections of the third nerve, obliquely longitudinal sections of the sixth, and nearly transverse sections of the ophthalmic branch of the fifth.

3. Frontal to the mid-brain; resulting in transverse sections of the third nerve, obliquely transverse sections of the sixth, and nearly longitudinal sections of the ophthalmic branch of the fifth.

2. DEVELOPMENT OF THE OCULOMOTOR NERVE, THE CILIARY GANGLION AND THE ABDUCENT NERVE; DESCRIBED BY STAGES.

Over fifty series of sections were made from chick embryos of various ages between the sixtieth hour and the seventh day of incubation, the period during which the third and sixth nerves and the ciliary ganglion assume both their distinctive histological characters and the most of their adult anatomical relations. From these series have been selected, for the purposes of the descriptions which follow, those best illustrating the successive steps in the development of the nervous structures with which we are dealing. For convenience in description I have divided the first five days of this period into five stages, which will be described in chronological order.

Stage I.

1. *Oculomotor Nerve.* The earliest indication of the origin of the oculomotor nerve was observed in an embryo of seventy-two and one-half hours' incubation. That the development of this embryo had been abnormally retarded cannot be doubted, since the third nerve in a more advanced stage was frequently met with in embryos of seventy hours and in one case in an embryo of sixty hours.

Parasagittal sections of the mid-brain at this stage show the thickness of its ventral wall to be about one-eighth the height of the neural canal. Entering into the composition of the medullary wall may be observed the elements first described by His and later studied in such detail by Schaper ('97). Near the internal limiting membrane lie numerous germinative cells in process of division, while the mantle layer, making up the greater part of the wall, is composed of ependymal cells which have assumed a supporting function by developing into a medullary framework, and of the products of the proliferating activity of the germinative cells, namely, indifferent cells, which later differentiate into either nervous or supporting elements. The structure of the medullary framework is not well brought out by the vom Rath method. Near the external limiting membrane there is a narrow zone free from nuclei, the marginal veil ("Randschleier"). In addition, at a distance of about 100 micra from the median plane on either side, is to be seen a small group of cells which the vom Rath stain renders distinguishable from the other elements of the medullary wall. Each cell shows, at one side of its nucleus, a variable amount of darkly colored cytoplasm, the characteristic feature of a neuroblast. Inasmuch as these neuroblasts occupy the position of those from which, at a slightly more advanced stage, the neuraxons of the oculomotor nerve take their origin, and since there is, even at this stage, evidence of the outgrowth of their processes from the neural tube, it follows that each group of cells is to be looked upon as the developing nidulus of the oculomotor nerve of that side. The niduli, then, at the very beginning of their development, are in a decidedly ventral position.

The neuroblasts on the right side of the median plane are more closely grouped together than those on the left, and even under low powers of the microscope stand out clearly from the rest of the medullary wall because of their darkly staining cytoplasm. Each group lies close to the external limiting membrane, projecting into the region of the marginal veil. On the right, the external limiting membrane remains intact, no processes of the neuroblasts having forced their way through it. On the left (Plate 3, Fig. 8), however, the external limiting membrane has been ruptured, and a part of the substance of the marginal veil protrudes. In the parasagittal section of the ventral mid-brain wall shown in Figure 8 there are included only a few of the several neuroblasts making up the nidulus. The letters *n'bl.'* designate a neuroblast with its cytoplasm drawn out, and directed toward the break in the medullary wall. Near it lie two cells, with cytoplasm tending in the same direction. The neuroblast marked *n'bl.''* shows a well-defined cytoplasmic process, narrowing toward its peripheral extremity, which has evidently pushed its way through the external limiting membrane. Of interest is a nucleus (*cl. med. mig.*), plainly medullary, lying in the material which is escaping from the neural wall through the aperture in the external limiting membrane to which reference has been made. This medullary nucleus appears to be making its way out of the neural tube at a very early stage in the development of the oculomotor nerve.

A little posterior to the oculomotor nidulus, at this stage, a few of the first fibres of the ventral fibre-tract can be seen running caudad toward the hind-brain.

2. *Eye Muscles.* As early as this stage, the fundament of the posterior rectus muscle has made its appearance, but since the series representing Stage II is more favorable for its study, description is deferred until then. Its character and relations in Stage I have not been altered in Stage II.

Stage II.

This stage is found in a series of seventy hours' incubation.

1. *Oculomotor Nerve.* Cross-sections of the mid-brain show the oculo-

motor niduli, lying in the ventral mid-brain wall, with their centres about 120 micra from the median plain. The niduli invade the marginal veil, which is now well developed. From the neuroblasts, cytoplasmic processes run out into the mesenchyme, as may be seen in Plate **3**, Figure 9. These appear to blend more or less, and, outside the neural tube, make a network with many nuclei lying along the threads of the net. This reticulated appearance of the nerve during its early development always follows fixation in Zenker's fluid or the corrosive-acetic mixture. In the present instance, the material was fixed in Zenker's fluid, and stained with Brazilin. Vom Rath preparations, on the contrary, exhibit the neuraxons of the growing nerve as separate elements, approximately parallel to one another, and not connected to form a network (comp. Plate **6**, Fig. 20).

The cells lying along the nerve strands are composed of rounded nuclei with which very little cytoplasm appears to be associated. For the sake of convenience, these cells will hereafter be called accompanying cells. Their nuclei resemble closely in form, size and staining qualities, the nuclei of the indifferent cells which lie inside the neural tube. Certain of the indifferent cells of the nidulus may be seen in the process of division (Plate **3**, Fig. 9, *cl.'*), and many lie near, and indeed in some cases (*cl.''*) immediately in contact with, the external limiting membrane.

The oculomotor may now be traced for some distance by its cytoplasmic threads and "accompanying" cells. It pursues a straight course through the mesenchyme in a ventral direction from the mid-brain. On account of the cephalic flexure, it lies nearly parallel to the axis of the hind-brain. After proceeding a short distance, it terminates in a slightly expanded distal extremity.

2. *Ophthalmic Branch of the Trigeminal Nerve.* In this stage the Gasserian ganglion, which has of course been present since its differentiation, much earlier, from the neural crest, shows plainly a partial division into a mesocephalic ganglion, giving rise to the ophthalmic branch of the trigeminus, and the ganglion of the maxillary and mandibular branches. The mesocephalic division is directed cephalad, and from its distal extremity the ophthalmic branch proceeds for a short distance along the outer wall of the anterior cardinal vein in the direction of the eyeball, but cannot be traced as far as the level of that organ. The maxillo-mandibular division of the Gasserian ganglion is directed ventrad and laterad, making approximately a right angle with the mesocephalic portion. It extends as far as the ectoderm, with a thickened patch of which (Plate **7**, Fig. 23, *gn. mx-md. Gas.*) it is directly connected.

The maxillary and mandibular branches of the trigeminus are poorly developed at this stage.

3. *Eye Muscles.* An isolated and compact accumulation of cells, staining deeply with haematoxylin, lies in the mesenchyme along the inner border of the anterior cardinal vein, not far from the ventro-lateral face of the anterior portion of the hind-brain (Fig. 23, *mu. rt. p.*). The distal extremity of the second division of the Gasserian ganglion lies laterad to this cell group, separated from it by the lumen of the anterior cardinal vein. The subsequent development of the mass proves it to be the fundament of the posterior rectus eye-muscle. No other eye-muscle fundaments are present, and not even the nidulus of the abducent nerve, which later innervates the posterior rectus muscle, has as yet appeared.

Stage III.

This stage is represented by two series of preparations, one of eighty-eight hours', the other of ninety-three hours', incubation. The two embryos had attained practically the same degree of development.

1. *Oculomotor Nerve and Ciliary Ganglion.* A fortunate section from the eighty-eight-hours' series, taken transversely to the axis of the mid-brain, shows the oculomotor cut longitudinally throughout its whole length (Plate 7, Fig. 24, *n. oc'mot.*). On either side of the median plane, and lying in the ventral wall of the mid-brain, the oculomotor niduli (*nidl. oc'mot.*) are seen as elliptical groups of cells, delimited by narrow areas comparatively free from medullary elements. These niduli present an elliptical outline whether viewed in transverse or parasagittal sections, but the ellipse seen in the latter plane has the longer principal diameter. Each nidulus measures approximately as follows: longitudinal diameter, 450 micra; transverse diameter, 135 micra; vertical diameter, 78 micra, the latter being more than half the thickness of the mid-brain wall, which here measures 117 micra. The centres of these niduli are slightly over 150 micra from the median plane. Allowing for increase in size due to growth, it is apparent that little, if any, change has taken place in their positions since their first appearance in Stage I. They then lay at the distance of 100 micra from the median plane.

The marginal veil is now invaded by the developing ventral fibre-tract, which forms a comparatively broad band of separation between the ordinary cells of the medullary wall and the external limiting membrane. The cells of the nidulus, however, project into this region, and extend to the very margin of the wall. Not all the neuraxons given off by the neuroblasts of the oculomotor nidulus pass out into the root of the nerve. Some are directed caudad, and contribute to the formation of the ventral fibre tract, as can easily be observed in vom Rath preparations (Plate 6, Fig. 20, *trt. fbr. v.*). No fibres were observed running cephalad from the nidulus.

The nerve, consisting of fibres densely crowded with nuclei, arises by a root which is spread out in a longitudinal direction into a fan-shaped form (Fig. 20). Seen in a plane at right angles to this, the root does not show this enlargement (Plate 7, Fig. 24). The trunk of the nerve pursues a straight course ventrad and laterad, terminating at the side of the ventral extremity of the infundibulum (which is brought by the cephalic flexure into a position ventral to the mid-brain). The distal end of the oculomotor is conspicuously enlarged, so that the whole nerve, seen in cross-sections of the mid-brain, may be said to have a clavate form (Fig. 24, *n. oc'mot.*) In parasagittal sections, the enlargement has the shape of an unsymmetrical spindle, the posterior side of which has the sharper curvature. This terminal swelling is the fundament of the ciliary ganglion (*gn. cil.*).

Examination of the root of the oculomotor nerve with high powers reveals conditions strongly suggesting the migration of medullary cells. Figure 11 (Plate 4) represents a section through the root of the third nerve shown in Figure 24 (Plate 7). In this preparation, which was fixed in the corrosive-acetic mixture and stained with Heidenhain's iron haematoxylin, the processes projecting out from the neuroblasts run together and blend in such a way as to lose their identities as neuraxons. Again, as in Stage II, we find nuclei lying on the nerve fibres, both within and without the brain wall. Not all of those within are the nuclei of neuroblasts, for some (as *cl.'*) are without cytoplasmic processes, and others appear to be lying peripherally on processes apparently originating from neuroblasts more centrally placed. These nuclei, with which very little cytoplasm is connected, answer to the description of the indifferent cells of Schaper, which are known to possess the power of locomotion, since, within the boundaries of the medullary wall, they pass from the region of the germinative cells, where they originate, into the mantle layer. In the present instance they can be traced beyond the mantle layer to the free surface of the neural tube. Indeed, now and then, one can be detected in the position of *cl.''* lying half within and half without the neural wall, in the same position in which Dohrn ('91) has figured emigrating cells in the root of the developing oculomotor nerve in selachians. Although there is little evidence of cell division within the nidulus, the germinative cells at the inner border of the medullary wall are numerous, and actively engaged in the production of indifferent cells.

Along the course of the nerve the "accompanying" cells may frequently be seen in process of mitosis, so that in case these are, as I believe, medullary and not mesodermal elements, it does not follow that the whole number present at this time have migrated from the neural tube, since their numbers are constantly increasing through cell division. A vom Rath preparation of the root of the oculomotor, in an embryo ninety-three hours old, shows a distinct difference in staining qualities between the "accompanying" nuclei and the adjacent mesodermal nuclei. While the "accompanying" nuclei take the stain readily, and are sharply defined, the surrounding mesodermal nuclei are, owing to their paleness, much less conspicuous (Plate **6**, Fig. 20). On the other hand, the nuclei of the medullary wall show in their affinity for the stain a striking resemblance to the "accompanying" nuclei.

It will be noticed that both the nuclei within the neural tube and those lying in the root of the oculomotor are more or less rounded in form. At least few, if any, exhibit a pronounced elongation. However, as we pass distally along the nerve, we find the most of the nuclei becoming more and more elongated, until the great majority are distinctly spindle-shaped. A few cells, distributed along the entire length of the nerve, retain the rounded form.

Taking into consideration the whole course of the nerve, the greatest amount of cell division occurs in the enlarged terminal (distal) portion (Plate **5**, Fig. 15), the fate of which proves it to be the fundament of the ciliary ganglion. Here, the majority of the nuclei are not as elongated as those lying among the fibres of the trunk of the nerve, many showing approximately circular outlines. All are nearly destitute of cytoplasm at this stage. It is evidently owing to the proliferation of these nuclei lying among the terminal nerve fibres that the enlargement in this region has taken place.

2. *Ophthalmic Branch of the Trigeminal Nerve.* The first branch of the fifth nerve (Plate **7**, Fig. 24, Plate **4**, Fig. 12, *rm. opth. trig.*) passes, in this stage, straight cephalad from the mesocephalic ganglion along the lateral wall of the anterior cardinal vein (*vn. crd. a.*). It terminates dorsad of the optic stalk between the fore-brain and eyeball, and just caudad of the laterally projecting vesicle of the hemisphere of that side. Its distal extremity is marked by a transitory fusiform ganglion (Plate **4**, Fig. 12, *gn. t'i.*), having an approximate length of 165 micra, and a greatest diameter of 75 micra. This Figure is drawn from several

sagittal sections of a vom Rath series, and represents about one-half the length of the ophthalmic branch of the trigeminus. In this particular case, the nerve, just after passing the level of the optic stalk, divides into two branches, which unite again at the ganglion; but I do not find this condition to be a constant one.

An examination of longitudinal sections of the ophthalmic branch of the trigeminus at this stage shows that, beside the elongated "accompanying" cells, resembling those of the oculomotor, there are to be found distributed along the whole length of the nerve, as well as in the transitory ganglion, ganglionic cells whose larger nuclei and more abundant and deeply staining cytoplasm make them easily distinguishable from the "accompanying" cells. The description of these ganglionic cells, and the discussion of the terminal ganglion, will be taken up under Stage IV.

