THE STRUCTURE OF THE SPINAL CORD OF THE OSTRICH.

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WITH 6 TEXT FIGURES.

It is related by Herodian how the Kaiser Commodus beheaded ostriches and then watched them with delight and wonder as they continued running about the amphitheater, apparently to no great extent inconvenienced by the loss of their heads. That which served Kaiser Commodus as barbarous amusement frames itself for us into an interesting anatomical problem, and calls to mind a similar phenomenon so often observed among the domestic fowls. What is, then, this arrangement of the nervous elements of the spinal cord of a bird that enables it to functionate so completely after separation from the higher centers?

Our present knowledge and methods do not suffice for a complete explanation of this problem, but we can lead the way toward a future solution if we study out what can be learned at present concerning the histology of the bird spinal cord. In this sense, under the suggestion and guidance of Professor Edinger, I have undertaken the investigation of the structure of the spinal cord of the ostrich (*Struthio camelus*). This, beyond all other birds, distinguishes itself by the great length of its spinal cord, and, in comparison with the brain, its great size.

In the literature, frequent reference is made to the spinal cord of birds. As early as 1868 *Stieda** presents what could be seen in unstained preparations. He gives a review of the previous literature reaching back to *Steno*, 1667, and *Perrault*, 1699. All of the older investigators of the spinal cord, such as *Stilling* and *Clarke*, have also studied more or less that of the bird, but it is the above mentioned work of *Stieda* that gave us first a clear and complete description. Of the more recent anatomists, mention is to be made of the works of *Gadow*¹ and *Kölliker*.² A number of investigations have been made which were limi-

* *Stieda*, Studien über das centrale Nervensystem der Vögel und Säugethiere.

¹ *Gadow*, Bronn's Klassen und Ordnungen des Thierreiches, Bd. 6, p. 406.

² *Kölliker*, Gewebelehre, 1896.

ted to various parts of the cord, as, for example, the study of *Duval*³ concerning the Sinus rhomboidalis, and an experimental work of *Friedländer*⁴ on the fibre tracts. To these may be added also the works of *Singer*, *Münzer*, and others who devoted themselves more particularly to the brain. It is, further, not to be forgotten that the studies of *Retzius*, *Ramon-y-Cajal*, *van Gehuchten*, and *v. Lenhossek* concerning the nerve-cells and fibres of the spinal cord in Golgi preparations were carried out largely on the chick. No attention, however, seems to have been directed toward the spinal cord of the ostrich. A cross-section, apparently of the thoracic region, is pictured by *Edinger*,⁵ but is not otherwise described.

The material on which this study is based consisted of three ostrich spinal cords taken from the neurological collection of the Anatomie. Two were practically intact; the third had been cut into segments. All three had been hardened in formol. After the macroscopic examination was completed, series of transverse sections were made in all segments. Unbroken sagittal and fronto-longitudinal series were prepared through three segments of the lumbar enlargement, and a fronto-longitudinal series of one segment in the cervical region. Sections were also prepared of a decalcified vertebra showing the cord *in situ* with its membranes, the nerve roots, and spinal ganglia. Where other than the usual stains were used they are specified in the text.

THE MENINGES.

The cord is supported in the vertebral canal by a connective tissue sheath which, like that in mammals, may be described as consisting of three separate membranes or envelopes. In order, from within outwards, they are the pia, arachnoidea, and dura. These structures are represented in Fig. 1.

Of the three envelopes the *dura* is by far the strongest. It is this that forms the tough fibrous sheath surrounding the cord, which one sees on the removal of the latter from the vertebral canal. It consists of a membrane .011 to .012 mm. thick, made of thickly-lying coarse fibres, and contains no blood-vessels. Outside the *dura* is a connective tissue layer which lines the vertebral canal, and forms the periosteum of the vertebræ. This, having the same histological character, may be described

³ Duval, Recherchés sur le Sinus Rhomboidal des Oiseaux, Journ. de l'Anat. et de la Phys., 1877.

⁴ Friedländer, Untersuch. über das Rückenmark und das Kleinhirn der Vögel, Neurolog. Centrabl., 1898.

⁵ Edinger, Nervöse Centralorgane, 1900, p. 76.

as belonging to the dura, and as forming its outer layer. The cleft between the two, the *epidural cavity*, is bridged over by loose strands of tissue supporting a plexus of blood-vessels.