In the transverse series of an eighty-eight-hours' chick there can be seen at this stage, on the left side of the body, an exceedingly slender offshoot of the ophthalmic branch of the trigeminus, passing to the fundament of the ciliary ganglion. The offshoot is apparently composed of a single neuraxon, to which a few "accompanying" cells are applied, and at the place of its origin from the ophthalmic branch lies a cluster of ganglion cells. On the right side of the body, on the contrary, the most careful search has failed to reveal any fibrous connection whatever with the fundament of the ciliary ganglion. Of interest, however, are two cells having the appearance of ganglion cells, both of which lie in the mesenchyme between the ophthalmic branch and the fundament of the ciliary ganglion, one being about midway between the two structures, and the other close to the surface of the ganglionic fundament. Both these cells differ markedly from mesodermal cells, and also from those of the fundament of the ciliary ganglion, on account of the larger size of their nuclei and their deeply staining cytoplasm; while their resemblance to ganglion cells seen in the ophthalmic branch, in the same sections, is very close. They appear to be migrating ganglion cells, and their origin from the ophthalmic branch seems very probable. Further evidence that ganglion cells do migrate from this nerve will be presented in Stage IV.

3. *Abducent Nerve.* The sixth nerve was first met with in a seventy-eight-hours' series, that is, in a stage intermediate between Stages II and III. It was observed on both sides of the head as a very small nerve, arising by five delicate roots from the ventral surface of the hind-brain, about 135 micra from the median plane. The nerve can be traced

cephalad for a very short distance only. In another series of the same length of incubation the abducens was not found. It will be noted that the abducens appears several hours after the differentiation of the fundament of its muscle, the posterior rectus.

In the ninety-three-hours' series, the nidulus of the abducens can be seen lying close to the ventral surface of the hind-brain wall. It is elongated in a longitudinal direction, and lies about 175 micra from the median plane. It is not possible, in my preparations, to make out its limits as definitely as in the case of the oculomotor nidulus.

The nerve itself is a slender one, springing from the ventral face of the hind-brain by a varying number of attenuated roots, placed one behind the other, and crowded with "accompanying" cells. As many as eight roots have been counted, the number differing in different embryos, and even on opposites sides of the body in the same embryo. The roots unite a short distance from the brain to form the trunk of the nerve, which passes straight cephalad, running parallel to the ventral face of the hind-brain. In vom Rath preparations the nerve can easily be traced as a slender bundle of a few darkly stained neuraxons with elongated "accompanying" cells to the posterior edge of the compact cluster of cells making up the fundament of the posterior rectus muscle. It will thus be seen that the abducens, though appearing later than the oculomotor, is the first of the two nerves to become connected with a muscle fundament. The fundament of this muscle, the posterior rectus, was already recognizable in the mesenchyme of Stage I, therefore, long before any of the other eye-muscle fundaments, none of which can be made out previous to the present stage.

4. *Eye Muscles.* The fundament of the posterior rectus eye muscle lies near the anterior portion of the hind-brain in a ventro-lateral position. It consists of a mass of modified mesodermal cells, which differ from surrounding ones in their closer association and their rather greater amount of cytoplasm. The absence of fibres in the muscle fundament, and their presence in that of the ciliary ganglion, make a notable difference in the appearance of these two structures. The muscle mass is elongated in an antero-posterior direction (Plate 7, Fig. 23, *mu. rt. p.*). It lies mostly caudad of the fundament of the ciliary ganglion, but its anterior end runs cephalad and laterad as a narrow prolongation, which, passing laterad of the posterior half of the ganglionic fundament, terminates between it and the anterior cardinal vein. The fundament of this muscle appears in Plate 7, Figure 24 (*mu. rt. p.*), where the section has passed very near its anterior extremity.

The fundaments of the dorsal rectus and dorsal oblique muscles, and the common fundament of the anterior and ventral rectus muscles, are now to be seen. These consist of small, local differentiations of mesodermal cells, which tend to become more closely associated, and, through their activities, produce an abundance of cytoplasmic material; this material represents the first stage in the formation of the contractile substance of the muscle cells. These muscle fundaments will be described and figured in Stage V, where my sections are in planes more favorable for showing their relations. Their positions in the later stage are practically the same as in the present one.

The fundament of the ventral oblique muscle cannot be distinguished at this stage.

It might here be stated that it has been impossible, in the chick, to assign the eye-muscle fundaments to their respective somites by the aid of the head cavities. These have not been present in the stages studied owing to the fact that, in the chick, they appear to be obliterated very early in development — much earlier than is the case in the embryos of ducks (van Wijhe, '86; Rex, :00) terns, gulls and lapwings (van Wijhe, '86).

Stage IV.

This stage occurs at about the one hundredth hour of incubation. It is described from two series, one of one hundred hours, the other of one hundred and one hours.

1. *Oculomotor Nerve.* The oculomotor nidulus retains its extreme ventro-median position. In fact it appears to have moved toward rather than away from the median plane. Although the neural tube has increased in size, the centre of the nidulus now lies nearly 50 micra nearer the median plane than in the stage last described, being distant only 105 micra from it. The ventral fibre tract has increased in thickness, and, while the nidulus of the oculomotor extends into it, the lower border of the nidulus does not lie as near the external limiting membrane as in Stage III. Neuraxons from the nidulus, passing through the ventral fibre tract — a region free from nuclei — are frequently seen to be accompanied by nuclei which have the rounded form of the indifferent elements in the nidulus dorsal to them, and of the "accompanying" cells of the root of the oculomotor ventral to them. Farther out on the trunk of the nerve, the great majority of the cells have become elongated, though occasional round ones are to be observed.

The oculomotor nerve pursues, as in the stage last described, a straight course, passing ventrad and slightly laterad (Plate 4, Fig. 13) through the mesenchyme, between the infundibulum on its median, and the lower half of the eyeball on its lateral side. The large accumulation of cells forming the ciliary ganglion lies mainly on the lateral, or ocular, side of the nerve trunk (Compare Plate 7, Fig. 25 *gn. cil.*). The neuraxons of the nerve continue for a short distance beyond the ganglion, and, bending somewhat laterad, terminate immediately mediad of the antero-ventral portion of the eyeball in the fundament of the ventral oblique muscle, which makes its first appearance in this stage. The oculomotor is as yet entirely without branches.

A histological change has by this time taken place in, at least, the distal two-thirds of the nerve. In early stages, especially in vom Rath preparations, the neuraxons of the nerve are to be seen, under high powers of the microscope, as relatively thick fibres with peripherally situated "accompanying" cells. The same powers now show, especially in the more distal parts of the nerve, that the relatively thick fibres no longer appear, their places having been taken by much finer fibrils. As a consequence, the fibrous components of the nerve are now greatly increased in number without a corresponding increase in the calibre of the nerve. I shall hereafter speak of these fine filaments as *fibrils* in contradistinction to the earlier *fibres* — the coarser structures which the fibrils have replaced. The histogenesis of the fibrils is considered under Stage V.

Lying at all depths within the nerve, "accompanying" cells may be seen closely applied to the fibrils. In the description of the preceding stage, evidence was brought forward to show that these "accompanying" cells have been derived through migration from the neural tube, where, it is maintained, they originate as rounded, indifferent cells, the descendants of the germinative cells, and where, according to Schaper, they may later differentiate into either nervous or supporting elements, i. e., neuroblasts or spongioblasts. Certain of these cells, through their power of locomotion, are capable of leaving the central nervous system, and, following the path of the neuraxons, of reaching the peripheral nerve trunk. Lying among the fibrils of the nerve, they increase in number by division. Knowing, as we do, the subsequent history of the indifferent cells remaining within the neural tube, an analogous fate might be expected, *a priori*, in the case of those which migrate out into the nerve trunk. That many of these emigrant indifferent cells do eventually subserve a supporting function, not in the form of neuroglia, but as the sheaths of Schwann, can hardly be doubted. Such cells become elongated soon after their escape from the medullary wall, and, during succeeding stages of development, can be observed adhering closely to the nerve fibrils, until finally, just before the hatching of the animal, they give evidence of participation in the formation of the sheaths of Schwann. The other possibility indicated by their identity with the indifferent cells of the neural tube — namely, their differentiation, in part, into ganglion cells — will be considered under the subject of the ciliary ganglion.

In the one-hundred-hours' series there occurs on the oculomotor nerve midway between its root and the ciliary ganglion, a group of cells worthy of attention. As is shown in Plate 5, Figure 17 — which is a longitudinal section through a portion of the oculomotor nerve — these cells are placed at the margin of the nerve trunk, and present a striking contrast to the "accompanying" cells lying along the fibrils. While the nuclei of the latter cells are drawn out into oval, elliptical and spindle forms, and possess very little cytoplasm, those of the cells forming the group have mostly an almost circular outline, and lie embedded in an abundance of granular cytoplasmic material, which stains deeply with haematoxylin. Proximal and distal to this group the nerve exhibits only fibrils and the ordinary elongated "accompanying" cells. I shall have occasion to refer again to this accumulation of differentiated cells when discussing the ciliary ganglion. The single layer of strikingly elongated cells at the periphery of the nerve is probably made up of mesodermal elements. The processes of these cells unite to form a thin envelope, which doubtless represents the connective-tissue sheath or perineurium of the adult nerve trunk.

2. *Ophthalmic Branch of the Trigeminal Nerve.* The transitory ganglion which appeared in Stage III still persists, but in one series it presents on the left side of the body a disorganized appearance, being represented by small clumps of ganglion cells, which lie scattered about in the mesenchyme in the immediate vicinity of the place on the ophthalmic branch where one would expect to find the ganglion. Possibly we have here the beginning of a process of disintegration. The ganglion on the right nerve in the same series is as compact and definitely limited a body as in the preceding stage, and it lies in the same position, immediately posterior to the laterally projecting vesicles of the cerebral hemispheres. The nerve continues beyond the ganglion as a slender strand, which runs ventrad of the lateral vesicle of the fore-brain, trending also laterad as it proceeds, and, before reaching the level of the anterior extremity of the fore-brain, terminates in a small swelling containing ganglion cells. Several small and rather indefinite

branches are given off immediately proximal to the large transitory ganglion. These branches can be followed for short distances into the mesenchyme.

As was stated in the description of Stage III, ganglion cells can be found scattered along the nerve from the mesocephalic to the transitory ganglion. These cells are more numerous near the mesocephalic ganglion; in fact, the transition from ganglion to nerve is a very gradual one, since so many ganglion cells have migrated outside the true limits of the ganglion. Comparison shows that the ganglion cells to be found in the mesocephalic ganglion are precisely like those of the transitory ganglion. Both have relatively large, rounded nuclei containing chromatin which is concentrated, for the most part, into one or two large masses. Surrounding the nucleus, but lying mostly on one side of it, is a considerable amount of finely granular cytoplasm, which becomes drawn out to a blunt extremity, and stains a deep blue with iron haematoxylin. The nucleus itself is much less deeply stained, with the exception of the included chromatin particles, which take on a dense, black appearance. Such ganglion cells are shown in Plate **2**, Figure 5, where α and β are cells from the transitory ganglion and γ, a cell from the mesocephalic ganglion. These ganglion cells are plainly in an early stage of development, being in the condition of neuroblasts the cytoplasm of which has become drawn out to one side preparatory to developing into neuraxons. In the mesocephalic ganglion many ganglion cells have already sent out their neuraxons, and these form the trunk of the ophthalmic division of the fifth nerve. There are also present, however, young ganglion cells which have not reached this stage of development, as the one to which attention has just been called (Fig. 5, γ). In fact, such ganglion cells seem to be forming here through the activities of proliferating cells, which can be seen in every section made through the Gasserian ganglion in this and preceding stages. Since, then, the mesocephalic ganglion is the scene of constant cell production, and since its young ganglion cells resemble exactly those of the transitory ganglion, and are connected with them by a continuous series of similar ganglion cells lying scattered along the nerve, the source of the component cells of the transitory ganglion does not seem to be open to question, especially when we remember that young ganglion cells possess an extraordinary capacity for locomotion (His, Jun., '**91**). All the evidence points to a migration of ganglion cells distally along the nerve to form the transitory ganglion and, similarly, any other smaller ganglia that may be found near it, If we look upon the proliferating cells in the mesocephalic ganglion as comparable, to a certain extent, with the germinative cells of the neural tube, and consider them, as Schaper has proved for the germinative cells, the producers of a generation of indifferent cells capable of becoming in part nervous, in part supporting elements, then we can easily account for the presence in the ganglion of many small, rounded cells, almost destitute of cytoplasm. It seems probable that these correspond to the indifferent cells of the neural tube. While some of them may change to ganglion cells, others may develop into the small, somewhat elliptical cells found in the ganglion, especially near its distal end, where they pass by an easy gradation into the more elongate cells lying among the fibrils of the nerve which here takes its origin. This leads to the supposition that the "accompanying" cells of the nerve, which later subserve a supporting function by developing the sheaths of Schwann, have been derived through migration from the ganglion. In support of this view I have introduced a drawing (Plate **2**, Fig. 6) made from sections of an embryo of Amblystoma punctatum. Group *A* is taken from the central part of the Gasserian ganglion. It will be noticed that here, lying within the limits of the ganglion, are to be found nuclei in all stages of transition between the rounded and the elongated forms. The nuclei of group *B* lie on the neuraxons at the proximal end of the ophthalmic branch of the trigeminal nerve, those designated by *cl. comit.'* and *cl. comit.''* being situated at the emergence of the nerve from the ganglion. The oval one (*cl. comit.'*) I take to represent a stage in the differentiation of a rounded cell into a long "accompanying" cell, such as those to be found in the remainder of the course of the nerve. Neither in the chick nor in Amblystoma is there at any point along the ophthalmic branch evidence of an intrusion of mesodermal cells.