More or less adherent to the inner surface of the dura is the *arachnoidea*. Whether or not this, in the fresh state, is completely adherent to and possibly a part of the dura, could not be decided, as all the material used in this study had been through a prolonged hardening in formol. In the preparations at irregular intervals, they were still adherent, but in the greater part there was a separation of the two membranes, having more the appearance of an artificial tearing apart, or shrinkage forma-

FIG. 1. Cross section through the 4th cervical vertebra of the ostrich, showing the spinal cord and its membranes. One side is drawn at a point somewhat higher than the other. Enlargement $\times 6$.

tion, than a natural cleft. In the space thus formed, there was no trace of serum, blood-cells, or other tissue. In cross-sections the arachnoidea shows itself as a delicate, thickly nucleated membrane, connected from its inner surface with the pia by a network of fine strands which form a meshwork of lymph spaces for the cerebro-spinal fluid, *subarachnoideal cavity*.

The rootlets forming the ventral and dorsal nerve roots take their course through this loose tissue caudad or cephalad to the nearest intervertebral foramen, where they pass outward, piercing the dural sheath. In their course they carry along with them a connective tissue contri-

bution from the pia and dura, which, through the intervertebral foramina, is directly continuous with the peripheral nerve-sheaths; this tissue furnishes the capsule and framework for the spinal ganglia, which are found just external to the foramina and attached to the fibres of the dorsal roots.

The *pia*, in contrast to the two more external membranes, forms, as we may say, an integral part of the structure of the cord, and serves to some extent as a framework, inasmuch as it is closely adherent to the peripheral layer of neuroglia and follows the outline of the cord entering all clefts and depressions. In the anterior median fissure it sinks to the bottom as a thick, strong lamella, *septum ventrale*, supporting, just ventral to the anterior commissure, the *arteria medullaris ventralis*.

The pia throughout is richly supplied with blood-vessels. Branches from these supply the cord, penetrating from the periphery inward and from the *arteria med. ventr.* outward. The vessels carry with them a connective tissue adventitia derived from the pia. In no case, however, were processes of pia seen entering the substance of the cord except as accompanying blood-vessels. This is easily demonstrated in specimens over-stained with iron hæmatoxylin and differentiated with picro-fuchsin. In such preparations the vessels, together with their connective tissue support, are stained brilliant red in contrast to the yellow-brown neuroglia septa which might otherwise be mistaken for pia.

At three places in its circumference, the pia receives an accession of thick dura like connective tissue fibres, producing ligamentous formations which extend as three longitudinal bands, lens-shaped in cross-section. Two of these are situated laterally, *ligamenta longitudinalia lateralia*, and one is situated at the attachment of the *septum ventrale*, *ligamentum longitudinale ventrale*. The former corresponds to what Berger^{*} has described as the *ligamentum dentatum* in reptiles. Between the 27th and 38th segments in the region of the lumbo-sacral enlargement, these bands reach a special development; they become much stronger and are modified in form. From the *ligamentum long. ventr.* pointed, tooth-like processes extend laterally to join the *ligamenta long. lat.* These processes fit closely in the intersegmental grooves, the sulci transversi, of the ventral surface of the cord. This is represented in Fig. 2, a.

A resemblance between this structure and the dural tissue is at once noticed, but it is identified as modified pia from the fact that the arach-

^{*} Berger, Ueber ein eigenthümliches Rückenmarksband en Reptilien und Amphibien, Sitzb. Wiener Akad. Wiss., Bd. lxxvii, 3 Abth.

noid lies external to it, and separates it from the dura proper. In the intervening spaces the pia becomes thinner and web-like; here the *eminentiæ ventrales* bulge forward and along their lateral border give off the ventral nerve roots which pierce the pia just ventral to the liga-

FIG. 2. Ventral and dorsal surfaces of the lumbo-sacral enlargement of the ostrich spinal cord, enlarged to $1\frac{1}{2}$ natural size. The pial sheath has in part been stripped off in order to show the *eminentiæ ventrales*. X indicates the situation of one of the *nuclei marginales majores*.

menta long. lat. Strong fibrous processes, *ligamenta denticulata*, extend also lateral from the *ligamenta long. lat.* to the dural sheath and thus render further support to this region of the cord. See Fig. 5.

Caudal to the lumbo-sacral enlargement, the pia returns to the more simple sheath-like form as seen in the thoracic and cervical regions.

A work on the comparative and embryological anatomy of the spinal cord meninges has recently been published by Sterzi.⁷

In the mammalian embryo (*Ovis aries*), 15 mm. long, the author describes a mesenchyma perimeningeale which first produces a definite spinal cord membrane in the embryo of 20 mm. This he calls *meninx primitiva*. In the 80 mm. long embryo this membrane is differentiated into an outer layer or *dura mater*, and an inner layer or *meninx secundaria*. The two are separated by an intradural space. The dural layer is separated externally by the epidural space from an *endorhachide* which Sterzi finds always distinct from the *dura*. In the 157 mm. embryo the *meninx secundaria* is further differentiated into an outer or arachnoideal layer and an inner or pial layer. In his comparative series the author finds the *Petromyzon* as representing the 20 mm. embryonal stage. The *Rana esculenta* and *Lacerta viridis* represent the 80 mm. stage. The development shown by the 157 mm. embryo with a differentiated arachnoid he finds only in the mammals. Our findings in the ostrich do not correspond with this. In Sterzi's series the birds are represented by *Gallus domestica* in which he describes a *meninx secundaria* not yet differentiated into pia and arachnoid. In the ostrich we find, as is above described, an arachnoidal layer which presents all the distinguishing features of that of the mammalian cord.

GENERAL MACROSCOPIC DESCRIPTION.

The abrupt change from the slender cervical spinal cord of the ostrich to the thick medulla oblongata gives a rather definite level at which the cephalic end of the cord may be said to be located. From this point extending caudally it stretches throughout the entire length of the spinal canal, its slender tapering end extending to the last coccygeal vertebra. It measures 81 cm. long in a small ostrich, the middle of whose back stands about 60 cm. above ground, and whose head in the ordinary upright position is 45 cm. higher, or 105 cm. above ground.⁸

From each side of the cord throughout its length is given off a series of fine rootlets which unite, within the dural sheath in segmental bundles, to form the dorsal and ventral nerve roots. These, together, pierce the

⁷ Sterzi, *Anatomia comparata ed all'ontogenesi delle Meningi midollari: Atti del Reale Istituto Veneto di Scienze, Lettere ed Arti, Tomo LX, 1900-1901.*

⁸ All the measurements hereafter stated are taken from this same specimen.

FIG. 3. Topography of the spinal cord of the ostrich. The transverse sections are all made on the same scale of enlargement and their proper levels are indicated on the drawing.

dural sheath, leave the spinal canal, and form the spinal nerves, as is described under the heading *Meninges*. Owing to the fact that the roots have a short intravertebral course, leaving the canal directly, a bundle of them forming a *cauda equina* is not here present, and the nerves thus correspond in position to the segments of the cord and to the vertebræ. There are in our specimens 51 pairs of nerves. We may classify the nerves and segments after the morphology of the vertebræ as follows:

Region.	No. of Nerve Pairs.	Segments.
Cervical	15	1st to 15th.
Thoracic	8	16th to 23rd.
Lumbo-sacral	19	24th to 42nd.
Coccygeal	9	43rd to 51st.

The topography of the cord is represented in Fig. 3. It will be observed that corresponding to the wings and legs the cord is in two places increased in size, the *brachial* and *lumbo-sacral enlargements*. The former is so barely visible that one notices at first only the enormously developed lumbo-sacral enlargement. A more careful observation however discloses a slight increase in size in the region lying between the 16th and 19th pairs of nerves. The difference in size is much more apparent in cross-sections.

Fürbringer⁹ describes the plexus brachialis of the ostrich as made up of the spinal nerves arising from the 17th to 21st segments, and this corresponds to our cervical enlargement. It is this region, therefore, that we must think of as the sensory and motor center for the wing musculature.

The remainder of the cervical and thoracic portion of the cord is nearly uniform in size, and on section shows a rounded circumference. A *fissura ventralis longitudinalis* is to be seen, but dorsally in this region no fissure is present. The segments in a way are marked off at the attachment of the spinal nerves by a slight dorso-ventral compression and a corresponding increase in size laterally.

In the lumbo-sacral region an entirely different appearance is presented. It is in this region of the cord that the crural and sacral plexuses are attached which supply nerve-fibres to the leg. The system of reflexes which is necessary for the control of the massive musculature of this member demands a large accumulation of nerve-cells and connecting nerve-fibres, and this accumulation forms the lumbo-sacral enlargement, the so-called "Lumbar Brain." As is stated above, the lumbo-sacral

⁹ Fürbringer, *Untersuchungen zur Morphologie und Systematik der Vögel*. Theil I., Amsterdam, 1888.

region of the cord extends from the 24th to the 42nd segment. About one-half of this space, from the 26th to 37th, is occupied by the lumbo-sacral enlargement.