It is quite possible that supporting derivatives of indifferent cells remain in the ganglia, and later, through their activities, form the nucleated capsules of the ganglion cells, just as the "accompanying" cells of the peripheral nerve form, in an analogous manner, the sheaths of Schwann about the neuraxons. The similar origin of the capsule of the ganglion cell and of the Schwann's sheath of its process would account for the continuity of the two structures. Those investigators who affirm the mesodermal derivation of the Schwann's-sheath cells have never been able, so far as I know, to obtain evidence of an invasion of cerebro-spinal ganglia by mesodermal elements destined to give rise to the envelopes of the ganglion cells.

The rôle played by the ophthalmic branch of the trigeminus in the development of the ciliary ganglion will be considered under the following heading.

3. *Ciliary Ganglion.* As has been stated, the ciliary ganglion lies mainly on the lateral side of the third nerve near its distal extremity. Its form in transverse section, and its general relation to the ophthalmic branch of the fifth nerve and to the eyeball, are shown in a diagrammatic way, for the right side of the head, in Plate **4**, Figure 13. The striated portion represents the fibrils of the oculomotor, while the ciliary ganglion is indicated by the evenly shaded part. The ganglion contains, now for the first time, cells so far advanced in differentiation that they can be declared without hesitation to be young ganglion cells (Plate **5**, Fig. 16, *E*). Interspersed among them are a few cells (*E*, *cl.′*, *cl.″*) exactly like the "accompanying" cells of the nerve fibrils. The ganglion is no longer, as in the preceding stage, the scene of active cell division. A few of the young ganglion cells lie along the median border of the nerve opposite the laterally placed body of the ganglion. Figure 13 (Plate **4**) also shows the ophthalmic branch of the trigeminus (*rm. opth. trig.*) cut transversely. A small offshoot is indicated, running from this nerve in the direction of the ciliary ganglion, which, however, it fails to reach. The fibrils of this branch become lost in the mesenchyme, so that it is not possible to trace them all the way to the ganglion, although, on the opposite side of the head, where development is a little more advanced, this can be done. I have also indicated in the figure all the ganglion cells to be found along that segment of the ophthalmic branch of the trigeminus which lies opposite the ciliary ganglion as well as all the ganglion cells that have become detached from the ophthalmic branch at this level. The number and positions of these cells were ascertained by studying the series of consecutive sections extending from the anterior to the posterior face of the ciliary ganglion, and recording the ganglion cells observed by projecting them on the plane of the diagrammatic section represented by Figure 13.

A comparison of the ganglion cells of the ophthalmic branch of the trigeminus with those of the ciliary ganglion will prove instructive. In Figure 16 at *A* are shown two ganglion cells (α, β), taken from the ophthalmic branch, their positions in that nerve being indicated by the same letters in Figure 13. The ganglion cells of the group *E* were taken at random from the ciliary ganglion. They exhibit the features characteristic of young ganglion cells, resembling those of the ophthalmic branch in the possession of deeply staining granular cytoplasm, accumulated at one side of the rounded nucleus. But an evident and consistent difference exists between the cells taken from the two sources. The cells of the ciliary ganglion are smaller than those of the ophthalmic branch of the trigeminus. This difference is to be seen at once in the drawings in Figure 16, in which the outlines of the cells were made with the aid of the camera lucida under precisely the same optical conditions for all groups. Not only is the amount of cytoplasm less in the ciliary-ganglion cells, but their nuclei are distinctly smaller than those of the ophthalmic cells. It is not an easy matter to compare accurately the two classes of cells by measurements of the diameters of their respective nuclei, since these are seldom exactly circular in outline. I have, however, made measurements in the cases of such nuclei as approached nearest to a circular form, and I find that while the diameters of the nuclei of the ciliary-ganglion cells fall between 5.2 micra and 6.5 micra, the nuclei of the ophthalmic cells show constantly a diameter of approximately 7.8 micra.

The ganglion cells lying in the mesenchyme, between the ophthalmic branch and the ciliary ganglion, are very evidently emigrant ophthalmic cells. Two such cells, having the positions γ and δ in Figure 13, are shown in *B* and *C*, Figure 16, each surrounded by mesodermal cells. A glance shows that they belong to the ophthalmic and not to the ciliary type. Within the boundaries of the ciliary ganglion, lying close to the exterior of the cell mass, on the side toward the ophthalmic branch of the trigeminus, are to be found among the smaller ganglion cells three cells with large nuclei, two of which are shown in Figures 16, *D*, and 13 (ϵ, in both figures). These appear to be ophthalmic ganglion cells, which have traversed the mesenchyme and entered the ciliary ganglion.

With the foregoing evidence before us, let us inquire into the source of the cells of the ciliary ganglion. We have seen that in the early stages of the growth of the oculomotor nerve a migration of medullary cells takes place from the neural tube into its root. I believe that in Stage I we have the first migratory cell forcing its way through the external limiting membrane of the neural tube (Plate 3, Fig. 8). In succeeding stages these cells seem to be migrating in considerable numbers. The rounded nuclei of the cells appear to be almost naked, for it is difficult to detect any cytoplasm surrounding them. These cells are as yet neither neuroblasts nor spongioblasts, but evidently the motile, indifferent cells of Schaper, i. e., they are descended from germinative cells, and are capable of differentiating later into either nervous or supporting elements. Many of these nuclei, once out on the nerve, become elongated as they move away from the neural tube. Such "accompanying" cells maintain throughout development their close proximity to the nerve fibrils, and in them we recognize, as has been pointed out, the nuclei of the future sheaths of Schwann. A large part, then, of the emigrant cells become supporting elements.

Do any of the emigrant indifferent cells become nervous elements? We have seen that at all stages rounded nuclei, resembling and continuous with the indifferent cells of the neural tube, occur abundantly at the root, and more sparingly along the trunk, of the oculomotor nerve, lying among the more numerous elongated supporting cells. In Stage III an accumulation of such cells was observed at the distal end of the nerve, causing at this place its enlargement into the fundament of the ciliary ganglion (Plate 7, Fig. 24, *gn. cil.*), the cells of which were undergoing active division (Plate 5, Fig. 15). Schaper, it will be remembered, shows that the indifferent cells of the central nervous system likewise possess the property of further propagation. In the present stage, IV, the ciliary ganglion of the right side contains undoubted ganglion cells. The right oculomotor has not yet come into connection with any other nerve, although the ophthalmic branch of the fifth is sending fibrils in the direction of the ciliary ganglion, and toward the latter a few ophthalmic ganglion cells are apparently making their way through the mesenchyme. Three, in fact, lie just within the borders of the ciliary ganglion, easily distinguishable by their larger size from the numberless ganglion cells about them. The vast majority of the cells of the ciliary ganglion, however, could have originated only by differentiation from the rounded, proliferating cells which are to be seen in Stage III occupying the site of the future ganglion, before there is the slightest trace either of a connection between the oculomotor and the ophthalmic branch of the trigeminus, or of the migration of ophthalmic ganglion cells through the mesenchyme toward the fundament of the ciliary ganglion. There is good evidence that the actively dividing cells of the latter ganglion had their origin in indifferent medullary cells which had escaped from the neural tube. If this be so, then a small portion of the indifferent cells migrating out from the mid-brain do become differentiated, after increase in numbers by division, into nervous elements, i. e., ganglion cells of the ciliary ganglion.

An accumulation of differentiating cells at the side of the third nerve, midway between its root and the ciliary ganglion (Plate 5, Fig. 17), during this stage, has been referred to in the account of the oculomotor nerve. This accumulation I believe to be composed of young ganglion cells, developing from indifferent cells stranded, as it were, on their way from the neural tube to the ciliary ganglion. Around each nucleus the characteristic deeply staining cytoplasm is in process of development. Whether these cells later disintegrate, or produce secondary ganglia, such as are sometimes found in fishes, amphibians, birds and mammals (Schwalbe, '79; Jegorow, '86–87), I do not know. Such an accumulation does not occur along the nerve of the opposite side.

4. *Abducent Nerve.* The sixth nerve emerges in this stage, as in the preceding, by several roots, crowded with "accompanying" cells. Its nidulus is not well defined. The roots of the nerve lie about 190 micra from the median plane, and have much the appearance seen in the following stage, which is shown in Figure 18 (Plate 6). They unite ventral to the hind-brain to form a straight, unbranched nerve, which runs horizontally cephalad, becoming more attenuated toward its distal end, and terminating in the postero-dorsal extremity of the posterior rectus muscle.

In the roots of the nerve can be seen evidence of cell migration from the neural tube. The more or less rounded cells found at the proximal end of the nerve pass rapidly into the elongated "accompanying" cells, which lie distally along its fibrils. Many of the "accompanying" cells show mitotic figures. At no place on the abducens is there an accumulation of rounded cells like that which in Stage III forms on the oculomotor the fundament of the ciliary ganglion. In the case of the sixth nerve the indifferent cells which migrate out from the hind-brain appear to develop exclusively into structures with the supporting function, the sheaths of Schwann.

5. *Eye Muscles.* In this stage first appears the fundament of the ventral oblique muscle, the most anterior of the four eye muscles which are innervated by the oculomotor nerve. At the same time we find that the free end of the nerve extends beyond the ciliary ganglion as far as this muscle mass.

The axis of the posterior rectus muscle now points in a postero-dorsal and antero-ventral direction, instead of nearly longitudinally, as in Stage III. The dorsal, anterior and ventral rectus muscles retain their primitive relations in both this stage and the following one; in the account of the latter they are described and figured, together with the ventral oblique muscle.

Stage V.

The conditions characteristic of the fifth stage of development are found in embryos of one hundred and eighteen to one hundred and twenty hours. The cephalic flexure has become less pronounced, so that the axis of the fore-brain makes with that of the hind-brain approximately a right angle, at the vertex of which the large vesicle of the mid-brain projects externally.

1. *Oculomotor Nerve.* The oculomotor nidulus is now about 200 micra from the median plane. The fibre tract of the ventral wall of the mid-brain is well developed, forming a third of the entire thickness of the wall. The processes of the oculomotor neuroblasts extend ventrad through this tract, the fibres of which run at right angles to the processes: Along the oculomotor neuraxons lie "accompanying" cells, which resemble in every respect the cells which are present in great abundance in the root of the nerve immediately outside the external limiting membrane.

However, within the neural tube the "accompanying" cells do not often extend along the neuraxons all the way to the limiting membrane. It appears that migration is by this time nearly over. The neuraxons of the third nerve are closely interwoven with numerous nerve fibres running at right angles to them. The "accompanying" cells, which measure approximately 4 micra in diameter, in order to pass from the mantle layer to the mesenchyme, would be obliged to force their way along the oculomotor neuraxons through a feltwork about 75 micra in thickness.

From its root, which is still spread out longitudinally, the oculomotor nerve runs caudad, ventrad and somewhat laterad. On reaching the level of the optic stalk, it turns toward the median plane, and, continuing its course ventrad and mediad for a short distance, ends in the ventral oblique eye muscle. About two-thirds of the way from the proximal to the distal end of the nerve, the unsymmetrically elliptical ciliary ganglion is to be seen lying on the nerve trunk. This portion of the nerve is seen in the parasagittal section shown in Plate **7**, Figure 26 (*n. oc'mot.*), which is viewed from the right face. The fundament of the dorsal rectus eye muscle (*mu. rt. d.*) and the common fundament of the ventral and anterior rectus muscles (*mu. rt. v.* + *a.*) lie in close contact with the dorsal side of the nerve, but no fibrils can be detected turning aside from the main trunk to penetrate these muscle masses. That is to say, so far as can be seen, the oculomotor remains at this stage an unbranched nerve.

Along the posterior margin of the root occurs a bundle of fibres rendered conspicuous by their freedom from "accompanying" cells. Along the external margin of this bundle a single layer of cells separates it from the mesenchyme.

A study of the oculomotor with high powers at this stage gives evidence of different histological conditions at different points along the nerve. These conditions are well brought out by the vom Rath method. A heavy black precipitate along the neuraxons differentiates these clearly against the less darkly colored stroma in which they appear to be imbedded.

The drawings shown in Plate 2, Figure 7, *A*, *B*, *C*, are from a chick of one hundred eighteen hours' incubation, stained by the vom Rath method. These drawings were made from different parts of the nerve: *A*, from the proximal end, *B*, farther distally, and *C*, near the peripheral termination. All were made with the aid of a camera lucida under precisely the same conditions of magnification. At *A*, are shown two neuraxons taken from the root as they appear under the $\frac{1}{12}''$ oil-immersion lens. It will be seen that these are compact cylinders in which fibrillation cannot be very satisfactorily made out, although indications of it are to be detected here and there, for instance, in the upper portion of the neuraxon lying on the right in the drawing. Closely applied to the neuraxons are numerous elongated "accompanying" cells.

Farther out on the nerve, in that portion which passes along the ventral margin of the common fundament of the ventral and anterior rectus muscles (comp. Plate 7, Fig. 26), the conditions are different. From this part of the nerve I have drawn two bundles of fibrils with the accompanying embryonic nuclei of Schwann's sheath. These possibly represent two neuraxons, though it is impossible to trace any one neuraxon with certainty through the series of sections from the root of the nerve to this place. A careful study of the preparations has, however, convinced me that the compact neuraxon which passes out from the brain into the root of the nerve becomes more and more expanded and more evidently fibrillar toward its peripheral extremity. In fact, close to this extremity the fibrils become so numerous that those belonging to the various component neuraxons of the nerve are inextricably intermingled. The appearance of the oculomotor upon reaching the ventral oblique muscle is shown at *C*, Figure 7. The bundles of fibrils which are the continuations of the comparatively large cylindrical neuraxons of the proximal portion of the nerve have here, at its distal end, lost their identity in the mass of fibrillar elements. Nevertheless, while the separate bundles of fibrils corresponding to the neuraxons are not well defined, there can be seen in the nerve a tendency toward the formation of more or less well-marked groups of fibrils, each of which may represent in the main a single neuraxon.

That the number of the fibrils arising from the splitting up of neuraxons is increased distally along the nerve by longitudinal division of the fibrils, can be asserted with a fair degree of confidence. It is possible to see in the preparations strong indications of such branching, though, as the fibrils concerned are very fine and lie closely associated with one another, it is difficult in most cases, even with the highest powers and most careful focusing, to be perfectly sure that the two branches into which the fibril appears to divide are really the continuations of that fibril.

In preparations fixed in Zenker's fluid and stained with iron haematoxylin the finely fibrillar condition of the entire nerve is plainly demonstrated, for not only are the identities of the neuraxons lost in the mass of fibrils in the distal and middle parts of the nerve, but they are with difficulty made out close to the root, where the fibrillar condition also appears.

It is interesting to compare with the conditions in the chick longitudinal sections through the oculomotor nerve of a pig embryo measuring 8 mm. (its greatest length in its normal curved position). This material was fixed in the corrosive-acetic mixture mentioned on p. 176 and stained with Brazilin. In Plate 4, Figure 14, *A*, the horizontal line (*mb. lim. ex.*) represents the external limiting membrane of the midbrain, and above it, on its way through the ventral fibre tract, is seen the proximal end of an oculomotor neuraxon. Upon leaving the neural tube, the neuraxon gradually grows thicker as it proceeds peripherally, and its fibrillation becomes more marked. It can be followed as a distinct process as far as has been indicated in the drawing, but at this point it comes into relation with other neuraxons forming the root of the oculomotor, and its identity becomes lost. The lower drawing, *B*, is that of a longitudinal section through the same nerve about midway in its course. It is plain that here the separate neuraxons cannot be distinguished. The whole nerve is simply a homogeneous bundle of fibrils.

A noticeable difference between the pig and the chick is the almost complete absence of nuclei among the nerve fibrils of the former. A few cells are to be seen lying along the periphery of the nerve, but it is only occasionally that one can be found among the fibrils in the interior of the bundle.

2. *Ophthalmic Branch of the Trigeminal Nerve.* The Gasserian ganglion is still bifurcated distally, but the two parts are more completely united proximally than in earlier stages. The ophthalmic branch extends forward from the extremity of the tapering mesocephalic ganglion, passes just mediad of the anterior cardinal vein, and dorsad of

the fundament of the posterior rectus muscle. Then the nerve, upon reaching the region of the ciliary ganglion, which is ventral to it, sends to this ganglion a strong fibrillar communicating branch (Plate **7**, Figure 25, parasagittal section, *rm. comn.*), indications of which were present in the preceding stage. The ophthalmic branch in its course next passes immediately ventral to the median end of the dorsal rectus muscle; then, passing on the dorsal side of the distal end of the optic stalk, and keeping close to the eyeball, it runs to the anterior region of the head, where it breaks up into a number of slender branches.

Ganglia are not to be seen along either the right or the left ophthalmic branches, although ganglion cells occur here and there along their courses. The ganglionic swellings observable in Stage IV have completely disappeared. At only two points on each nerve are there accumulations of ganglion cells, and these are so small as to cause no enlargement of the nerve trunk. The ganglionic groups occur at the origin of the communicating branch (Fig. 25, β), and at the origin of a small ramus which extends into the mesenchyme opposite the dorsal rectus muscle. Both of these localities are far proximad of that of the transitory ganglion of Stages III and IV, no trace of which now remains. It will be remembered that in Stage IV one of the two ophthalmic nerves showed a disorganized transitory ganglion, which, as was suggested, might be considered in process of disintegration.

In a series from a chick incubated one hundred nineteen and one-half hours, the communicating branch between the ophthalmic division of the trigeminus and the ciliary ganglion is of considerable size, its diameter on the right side of the body, where it is a single trunk, being rather more than one-fourth that of the ophthalmic branch. On the left side, it consists of two separate bundles of fibrils. In both cases it presents the same appearance as the trunk of the ophthalmic branch, being made up of fine fibrils with elongated "accompanying" cells. The very small number of migrant ganglion cells to be found along the communicating branch is significant. Instead of affording a highway along which quantities of cells from the ophthalmic branch pass over into the third nerve to form the ciliary ganglion, it serves for the transit of very few of these cells. On the left side of the body there can be counted along the communicating branch only five ganglion cells, while, on the right side, only one undoubted cell of this nature can be made out. In the trunk of the ophthalmic branch, at the place of origin of the communicating ramus, there are present, on the left side of the body, twenty-one ganglion cells; on the right side, only two.

3. *Ciliary Ganglion.* The ciliary ganglion projects as a large mass of cells from the lateral and dorsal sides of that portion of the oculomotor nerve which lies between the fundament of the dorsal rectus muscle and the combined fundaments of the ventral and anterior rectus muscles (Plate **7**, Fig. 26, *gn. cil.*). The communicating ramus from the ophthalmic branch of the trigeminus connects with its lateral face. A comparison of its ganglion cells with those found along the ophthalmic branch shows, as in Stage IV, a marked difference both in the size of nuclei and in the amount of distinctive cytoplasm. In Plate **3**, Figure 10, the three upper ganglion cells, α, β, γ, are from the ophthalmic branch, the three lower ones, δ, from the ciliary ganglion. Cell α, near which are shown several future Schwann's-sheath cells applied to the neuraxons, is taken from the nerve close to the Gasserian ganglion. Cell β is found at the base of the communicating branch running to the ciliary ganglion, in the position indicated in Plate **7**, Figure 25, by β; while cell γ occurs distal to β at the point indicated by γ in the same figure. The smaller size of the ciliary ganglion cells, δ, is apparent. Both along the ophthalmic branch and within the ciliary ganglion, occasional "accompanying" cells can be observed in the act of dividing. One from the ophthalmic branch is shown at *cl. comit.′*, one from the ciliary ganglion at *cl. comit.″*

Ganglion cells of the ophthalmic type lying along the communicating branch have been mentioned above. In one case ophthalmic ganglion cells can be traced along the branch to the boundary of the ciliary ganglion, but none can be detected within it; in another, there can be seen within the boundaries of the ganglion near the entrance of the communicating branch two cells, which can with certainty be assigned to the ophthalmic class. It is apparent that there is not a large contribution of cells from this source to the ciliary ganglion; yet it seems probable, in view of the evidence derived from Stage IV, that at least a few ophthalmic ganglion cells have from that time on been making their way into the ciliary ganglion. If this be so, the large invading cells must soon become modified, through decrease in size, into cells closely resembling those of the ciliary ganglion, which have arisen *in situ*, for careful search through the entire ganglion at this stage fails to reveal more than two cells of the ophthalmic type within its precincts, and these lie close to the entering end of the communicating branch, and hence appear to be new arrivals.

4. *Abducent Nerve.* Except for some increase in size, the sixth nerve has not changed its appearance since the last stage. It springs from its

longitudinally elongated nidulus in the floor of the hind-brain by five or more roots placed one behind the other (Plate 6, Fig. 18, *n. abd.*). These roots often become divided near their region of emergence from the neural tube, so that a strict count of their number is made difficult. The number of roots differs in different individuals, and even on opposite sides of the same individual. Although Figure 18 shows but five roots, on the other side of the embryo six can be counted. This figure shows the manner in which the roots unite to form the nerve, which is now of comparatively large size, although previously it has been remarkable for its small calibre. The nerve trunk (Plate 7, Fig. 26, *n. abd.*) runs cephalad, laterad, and slightly ventrad to end in the fundament of the posterior rectus muscle (*mu. rt. p.*). In one case, the nerve bifurcates just before reaching the fundament, and while one division continues the course of the nerve straight into the muscle mass, the other runs on the dorsal side of it for some distance, and then turning ventrad enters the fundament, dividing again as it does so. The fibrils of the nerve can be traced far into the mass of differentiated mesodermal cells constituting the muscle fundament.

The evidence for cell migration into the roots of the abducens is still good at this stage, the ventral fibre tract in the region of the nidulus being less thick than where the oculomotor emerges. Figure 19 (Plate 6), drawn from a preparation fixed in the picro-sulphuric mixture and stained with Delafield's hæmatoxylin, shows that rounded nuclei in the wall of the neural tube extend down from the nidulus into the ventral fibre tract, and, indeed, to the very surface of the tube, where they become continuous with similar nuclei lying outside the tube along the nerve. Farther out on the nerve these nuclei become elongated. As has been said, all the indifferent cells escaping in connection with the sixth nerve appear to assume a supporting function, developing into the sheaths of Schwann. At no time during the growth of the nerve can young ganglion cells be discovered at any place along its course.

5. *Eye Muscles.* The section represented in Plate 7, Figure 26, shows in one plane the fundaments of the posterior rectus eye muscle and the four eye muscles innervated by the oculomotor nerve. All the eye-muscle fundaments consist of clusters of crowded elongated mesodermal nuclei, the interstices between which are filled with differentiating cytoplasm, which stains deeply with hæmatoxylin.

The first, in order of development, is the posterior rectus muscle (*mu. rt. p.*). This was present in Stage I, and its position and appearance during succeeding stages have been described. In the present stage, it lies caudad and mediad of the eyeball. The main mass of the muscle extends laterad until its outer extremity comes to lie just ventrad of the ophthalmic branch of the trigeminus (Plate 7, Fig. 25, *mu. rt. p.*). From this main portion an arm extends mediad and caudad to meet the abducent nerve; the nerve penetrates the muscle mass, and its fibrils become thoroughly intermingled with the cells of the fundament.

The fundaments of the dorsal, ventral, and anterior rectus and the dorsal oblique muscles were all seen for the first time in Stage III. The dorsal rectus (Plate 7, Fig. 26, *mu. rt. d.*) extends in a transverse direction, its outer end lying dorsad of the ophthalmic branch of the trigeminus, and its inner end dorsad of, and in close contact with, the oculomotor, immediately before that nerve reaches the ciliary ganglion.

The common fundament of the ventral and anterior rectus muscles (*mu. rt. v.* + *a.*) is comparatively large, and lies along the ventral side of the optic stalk, reaching laterad as far as the third nerve, which lies along its ventral border.

The most superficial of all the muscle fundaments is that of the dorsal oblique, which lies in the same parasagittal plane as the Gasserian ganglion, and is dorsal to the eyeball at a point a little anterior to one opposite the choroidal fissure. This is the only eye-muscle fundament which does not appear in the plane of the section of which Figure 26 is a photograph. It has no connection with its nerve, the trochlear, which, indeed, I have not been able to detect up to this stage of development. In appearing thus before its nerve, it resembles the posterior rectus muscle, and differs from the muscles innervated by the oculomotor.

The last muscle to develop is the ventral oblique (Fig. 26, *mu. ob. v.*), which first appeared in Stage IV. Its fundament is antero-ventral to the optic stalk, and much nearer the median plane than the dorsal oblique. The axis of the muscle fundament extends transversely, and near its median end receives the spreading fibrils of the extremity of the oculomotor nerve. It is the only one of the muscles finally innervated by the third nerve into which fibrils from the nerve can at the present time be traced.

Notes on Later Development.

1. *Oculomotor Nerve.* In Stage V (about five days' incubation) none of the branches of the third nerve found in the adult were present. In series of about seven days' incubation it can be seen that the eye-muscle fundaments, which in Stage V were in contact with the sides of the

nerve, have now drawn away from it. Fibrils can be detected turning aside from the trunk of the oculomotor and entering the fundament of the dorsal rectus. The nerve also sends a bundle of fibres to the fundament of the ventral rectus, which has now become distinct from that of the anterior rectus. The branch of the oculomotor which in the adult innervates the latter muscle must develop later, since I have not been able to detect it in three series of sections of about seven days' incubation. At this time, then, the third nerve exhibits all of the branches found in the adult, with the single exception of that to the anterior rectus muscle.

The first indications of the formation of the sheaths of Schwann were discovered only in the oldest embryo I have examined — one of eighteen days' incubation. In longitudinal sections of the oculomotor stained by the van Gieson method, it is apparent that the elliptical "accompanying" cells lying among and parallel to the fibrils are sending out cytoplasmic processes from both ends. These processes have not, however, developed the longitudinal laminae, which mark the next step in the formation of the sheaths of Schwann in mammals, as was first shown by Gurwitsch (:00). Bardeen (:03) using the van Gieson stain, has confirmed the conclusions of Gurwitsch. When present the laminae, exhibiting their cut edges in cross-sections of the nerve fibrils, separate the latter into bundles which are later bound closely together to form the neuraxons. Cross-sections of the oculomotor nerve at this stage give no evidence of the subdivision of the fibrils into such bundles.

2. *Ophthalmic Branch of the Trigeminal Nerve.* The direct connection between the ophthalmic branch and the ciliary ganglion persists at least up to the eighteenth day of incubation, which is the oldest series in which I have looked for it. It will be remembered that in the adult such a direct connection does not exist, the communicating branch entering the ciliary nerve some distance distal to the ciliary ganglion. (Plate 1, Fig. 2).

3. *Ciliary Ganglion.* The ciliary ganglion retains throughout life its situation immediately on the trunk of the oculomotor nerve; that is to say, no radix brevis is ever developed. In fact it often appears, even in the adult, as though the main trunk of the oculomotor ends in the ciliary ganglion, while its continuation to the ventral oblique muscle has the appearance of a large branch leaving the trunk just before the ciliary ganglion is reached. It is, however, more in accordance with the facts of comparative anatomy to regard the nerve as dividing into two main branches at the region of the ramus to the dorsal rectus muscle.

One of these main branches is the latter ramus, the one innervating the dorsal rectus muscle; the other is the ventral ramus, which extends to the ventral oblique muscle. The ciliary ganglion should, then, be considered as sessile on the ventral division of the nerve.

At seven days I have seen no evidence of the ciliary nerve. At eighteen days it is present as a comparatively large bundle of fibrils, which runs from the ciliary ganglion to the eyeball. The fibrils penetrate the sclerotic coat caudad of the entrance of the optic nerve, and continue their course between the sclerotic and choroid tunics.

In the seven-days' stage the difference in size between the ganglion cells of the ciliary and Gasserian ganglia is striking.

In the ciliary ganglion of an eighteen-days' embryo, small cells with crescentic nuclei can be seen arranged about the ganglion cells. Their processes are continuous, forming a complete envelope, the nucleated capsule of the ganglion cell. Retzius ('81) figures these nucleated capsules around the bipolar ciliary-ganglion cells of the adult fowl.