A feature which contributes largely to the peculiar appearance of this part of the cord is the change occurring in the posterior longitudinal sulcus. What was a barely-perceptible furrow in the cervical and thoracic cord becomes, at the beginning of the lumbo-sacral region, more distinct, and, where the 31st pair of nerves are given off, it rather abruptly widens out into a broad boat-shaped groove, the *sinus rhomboideus sacralis*. This reaches ventrally to the commissura anterior, and spreads apart the posterior funiculi from the 31st to 36th segment, at which point the sides again come together and are continued as the posterior longitudinal furrow. This sinus is filled with a delicate gelatinous tissue, the structure of which will be discussed later.

A drawing of the dorsal surface is reproduced in Fig. 2, b; lateral to the sinus can be seen the sharply-defined dorsal funiculi increasing in size from below upward. Each dorsal funiculus is bounded laterally by a dorso-lateral groove, at a point corresponding to the tip of the dorsal horn. Entering this groove are the enormous dorsal nerve roots, grouped into segmental fibre bundles.

Fig. 2, a shows the ventral surface of the enlargement. At two places the pial sheath has been left intact. In this part of the cord the pia is considerably modified from the form which is present in other regions. Beginning at the 26th segment there is a marked increase in the size of the thickened strips of the pial sheath, or ligamentous bands. The pia in the intervening spaces becomes thinner and more web-like. Between the 30th and 37th segments the ligamentum long. ventr. sends out tooth-like intersegmental processes which join the ligamenta long. lat., and the ligamentous structure thus formed affords a strong support where, owing to its specialized character, the cord demands more than ordinary protection.

On removing the pia, there is seen an enlargement of the fissura longitudinalis ventralis, which forms a sinus resembling, to some extent, the sinus rhomboideus of the dorsal surface, though it is shorter and narrower. Moreover it is not filled with the gelatinous semi-transparent tissue as seen in that sinus, and at the bottom one can see the cross-fibres of the commissura anterior. The space where the fissura long. ventr. may be called a sinus, extends from the 31st to the 35th segment, and is 1.3 mm. wide.

The great increase in the anterior horn elements, which occurs in the enlargement, is segmental in character, and forms segmentally projecting

masses of grey substance whose outline can be seen on the ventral surface of the cord as rounded elevations, *eminentiae ventrales*, which bulge forward through the ligamentous framework. There is thus formed a series of hill-like prominences separated by intersegmental grooves, *sulci transversi*. In the grooves lie the lateral prongs of the ligamentum long. ventr. From the lateral border of the segmental elevations arise the motor nerve roots as a row of fine rootlets which pass through the web part of the pial sheath just ventral to the ligamenta long. lat.

On examining the lateral surface of the cord in the region from the 31st to 36th segment, one sees, just dorsal to the ligamenta long. lat., at the level of each sulcus transversus, a small oval greyish projection measuring 1.4 mm. long and 0.4 mm. wide. These projections are the *nuclei marginales majores*, or the Large Hofmann Nuclei. They are easily seen with the naked eye, but better with a lens and under water. A description of them will be included under the heading Nerve-Cell Groups.

Caudal to the lumbo-sacral enlargement the cord decreases abruptly in size and extends, gradually tapering, to the end of the spinal canal. There is no cauda equina. A section of the most caudal pieces of our specimen shows a central canal and a similar general arrangement of grey and white matter as present in other parts of the cord.

From Gadow's¹⁰ work we can localize the peripheral parts that are controlled by this region of the cord. Gadow describes the sacral plexus as consisting of three individual groups: plexus cruralis; plexus ischiadicus; plexus pudendus. The nervus sacralis, which, by means of its bifurcated root, joins the latter two plexuses, he locates in the ostrich at the 37th segment. The nervus furcalis, which separates the plexus ischiadicus from the plexus cruralis, he places at the 31st segment. Thus the plexus cruralis is attached to the cord from the 27th to the 31st segment, or the cephalic half of the enlargement. We may, therefore, locate here the nerve-cell groups belonging to the trochanter muscles and the muscles situated on the medial and anterior side of the femur, to which area the plexus cruralis is distributed. The plexus ischiadicus arises by 7 roots from the caudal half of the enlargement, the 31st to 37th segment. The roots of this plexus unite to form nervus ischiadicus which supplies the massive group of muscles on the lateral and posterior sides of the femur and the muscles of the lower leg. Caudal to the 37th segment is situated the pudendal plexus which innervates the anal and genital musculature. Beyond the 43rd segment arise the delicate caudal nerves which supply the coccygeal muscles.