4. *Abducent Nerve.* The sixth nerve had reached in Stage V its adult condition, as far as its relations to the posterior rectus muscle and surrounding structures were concerned, except that its branch to the muscles of the nictitating membrane had not appeared. I have not observed the formation of this branch. It could not be found at the end of seven days' incubation.

5. *Eye Muscles.* As has been said in the description of the oculomotor nerve, at some period between Stage V (about one hundred nineteen hours) and one hundred sixty-eight hours, the common fundament of the ventral and anterior rectus muscles becomes divided into two parts, from which develop the separate muscles of the adult.

6. *Trochlear Nerve.* In sections of seven-days' embryos, the fourth nerve can be traced from its dorsal superficial origin between the mid-brain and the hind-brain to its termination in the dorsal oblique muscle. Before reaching the muscle the nerve spreads out into a loose brush of fine fibrils, which, even in vom Rath preparations, are not easily traceable through the mesenchyme.

Discussion of Results.

Migration of Medullary Cells. Frequent allusions to the migration of cells from the embryonic neural tube are to be found in neurological literature since the time of Balfour. That pioneer among the investigators of the histogenesis of nerves believed he found in elasmobranchs clear evidences of the escape of nerve-forming cells from the spinal cord

(Balfour, **'75**). In this view he was supported by Beard (**'88**). Dohrn (**'88**[a], **'91**) also saw the migration of medullary elements in selachians, and C. L. Herrick (**'93**) affirms that in amphibians, reptiles and mammals nerve-forming cells issue from the niduli of ventral nerve roots. Platt (**'96**) is of the opinion that in Necturus the motor nerves are formed by emigrant bipolar cells derived from the neural tube. Among recent observers who have likewise seen medullary cells migrating out into the ventral roots of spinal nerves may be mentioned Harrison (**:01**) and Neal (**:03**). The former made his observations upon Salmo salar, the latter upon Squalus acanthias.

The interpretations put upon these emigrant cells have been various. They have been thought by some observers to be the cells which, assuming a moniliform arrangement, give rise to the neuraxons of the nerves; they have been considered to be ectodermal additions to the mesodermal cells which lie among the peripheral processes of centrally located neuroblasts, and to be destined later to participate in the formation of the sheath of Schwann; and, finally, they have been looked upon, in part at least, as undeveloped ganglion cells.

It is not unusual to meet with ganglion cells in the ventral roots of the spinal nerves of adult animals. Freud (**'78**) describes such cells in the ventral roots of the spinal nerves of Petromyzon. Schäfer (**'81**) and Kölliker (**'94**[a]) found ganglion cells similarly situated in the cat. Thompsen (**'87**) figures what he believes to be ganglion cells in various stages of degeneration in the roots of the third and fourth cranial nerves in man, and his interpretation has been accepted by Gaskell (**'89**), and more recently by Barratt (**:01**), to account for the presence of amorphous fibrillar or granular masses observed by them in the human oculomotor and trochlear nerves. Taking into consideration the observations which have been made on the growth of the oculomotor nerve in the chick, the suggestion is here offered that these degenerated ganglion cells may have had their origin as indifferent cells migrating out from the mid-brain into the roots of these nerves in an early embryonic stage. Becoming differentiated here into ganglion cells, they may later have undergone a more or less complete disintegration, owing to their failure to attain to a condition of functional activity.

The chief opponent of the view that medullary cells migrate out from the neural tube has been W. His (see His, **'89**), and it is doubtless largely owing to his prestige that the fact of migration, together with the rôle played by the emigrant cells in nerve formation, has attracted comparatively little attention. The followers of His have accounted for the origin of all the parts of a peripheral neuron in the following manner: The neuraxon arises as a process from a centrally situated neuroblast, which becomes the ganglion cell. Cells of mesodermal origin form around the neuraxon the sheath of Schwann (Vignal, '83; Kolster, '99; Gurwitsch, :00; Bardeen, :03; and others). Between the central neuraxon and the enveloping sheath of Schwann the non-cellular medullary substance is developed, possibly as the result of differentiation in the homogeneous stroma immediately surrounding the neuraxon. The participation of emigrant medullary elements in the formation of the nerves appears, then, to be quite unnecessary.

Recent writers on the histogenesis of nerves generally take into account, however, the indisputable evidence that has been offered in favor of the immigration of cells into the developing nerves of elasmobranchs. Bardeen (:03) admits that even in mammals, as well as in the lower vertebrates, a certain number of cells migrate out from the spinal ganglia and cord, but believes that in mammals the cells of Schwann's sheath arise in the main at least from the mesoderm. Neal (:03) is of the opinion that in elasmobranchs both mesodermal and emigrant ectodermal cells participate in the production of the sheath of Schwann. He saw few mitoses among the emigrant cells, and consequently concludes that ectodermal elements are not present in sufficient numbers to furnish all the sheath cells. In the developing oculomotor and abducent nerves in chick embryos however, mitotic division among the "accompanying" cells is of frequent occurrence. If, as the appearances lead me to believe, the "accompanying" cells are medullary derivatives, it follows that here ectodermal elements might easily be multiplied until they became numerically equal to the nuclei of the Schwann's sheaths of the definitive nerve. Proof that the Schwann's-sheath cells of the lateral line in Amblystoma are to be regarded as ectodermal derivatives has been adduced by Harrison (:03) in a recent paper.

In an earlier paper Neal (:00) concluded from his own researches, and from a review of the literature, that anamniote embryos differ from amniote embryos in deriving a part of their sheath cells from the neural tube. That migration is more easily observable in lower forms than in mammals is undoubtedly true. In this connection it should be borne in mind that His ('89), who controverted the interpretations of Dohrn ('88^a) in respect to migration in selachians, must have been largely influenced by his extended researches on the histogenesis of mammalian nerves. But if it be admitted that medullary cells migrate out of the neural tube into the roots of the third and sixth nerves in the chick, Neal's limitation of such a phenomenon to anamniote embryos no longer holds.

Histogenesis of the Neuraxons. As regards the growth and internal differentiation of the neuraxons, my results are in general accordance with those of Vignal ('83), and especially with those of Bardeen (:03), both of whom followed the development of cerebro-spinal nerves in mammalian embryos. The neuroblasts of the oculomotor nidulus send out into the mesenchyme, to form the third nerve, compact homogeneous processes of considerable calibre. These soon break up, apparently by a longitudinal splitting, into fine fibrils; this differentiation begins at the distal end of the nerve. Bardeen's statement as to the effect of this upon the appearance of a cerebro-spinal mammalian nerve applies equally well to the oculomotor or abducent nerve in the chick. He says (p. 247): "During the early stages of development these fibrils may either be gathered in small compact groups, each of which represents an axis-cylinder process, or they may be so scattered within the nerve that it is impossible to distinguish definite groups of fibrils corresponding to axis-cylinder processes." The first statement we have seen to be true of the middle portion of the developing oculomotor nerve; the second, of its distal extremity. Bardeen is also of opinion that the fibrils may increase in numbers by longitudinal division. As he has pointed out, these fibrils seem to be of larger calibre than the "primitive" fibrils of Apáthy and Bethe occurring in adult neuraxons. According to the observations of Vignal ('83), Gurwitsch (:00) and Bardeen the embryonic nerve trunk in mammals becomes invaded by cells which divide the fibrils into small bundles, each of which becomes surrounded by a special envelope (Schwann's sheath) formed by the invading cells. The fibrils making up the bundle are closely bound together in this way into a compact neuraxon. It is possible that the fibrillation of the adult neuraxon may bear some relation to the embryonic fibrils out of which the neuraxon is formed, but the precise nature of this relation remains to be ascertained.

Nature of the Ciliary Ganglion. The evidence derived from the study of both its development and its histology points to the double nature of the ciliary ganglion of the fowl. I shall now consider, first from an embryological, and then from a histological point of view, the character of the two kinds of elements that enter into the composition of the ganglion.

We have seen that during development the fundament of the ciliary ganglion receives contributions of cells from the Gasserian ganglion *via* the ophthalmic branch of the fifth nerve. Their origin from a cerebro-spinal ganglion, their migration, their final incorporation into a ganglion whence proceed motor peripheral fibres, are all strong indications of the sympathetic nature of these cells. Yet, as His ('**88**^{a}) has observed, errant cerebro-spinal cells, which may remain cerebro-spinal in character throughout life, cannot with certainty be distinguished in the embryo from cells destined to become sympathetic. We must apply in addition the tests of histology after the cells have reached their adult development.

The greater part of the cells of the ciliary ganglion do not originate, like those to which reference has just been made, from a cerebro-spinal ganglion. It has been shown that a large proportion of the ciliary cells become gradually differentiated *in situ* in the third nerve. The evidence in favor of regarding these as migrant medullary elements has been given. These ganglion cells, therefore, resemble in their development neither cerebro-spinal cells, which stand in direct genetic relation to the neural crest, nor sympathetic cells, the derivation of which from cerebro-spinal ganglia can scarcely be questioned since the researches of Onodi ('**86**), His, Jun. ('**91**), and others.

The histological conditions which obtain in the ciliary ganglion of the adult fowl bear out well the idea of its double nature. The occurrence in the ganglion of two regions, which were described in Part I of this paper, is readily explained on developmental grounds. The smaller, dorsal portion of the ganglion, whose small cells, slightly medullated neuraxons and pericellular fibrils give evidence of its sympathetic character, lies on the side next the ophthalmic branch of the trigeminus, and receives from that nerve the communicating ramus which so clearly resembles a ramus communicans of the thoracic region. It is true, however, that the neuraxons given off peripherally lack the abundant medullation characteristic of the post-ganglionic sympathetic neuraxons of the thoracic region. If we consider that this part of the ganglion has originated from those cells which, in the embryo, migrated into it from the Gasserian ganglion, it then may be said to conform to the sympathetic type in its manner of development, as well as in nearly all its adult histological details. One evidence of the sympathetic nature of this region of the ciliary ganglion has not been adduced. The multipolarity of its cells still remains a matter of assumption. Holtzmann ('**96**), it is true, found both large and small cells in the ciliary ganglion of birds. While the large cells are shown to be bipolar with large, medullated processes, a typical small cell is figured with a single, slender, apparently non-medullated process. The possibility that other fine processes might have been torn off in the macerating and teasing method employed suggests itself. Except for its unipolar condition this cell bears a close resemblance to a sympathetic cell.

The larger, ventral region of the ciliary ganglion bears little resemblance to a sympathetic ganglion. The cells in it are of greater size, pericellular fibrils are not abundant, and its neuraxons are heavily medullated. It seems safe to assume that from this portion of the ganglion were obtained by maceration the large bipolar cells with medullated processes, the description of which has been given. While the neurons in question resemble in medullation and size of ganglion cells those of cerebro-spinal ganglia, some points of difference exist, the chief one being the bipolarity of the former and the unipolarity of the latter. As has been stated, even when the ciliary-ganglion cells approach an unipolar condition, the single stem does not divide at right angles to form the typical **T** of a cerebro-spinal neuron. Inasmuch as we have assigned to the dorsal or sympathetic portion of the ciliary ganglion the cells which in the embryo migrate into it from the Gasserian ganglion, this larger ventral region must have had its origin from those other and more numerous cells which differentiate into nervous elements *in situ* within the third nerve. These, as has been shown, appear to be migrant cells from the ventral wall of the neural tube, a source from which neither cerebro-spinal nor sympathetic ganglion cells are derived.

It must be borne in mind, however, that the definition of an embryonic sympathetic cell which is here implied, namely, a ganglion cell which migrates out from a "stationary" cerebro-spinal ganglion into a "vagrant" ganglion (Gaskell), may be found by later researches to be inadequate. If later researches prove Harrison (:**01**) to be right in his supposition that sympathetic ganglia receive contributions of migrant motor cells from the neural tube *via* the ventral roots of spinal nerves, then the two sources of the cells in the ciliary ganglion become identical with the two sources of sympathetic cells. But the participation of medullary elements in the formation of sympathetic ganglia has never been actually observed. Investigators such as Onodi (**'86**), His, Jun., und Romberg (**'90**), and His, Jun. (**'91**), who have made special studies of the development of the sympathetic system, agree in deriving the cells entirely from spinal ganglia. Their conclusions have been generally accepted.

The ciliary ganglion of the fowl is, then, to be considered as composed of cells which fall into two categories, one being, as far as the evidence goes, in all essential respects typically sympathetic, the other belonging to neither the sympathetic nor cerebro-spinal systems. This conception of the double nature of the ciliary ganglion differs from that of Krause ('81) who, on anatomical grounds, regards the ganglion in mammals as mainly sympathetic, but also in part cerebro-spinal. He looks upon the ganglion in vertebrates lower than mammals as a homologue of a spinal ganglion. But in the light of the foregoing observations on its development in the chick, the direct genetic connection of a portion of the ciliary ganglion with the neural crest in vertebrates appears open to question. No embryologist who has distinguished between the ciliary and the mesocephalic ganglia has ascribed to any of the cells of the former a cerebro-spinal origin.

In birds, as we have seen, only a small proportion of the ciliary cells enter the ganglion from the ophthalmic branch of the trigeminal nerve. But if Hoffmann ('85) has described correctly the development of the ciliary ganglion in Lacerta, it is evident that in reptiles, at least, the greater part of the cells are derived by migration from the Gasserian ganglion. In view of this fact the large number of ganglion cells which, in chick embryos, migrate out along the ophthalmic branch of the fifth nerve, but do not take part in the building of the ciliary ganglion, may possibly possess a phylogenetic significance; for it is difficult to account for the migration of these short-lived cells into the ophthalmic branch, except upon the supposition that the cells were of functional importance earlier in the history of the race. The majority now fail to reach the ciliary ganglion, and soon disappear. It seems possible that a change in the relative numbers of ciliary cells from the two sources, the Gasserian ganglion and the neural tube, may have been in some way connected with the striking development in birds of the intrinsic muscles of the eye, to which the ciliary nerves are distributed. It is characteristic of the group that these muscles are striated. The radial dilator muscle of the iris is remarkably well developed. The latter organ appears to be under voluntary control (Coues, :03).

Rubashkin (:03) has recently shown that in the chick certain cells derived from the Gasserian ganglion form, at the extremity of a ramus of the ophthalmic branch of the fifth nerve, a "ganglion olfactorius nervi trigemini." According to his account, these cells do not leave the Gasserian ganglion before the seventh day of incubation. They are consequently not connected with the cells which, much earlier, migrate out along the ophthalmic branch during the development of the fundament of the ciliary ganglion. Many of these, as has been shown, are grouped together in one or more transitory ganglia, which are observable at the ninety-third and at the one-hundredth hour. By the end of the fifth day, the transitory ganglia and the majority of the cells scattered along the nerve have disappeared.

Homologies of the Oculomotor and Abducent Nerves. A consideration of the homologies of the third and sixth nerves does not lie within the scope of this paper. Nevertheless, I have thought it well to reproduce here from Fürbringer (:02, p. 124) a concise summary of the various interpretations given these nerves and their musculature. I have slightly modified the arrangement.

I. Oculomotor Nerve.
  1. Ventral-motor nerve (somatic musculature).
    a. Based on ontogeny: van Wijhe ('82), Beard ('85), Hoffmann ('85, '94, '96, '97, '99, :00), His ('88), Martin ('90, motor [sensory ?] root in addition), Dohrn ('90, represents in Torpedo a multiplum equivalent to from three to four, if not more, spinal nerves, '91), Zimmermann ('91), Kölliker ('96), Neal, ('96, '98).
    b. Based on anatomy in adult: Bell ('30), Stannius ('49), Huxley ('74–75), Schneider ('79), Gaskell ('86, '89), Strong ('90) Fürbringer ('97), Wiedersheim ('98), Gaupp ('97–99).
  2. Ventral-motor nerve (visceral musculature).
    a. Based on ontogeny: von Kupffer ('94 ?, '95).
    b. Based on histology of eye muscles: Stannius ('51), Langerhans ('73).
  3. Lateral-motor nerve (visceral musculature).
    a. Based on ontogeny: Balfour ('78), Marshall ('81, '82), Dohrn ('85, '87), Houssay ('90), Hatschek ('92, probably descended from the visceral constrictions), Sewertzoff ('98–99, not entirely decided).
  4. Arising as a dorso-sensory or mixed (dorso-sensory and motor) nerve, with secondary reduction of the sensory component.
    a. Based on ontogeny: Marshall ('82), possibly Rabl ('89), Martin ('90), Platt ('91), Mitrophanow ('92, '93), Sedgwick ('94), perhaps Sewertzoff ('98–99).
    b. Based on comparative anatomy: Schwalbe ('79, '81), Gaskell ('89), [Haller ('98)].

II. Abducent Nerve.
  1. Ventral-motor nerve (somatic muscle).
    a. Based on ontogeny: van Wijhe ('82), Beard ('85), His ('88), Dohrn ('88, '90, p. 344: represents in Torpedo a multiplum equivalent to three or four motor spinal nerves), Martin ('90), Oppel ('90), Zimmermann ('91), Platt ('91), Hatschek ('92,

pro-otic myomere), Hoffmann (**'94**, **'96**, **'97**, **'99**, **:00**), von Kupffer (**'94**, p. 58 : probably a lateral body muscle, but derivation from a velar muscle not entirely disproved; **'95**, pp. 36, 72: m. rect. ext. of Petromyzontes identical with that of Gnathostomi), Sewertzoff (**'95**, **'98–99**, formed from one somite in sharks, from at least two in Torpedo), Kölliker (**'96**), Neal (**'96**, m. rect. ext. formed from four metameres).

b. Based on anatomy in adult: same as oculomotor nerve (I. 1. b.).

2. Lateral-motor nerve (visceral muscle).

a. Based on ontogeny: Balfour (**'78**), Marshall (**'81**), Dohrn (**'85**, p. 447: m. rect. ext. formerly a gill muscle), von Kupffer (**'94**, p. 58: derivation from the velum not disproved, though probably from a lateral body muscle).

b. Based on histology of external rectus muscle: Stannius (**'51**), Langerhans (**'73**). Schneider (**'79**) maintains the contrary [ventral motor nerve].

Summary of Results.

I. OCULOMOTOR NERVE.

1. The oculomotor nerve of the chick first appears during the third day of incubation as a small bundle of peripheral processes of neuroblasts on either side of the median plane. These neuroblasts are grouped to form the oculomotor nidulus, which is situated in the ventral wall of the mid-brain near the median plane.

2. Rounded medullary cells (indifferent cells of Schaper) migrate from the neural wall into the root of the developing oculomotor nerve. During the peripheral growth of the neuraxons, these escaped medullary elements continue their migrations, and become distributed along the nerve as "accompanying" cells. In vom-Rath preparations the "accompanying" cells exhibit staining qualities which differentiate them from the neighboring cells of the mesenchyme.

3. The majority of the "accompanying" cells become elongated, and remain during development closely applied to the neuraxons. They are recognizable in later stages as the cells from which the sheaths of Schwann are derived. The sheaths of Schwann are consequently, like the other parts of the oculomotor neurons, ectodermal in origin. A small number of the "accompanying" cells retain their rounded form, and through increase in numbers by mitotic division give rise to a cluster of cells near the distal end of the oculomotor nerve. In this way the fundament of the ciliary ganglion is formed, many of the cells of the enlarged extremity of the nerve developing into ganglion cells.

4. The processes of the oculomotor neuroblasts grow out into the mesenchyme as compact neuraxons. After they have attained a considerable length they begin to break up, apparently by longitudinal splitting, into fine fibrils. The process of fibril formation seems to begin at the free extremity of the nerve and proceed toward the proximal end. As a consequence the whole nerve trunk, especially in its more distal regions, presents the appearance of a large bundle of fine fibrils, among which the fibrils belonging to individual neuraxons cannot with certainty be recognized.

5. The fundaments of the muscles to which the oculomotor nerve is distributed in the adult appear after the development of the nerve has begun. The last of these muscle fundaments to be differentiated, that of the ventral oblique muscle, is the first with which the third nerve becomes connected. The branches of the nerve to the dorsal and ventral rectus muscles are developed between the fifth and seventh days of incubation.

6. The oculomotor nerve in the adult fowl is composed of large and small medullated neuraxons. The majority of the small neuraxons form a peripheral layer along the lateral margin of the nerve, and are continued into the ciliary ganglion.

II. Ciliary Ganglion.

1. The fundament of the ciliary ganglion appears during the fourth day as a collection of actively dividing "accompanying" cells near the distal extremity of the oculomotor nerve. There is evidence that these "accompanying" cells are to be regarded as indifferent medullary cells which have migrated into the nerve from the neural tube. During the fifth day nearly all the cells become differentiated into young ganglion cells, characterized by a comparatively large amount of deeply staining, granular cytoplasm, which is accumulated, for the most part, at one side of the rounded nucleus. A few of the indifferent cells do not become ganglionic nervous elements, but assume the characters of elongated supporting cells, similar to those which develop the sheaths of Schwann along the trunk of the nerve. These cells may later participate in the formation of the nucleated capsules of the ciliary-ganglion cells.

2. While the fundament of the ciliary ganglion is undergoing development, young ganglion cells migrate out from the Gasserian ganglion along the ophthalmic branch of the trigeminal nerve. These cells are characterized by the same deeply staining, granular cytoplasm and rounded eccentric nuclei observable in the ciliary cells, but they are

easily distinguished from the latter by reason of the larger size of their nuclei and the greater abundance of their cytoplasm. A comparatively small number of the ophthalmic ganglion cells migrate into the fundament of the ciliary ganglion, passing at first through the mesenchyme, and later along the neuraxons of a communicating ramus, which grows from the ophthalmic branch of the trigeminus to the fundament of the ciliary ganglion. In their origin from a cerebro-spinal ganglion, and in their capacity for locomotion, these cells resemble those which, in the trunk region, give rise to sympathetic ganglia. Of the ganglion cells migrating along the ophthalmic branch, those which fail to reach the ciliary ganglion are in part accumulated to form one or more transitory ganglia in the distal portion of the nerve. By the end of the fifth day the transitory ganglia, and nearly all the migrant ganglion cells distributed along the nerve, have disappeared.

3. In the adult fowl the ciliary ganglion is situated directly upon the oculomotor nerve without the intervention of a radix brevis. Two regions are distinguishable in the ganglion, a smaller dorsal region and a larger ventral one. The first region presents many sympathetic characters, containing, as it does, small ganglion cells, slightly medullated neuraxons and many pericellular fibrils. It receives neuraxons of small calibre through the communicating branch from the trigeminus. The communicating branch resembles histologically a ramus communicans of the sympathetic system. From this region of the ganglion practically non-medullated neuraxons proceed to the eyeball in company with the other neuraxons constituting the oculomotor ciliary nerve. This portion of the ciliary ganglion may have arisen from the migrant ophthalmic cells which enter the fundament of the ganglion during development. The larger ventral region of the ganglion contains large cells, fine but well-medullated neuraxons, and few pericellular fibrils. From this region are doubtless derived the large bipolar ganglion cells with medullated processes which are to be obtained from the ciliary ganglion by maceration methods. The greater part of the oculomotor ciliary nerve passes out from this portion of the ganglion in the form of a large bundle of fine medullated neuraxons. It is probable that the cells of this region had their origin in the migrant cells from the embryonic neural tube.

4. The oculomotor ciliary nerve passes from the distal end of the ciliary ganglion to the intrinsic muscles of the eye. It comprises fine, well-medullated neuraxons together with a small number of neuraxons with little if any medullation. In its course through the orbit it gives

rise to a variable number of very small branches, which accompany it to the eyeball.

III. Abducent Nerve.

1. The sixth nerve arises at the beginning of the fourth day of incubation as a slender bundle of processes of neuroblasts, which emerge from the ventral face of the hind-brain. The abducent nidulus is situated in the ventral wall of the hind-brain near the median plane. The nerve exhibits a number of attenuated roots arranged in a longitudinal series.

2. Indifferent medullary cells migrate out into the roots of the abducent nerve. These distribute themselves along the nerve trunk, assume an elongated form, and become recognizable as the cells which later develop the sheaths of Schwann. None of these indifferent cells give rise to ganglion cells.

3. The fundament of the posterior rectus muscle becomes differentiated during the third day before the appearance of the abducent nerve. The embryonic abducent neuraxons, upon emerging from the neural tube, grow rapidly cephalad to connect with the muscle fundament.

4. The abducent nerve of the adult is composed of both large and small medullated neuraxons.

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1. Cells resembling the indifferent cells of the neural tube are present in the embryonic Gasserian ganglion. Certain of these cells may, by differentiation, give rise to ganglion cells. Others appear to migrate from the Gasserian ganglion into the ophthalmic branch of the trigeminal nerve, and there assume the characters of Schwann's-sheath cells. Similar cells remaining within the Gasserian ganglion possibly develop later into the nucleated capsules of the ganglion cells.

2. In the adult the communicating ramus from the ophthalmic branch of the trigeminus does not pass directly to the ciliary ganglion, as in the embryo, but to the oculomotor ciliary nerve, with which it connects about one mm. from the distal extremity of the ganglion. Certain of the neuraxons of the communicating ramus, however, turn centrally and enter the sympathetic region of the ciliary ganglion; the remaining neuraxons accompany those of the oculomotor ciliary nerve to the eyeball.

3. A trigeminal ciliary nerve is given off by the communicating ramus about midway in its course. A second trigeminal ciliary nerve is occasionally to be seen arising from the communicating ramus near the termination of the latter in the oculomotor ciliary nerve.

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EXPLANATION OF PLATES.

All figures are from preparations of chick embryos except when otherwise stated. All, with the exception of the photomicrographs and diagrams, were drawn with the aid of the camera lucida. The magnifications follow the descriptions of the figures.

ABBREVIATIONS.

cl.	Indifferent cell.
cl.′	Indifferent cell. (See explanation of Fig. 16.)
cl.″	Indifferent cell. (See explanation of Fig. 16.)
cl. comit.	"Accompanying" cell.
cl. comit.′	"Accompanying" cell.
cl. comit.″	"Accompanying" cell.
cl. gn.	Ganglion cell.
cl. gn. cil.	Ganglion cell of ciliary ganglion.
cl. med. mig.	Migrant medullary cell.
ec'drm.	Ectoderm.
gn. cil.	Ciliary ganglion. (See explanation of Fig. 17.)
gn. cl.″	Erroneously engraved for *gn. cil.* (Fig. 2).
gn. Gas.	Gasserian ganglion.
gn. mx-md. Gas.	Maxillo-mandibular portion of Gasserian ganglion.
gn. t'i.	Transitory ganglion.
ifb.	Infundibulum.
l.	Lateral.
m.	Median.
mb. lim. ex.	External limiting membrane.
ms'e.	Mid-brain.
ms'ench.	Mesenchyme.
mt'e.	Hind-brain.
mu. ob. d.	Dorsal oblique muscle.
mu. ob. v.	Ventral oblique muscle.
mu. rt. a.	Anterior rectus muscle.
mu. rt. d.	Dorsal rectus muscle.
mu. rt. p.	Posterior rectus muscle.
mu. rt. v.	Ventral rectus muscle.
mu. rt. v. + a.	Ventral and anterior rectus muscles.
n. abd.	Abducent nerve.
n. cil. oc'mot.	Oculomotor ciliary nerve.
n. cil. trig.	Trigeminal ciliary nerve.
n. oc'mot.	Oculomotor nerve.

n. opt.	Optic nerve.
n. trch.	Trochlear nerve.
n'ax.	Neuraxon.
n'ax med.	Medullated neuraxon.
n. b'l.	Neuroblast.
n. b'l.'	Neuroblast.
n. b'l.''	Neuroblast.
nd. Rnv.	Node of Ranvier.
nidl. oc'mot.	Oculomotor nidulus.
nl.	Nucleus.
par. ms'e. v.	Ventral wall of mid-brain.
par. mt'e. v.	Ventral wall of hind-brain.
par. rtn. ex.	Outer wall of retina.
par. rtn. i.	Inner wall of retina.
pdl. opt.	Optic peduncle.
phx.	Pharynx.
pi'n.	Perineurium.
prose.	Fore-brain.
rm. comn.	Communicating ramus.
rm. f.	Frontal branch.
rm. mu. qd. + pyr.	Branch to quadratus and pyramidalis muscles.
rm. mu. rt. a.	Branch to anterior rectus muscle.
rm. mu. rt. d.	Branch to dorsal rectus muscle.
rm. mu. rt. p.	Branch to posterior rectus muscle.
rm. mu. rt. v.	Branch to ventral rectus muscle.
rm. na.	Nasal branch.
rm. n. cil. oc'mot.	Branch from oculomotor ciliary nerve.
rm. opth. trig.	Ophthalmic branch of trigeminal nerve.
rm. v.	Ventral ramus.
trt. fbr. v.	Ventral fibre tract.
vel. marg.	Marginal veil.
vn. crd. a.	Anterior cardinal vein.

PLATE 1.

FIG. 1. Eye-muscle nerves of adult fowl viewed from left side. × 4.

FIG. 2. Portion of Figure 1 enlarged. × 16.

NOTE. — The dotted line from *rm. comn.* is carried a little too far.

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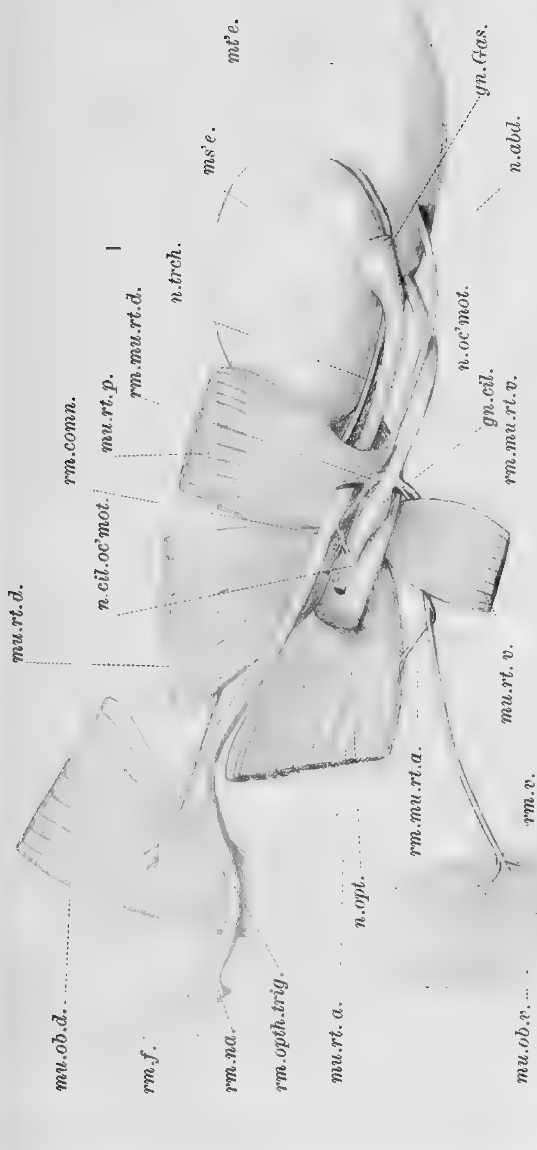

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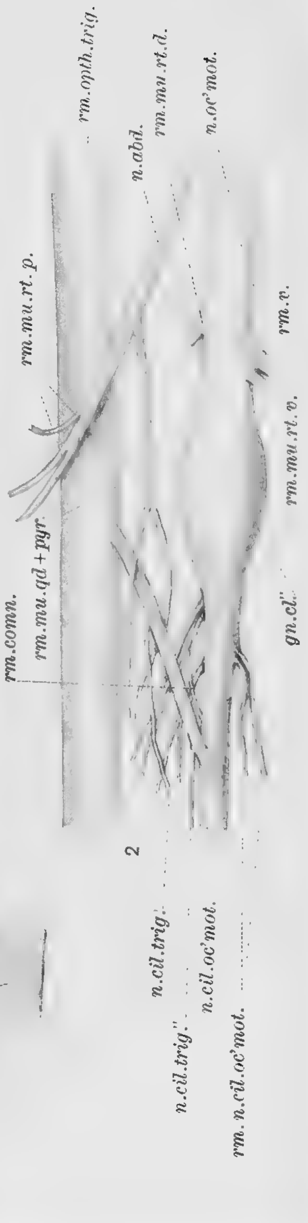

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PLATE 2.

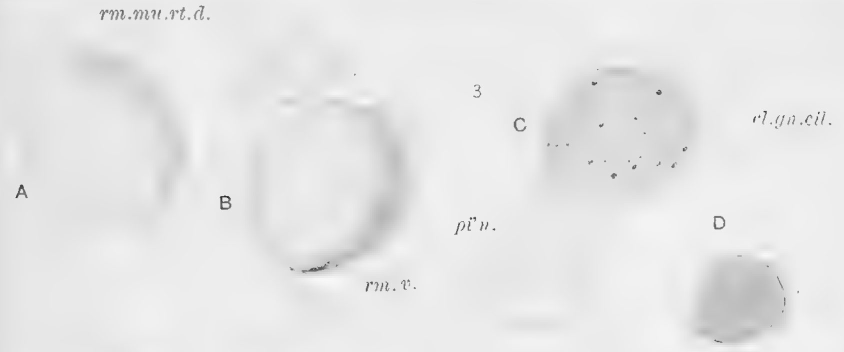
FIG. 3. *A*, *B*, *C*, Transverse sections of oculomotor nerve of fowl at different points along its course, nerve tracts and cells diagrammatic (*A*, most proximal; *C*, most distal). *D*, Transverse section of oculomotor ciliary nerve. Shaded areas indicate regions of small neuraxons; unshaded areas, regions in which large neuraxons predominate. × 33.

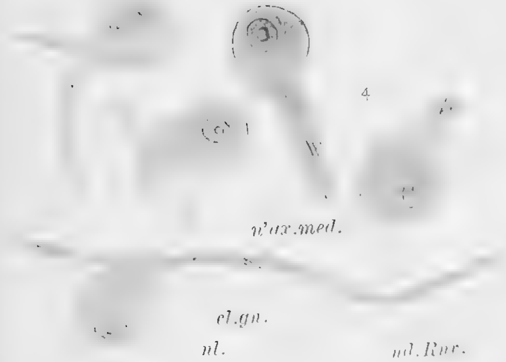
FIG. 4. Isolated ganglion cells from ciliary ganglion of fowl. × 233.

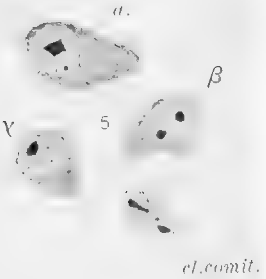
FIG. 5. Cells from an embryo in Stage IV (101 hrs. incubation). α, β, Ganglion cells of transitory ganglion of ophthalmic branch of trigeminal nerve. γ, Ganglion cell of mesocephalic ganglion. *cl. comit.*, "Accompanying" cell of ophthalmic branch of trigeminal nerve. Fixed in Zenker's fluid and stained with iron hæmatoxylin. × 933.

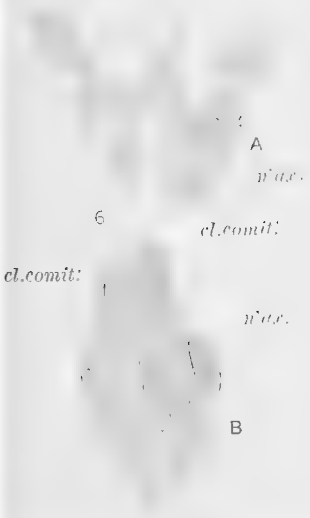
FIG. 6. From an embryo *Amblystoma*. *A*, Cells from Gasserian ganglion. *B*, Cells from proximal end of ophthalmic branch of trigeminal nerve. Fixed and stained in vom Rath's fluid. × 600.

FIG. 7. Portion of a section from an embryo in Stage V (118 hrs. incubation), showing neuraxons and fibrils from different points along course of the oculomotor nerve. *A*, proximal; *B*, intermediate; *C*, distal. Fixed and stained in vom Rath's fluid. × 933.









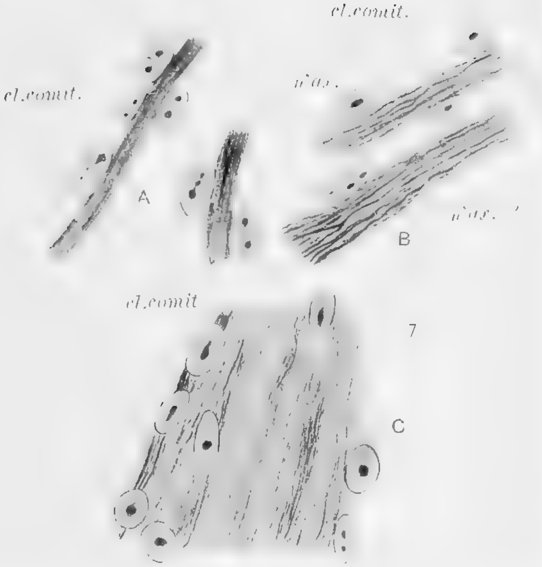


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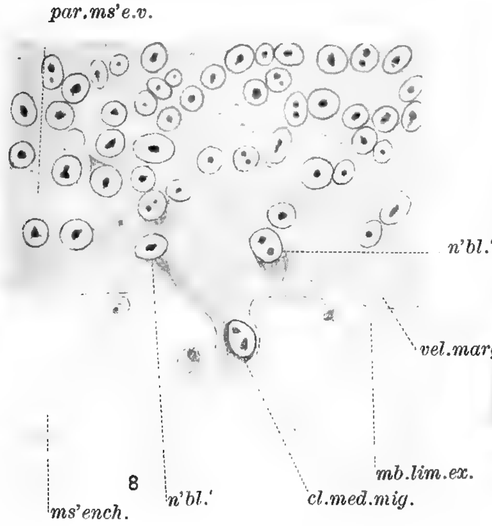
PLATE 3.

FIG. 8. Parasagittal section through ventral wall of mid-brain of an embryo in Stage I (72½ hrs. incubation), viewed from the left side. Early neuroblasts of oculomotor nidulus. Fixed and stained in vom Rath's fluid. × 1300.

FIG. 9. Section transverse to longitudinal axis of mid-brain of an embryo in Stage II (70 hrs. incubation), showing root of oculomotor nerve. Fixed in Zenker's fluid, and stained with Brazilin. × 800.

FIG. 10. From an embryo in Stage V (119½ hrs. incubation). α, β, γ, Ganglion cells in ophthalmic branch of trigeminal nerve; α, near Gasserian ganglion; β, opposite ciliary ganglion in position marked β in Figure 25; γ, more distal, in position marked γ in Figure 25. δ, Ganglion cells in ciliary ganglion. Fixed in Zenker's fluid and stained with iron hæmatoxylin. × 1400.



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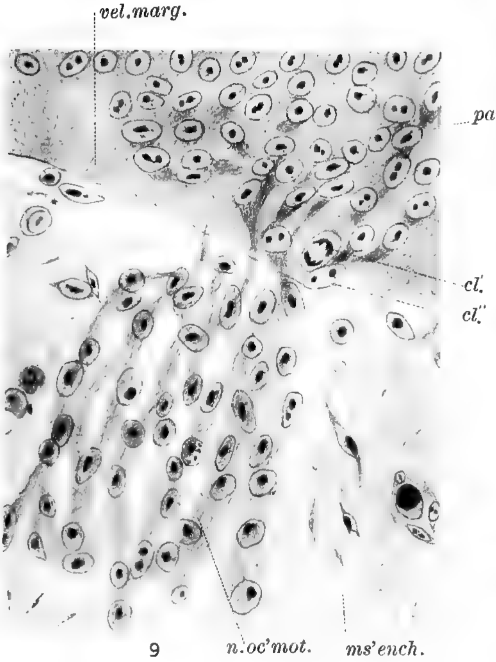

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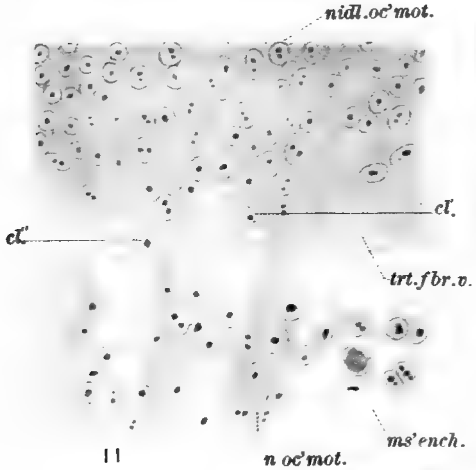
PLATE 4.

FIG. 11. Section transverse to longitudinal axis of mid-brain of an embryo in Stage III (88 hrs. incubation), showing root of oculomotor nerve. Fixed in corrosive-acetic mixture and stained with iron hæmatoxylin. × 600.

FIG. 12. Reconstruction from seven consecutive parasagittal sections through an embryo in Stage III (93 hrs. incubation), viewed from left side, and showing longitudinal section through distal portion of ophthalmic branch of trigeminal nerve. Fixed and stained in vom Rath's fluid. × 66.

FIG. 13. Diagram of relations between fundament of ciliary ganglion and ophthalmic branch of trigeminal nerve. Reconstructed from 28 consecutive sections transverse to longitudinal axis of mid-brain of an embryo in Stage IV (100 hrs. incubation). In the Figure dorsal is up, median to the left. Ganglion cells α, β, γ, δ, ϵ, correspond to ganglion cells with the same designations in Figure 16 (Pl. **5**). × 200.

FIG. 14. From an embryo *pig*. *A*, Proximal end of neuraxon of oculomotor nerve. *B*, Longitudinal section through oculomotor nerve midway in its course. Fixed in corrosive-acetic mixture and stained with Brazilin. × 733.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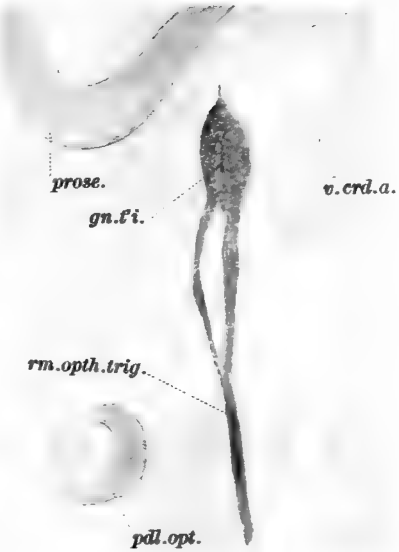
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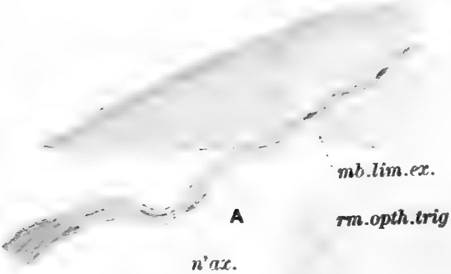
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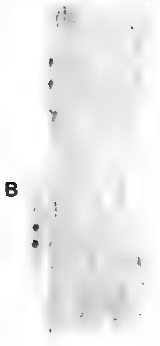
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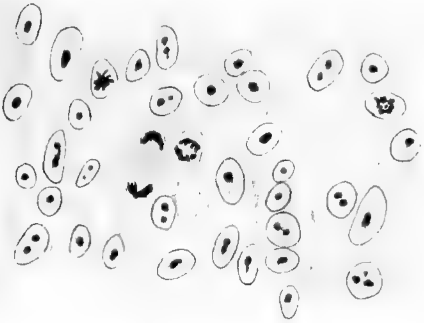
PLATE 5.

FIG. 15. From an embryo in Stage III (88 hrs. incubation), showing cells of distal enlargement of oculomotor nerve. Fixed in corrosive-acetic mixture and stained with iron hæmatoxylin. × 900.

FIG. 16. From an embryo in Stage IV (100 hrs. incubation). *A*, Ganglion cells in ophthalmic branch of trigeminal nerve; *B*, *C*, cells in mesenchyme between ophthalmic branch of trigeminal nerve and fundament of ciliary ganglion (γ, δ, ganglion cells); *D*, ophthalmic-ganglion cells within ciliary ganglion; *E*, ganglion cells of ciliary ganglion (*cl.′*, *cl.″*, "accompanying" cells in ciliary ganglion, which should have been lettered *cl. comit.*). Fixed in corrosive-acetic mixture and stained with iron hæmatoxylin. × 1400.

FIG. 17. Longitudinal section through left oculomotor nerve proximal to ciliary ganglion. From an embryo in Stage IV (100 hrs. incubation). Fixed in corrosive-acetic mixture and stained with iron hæmatoxylin. × 900. NOTE. — The lettering *gn. cil.* should have been *cl. gn.*



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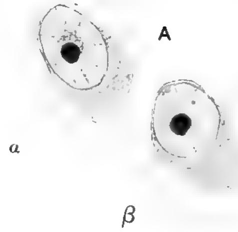

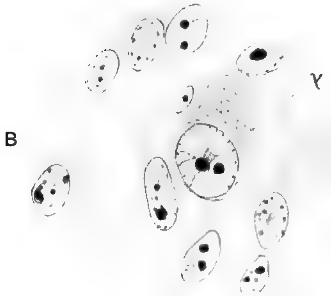

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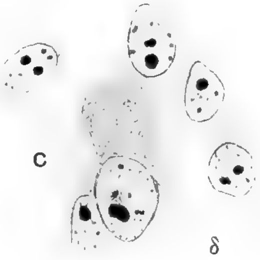

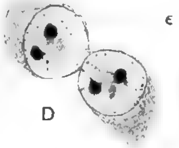

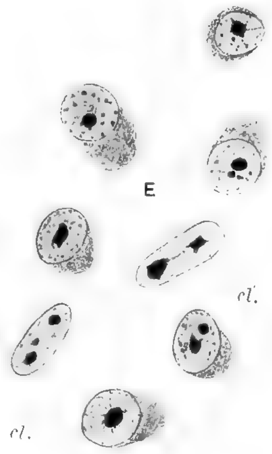

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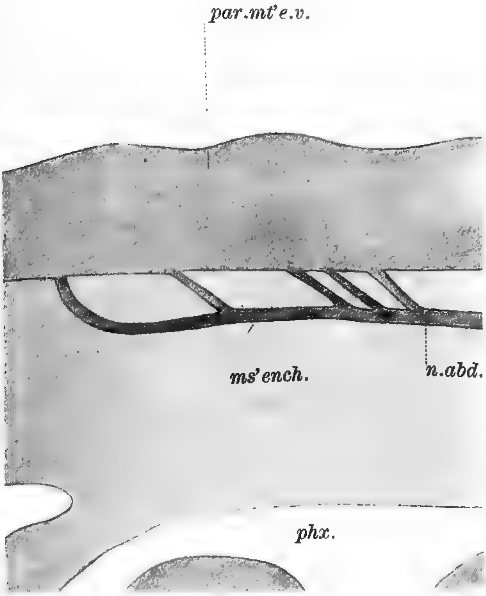
PLATE 6.

Fig. 18. Reconstruction from five consecutive parasagittal sections through ventral wall of hind-brain of an embryo in Stage V (118½ hrs. incubation), giving a diagrammatic view of proximal end of left abducent nerve, viewed from right side. × 150.

Fig. 19. Enlarged view of a root of the abducent nerve shown in Figure 18. Fixed in picro-sulphuric mixture and stained with Delafield's hæmatoxylin. × 800.

Fig. 20. Parasagittal section through an embryo in Stage III (93 hrs. incubation), viewed from left side, showing root of oculomotor nerve. Fixed and stained in vom Rath's fluid. × 160.



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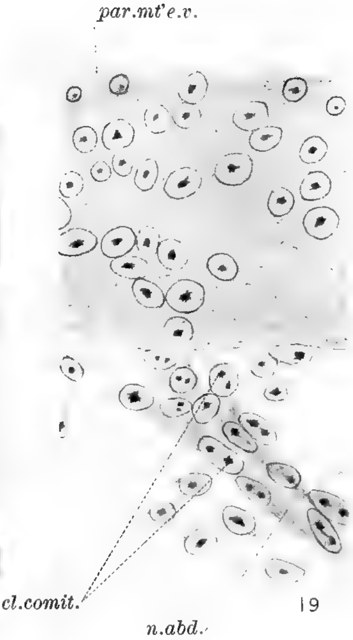

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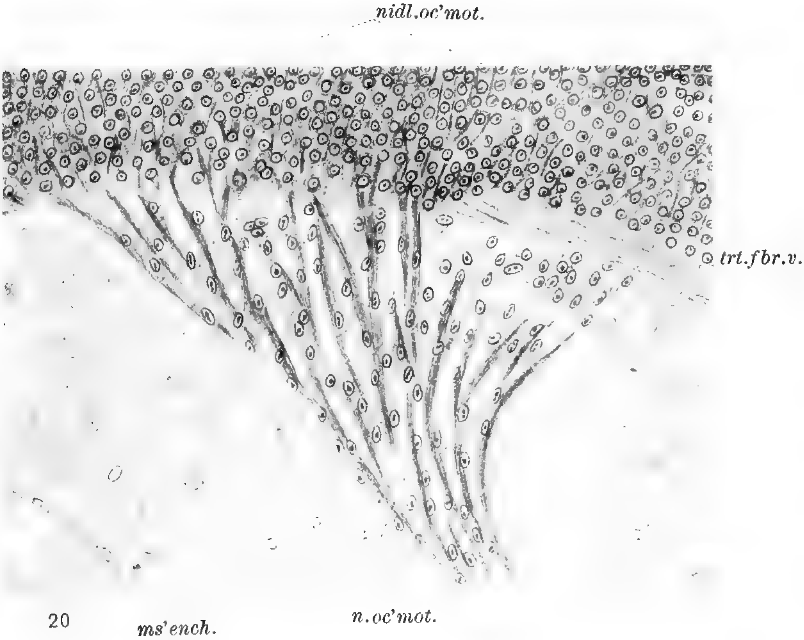

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PLATE 7.

All the Figures of this Plate are from photomicrographs.

FIG. 21. Transverse section of oculomotor nerve of fowl corresponding to *A*, Figure 3 (Pl. **2**). × 86.

FIG. 22. Transverse section of branch of oculomotor nerve of fowl supplying dorsal rectus muscle. × 86.

FIG. 23. Section frontal to hind-brain of an embryo in Stage II (70 hrs. incubation), showing connection of maxillo-mandibular portion of Gasserian ganglion with ectoderm, and fundament of posterior rectus muscle. Stained in hæmalum. × 266.

FIG. 24. Section transverse to longitudinal axis of mid-brain of an embryo in Stage III (88 hrs. incubation), showing longitudinal section through entire length of oculomotor nerve. Fixed in corrosive-acetic mixture and stained with iron hæmatoxylin. × 44.

FIG. 25. Parasagittal section of an embryo in Stage V (119½ hrs. incubation), viewed from right side, and showing longitudinal section through communicating ramus between ophthalmic branch of trigeminal nerve and ciliary ganglion. For significance of β and γ, see explanation of Figure 10 (Pl. **3**). Fixed in Zenker's fluid and stained with iron hæmatoxylin. × 173.

FIG. 26. Parasagittal section through an embryo in Stage V (119½ hrs. incubation), viewed from right side, and showing oculomotor nerve, ciliary ganglion, abducent nerve, and fundaments of eye muscles. Fixed in Zenker's fluid and stained with iron hæmatoxylin. × 40.

NOTE. — By an oversight the *plus* sign (+) has been omitted from the Plate in the abbreviation *mu. rt. v.* + *a.*

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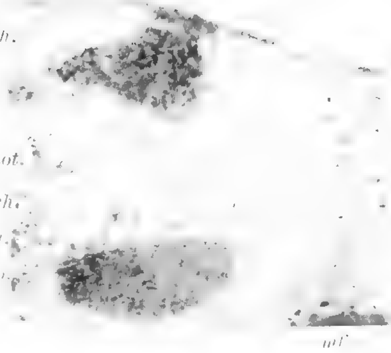

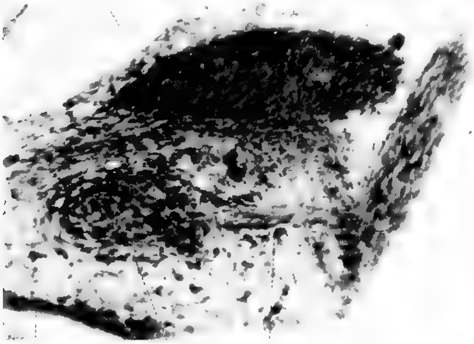

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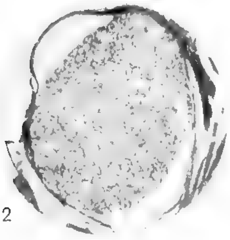

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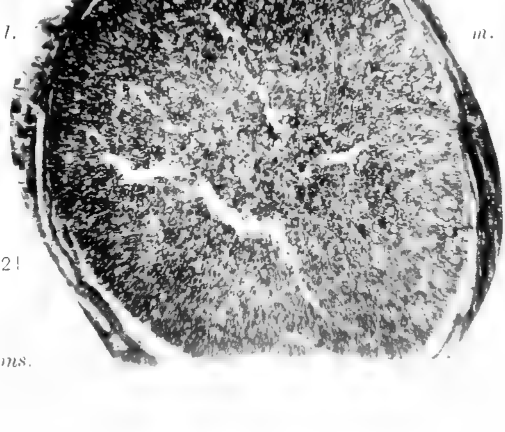

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The following Publications of the Museum of Comparative Zoölogy are in preparation: —

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H. AUGENER. The Annelids of the "Blake."
C. HARTLAUB. The Comatulae of the "Blake," with 15 Plates.
H. LUDWIG. The Genus Pentacrinus.
A. MILNE EDWARDS and E. L. BOUVIER. The Crustacea of the "Blake."
A. E. VERRILL. The Alcyonaria of the "Blake."

Reports on the Scientific Results of the Expedition to the Tropical Pacific, in charge of ALEXANDER AGASSIZ, on the U. S. Fish Commission Steamer "Albatross," from August, 1899, to March, 1900, Commander Jefferson F. Moser, U. S. N., Commanding.

LOUIS CABOT. Immature State of the Odonata, Part IV.
E. L. MARK. Studies on Lepidosteus, continued.
" On Arachnactis.
R. T. HILL. On the Geology of the Windward Islands.
W. McM. WOODWORTH. On the Bololo or Palolo of Fiji and Samoa.
AGASSIZ and WHITMAN. Pelagic Fishes. Part II., with 14 Plates.

Reports on the Results of the Expedition of 1891 of the U. S. Fish Commission Steamer "Albatross," Lieutenant Commander Z. L. TANNER, U. S. N., Commanding, in charge of ALEXANDER AGASSIZ, as follows: —

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" The Panamic Deep-Sea Fauna.
H. B BIGELOW. The Siphonophores.
K. BRANDT. The Sagittae.
" The Thalassicolae.
W. R. COE. The Nemerteans.
W. H. DALL. The Mollusks.
REINHARD DOHRN. The Eyes of Deep-Sea Crustacea.
H. J. HANSEN. The Cirripeds.
HAROLD HEATH. Solenogaster.
W. A. HERDMAN. The Ascidians.
S. J. HICKSON. The Antipathids.
J. P. McMURRICH. The Actinarians.
E. L. MARK. Branchiocerianthus.
JOHN MURRAY. The Bottom Specimens.
P. SCHIEMENZ. The Pteropods and Heteropods.
THEO. STUDER. The Alcyonarians.
M. P. A. TRAUSTEDT. The Salpidae and Doliolidae.
H. B. WARD. The Sipunculids.
W. McM. WOODWORTH. The Annelids.

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Vols. XLIII., XLVI., XLVIII., XLIX., and L. of the BULLETIN, and Vols. XXV., XXVI., XXVII., XXX., XXXIII., XXXIV., and XXXV. of the MEMOIRS, are now in course of publication.

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