¹⁰ L. c., p. 406

ARRANGEMENT OF WHITE AND GREY SUBSTANCE.

A cross-section of the cord shows, in a general way, a central four-horned area of grey matter surrounded by a much larger area of white matter. The two dorsal horns of grey matter separate off a portion of the latter forming the dorsal funiculi, so called in distinction to the remainder of the white matter, or ventro-lateral funiculi. The outline and relative size of these individual areas in different levels of the cord are shown in Fig. 3.

A great variation exists in the size of the dorsal and ventral horns, as well as the anterior commissure. These structures are apparently closely interrelated, as they undergo the size-variation in unison. All of them reach their greatest development in the lumbo-sacral enlargement. Of the ventral and dorsal horns, the latter show less increase in size in the two enlargements. In the cervical region the dorsal horns are reduced to a narrow strand of grey matter and fail to reach the border of the cord. The white commissure, *commissura ventralis*, connecting the two halves of the cord is present at all levels, and will be described more in detail in connection with the fibre tracts. The grey commissure from the 31st to the 36th segments entirely fails. Its place is filled by the tissue of the sinus rhomboideus.

A more exact knowledge of the total area of transverse sections made at different levels, and the relative area of the antero-lateral funiculi, the dorsal funiculi, and the grey substance was obtained by a method which allows the calculation of the areas in square mms.

In this method one makes a series of outline drawings (in our case the Edinger drawing apparatus was used) of the various segments on a sheet of evenly-rolled lead or tin foil. Thick cardboard can also be used when the drawings are large. The drawings of the individual segments thus outlined on the sheet of lead are all magnified on the same scale. A drawing is also made in a similar way and with the same enlargement of a square cm. which has been outlined in ink on a glass slide. The drawings of the different segments and of the square cm. are then cut out from the lead sheet, and the segments further cut apart into the different areas. These pieces are all separately weighed. The ratio then, between the weight of each individual part and the weight of the piece representing the square cm., is equivalent to the area of this part.

Sections were taken from each segment of the ostrich cord, and the area of the various fields was thus calculated. The sections were taken uniformly near the departure of the nerve to avoid the discrepancy that might occur from differences in the same segment. This variation in the upper part of the cord is hardly appreciable. In the lumbo-sacral enlargement, however, it is more marked, and we have a distinct segmental character given to the cord by the increase in the size of the ventral horns, which occurs in the middle of the segment. Taking the sections at the level of the roots has the

further advantage that here the boundary of the dorsal funiculi is more sharply defined, owing to the larger number of entering dorsal root-fibres.

The results of the method in our case are represented in the adjoining table:

TABLE
SHOWING SIZE OF VARIOUS AREAS OF CROSS-SECTIONS OF CORD AT DIFFERENT LEVELS.
THE NUMBERS GIVEN INDICATE SQUARE MMS.

Segment.	Grey Matter.	Ventro-lateral Funiculi.	Dorsal Funiculi.	Total Area.
3	.7	8.7	.7	10.1
5	.7	9.1	.7	10.5
7	.7	9.1	.7	10.5
12	.8	9.2	.7	10.7
13	.9	8.8	.7	10.4
14	.9	8.9	.7	10.5
16	1.3	10.9	.9	13.1
17	1.9	12.2	1.1	15.2
19	1.7	10.9	.9	13.5
20	1.3	9.9	.7	11.9
21	1.2	9.9	.6	11.7
22	1.2	8.9	.5	10.6
24	1.5	10.5	.7	12.7
26	2.1	11.9	1.1	15.1
27	4.4	14.9	2.1	21.4
28	6.3	18.3	3.1	27.7
29	8.6	21.9	4.3	34.8
30	9.6	23.5	5.4	38.5
31	7.8	18.9	4.4	31.1
32	7.2	16.6	3.5	27.3
33	5.9	14.2	3.1	23.2
34	4.8	9.3	2.1	16.2
35	3.5	6.9	1.1	11.5
36	1.9	5.2	.6	7.7
38	1.0	3.1	.5	4.6
44	.4	.9	.2	1.5

These areas and their relative size are more graphically represented in the diagram given in Fig. 4. The size of the grey substance, the ventro-lateral funiculi, and the dorsal funiculi in typical segments are represented by curves, the height of which signifies square mms. as shown by a scale on the left.

From this diagram it is apparent that the ventro-lateral funiculi form by far the greatest area at all levels. The proportion is much greater above than below the lumbo-sacral enlargement. This could be accounted for in part by the presence of tracts connecting the enlargement with the brain centers. In both the cervical and lumbo-sacral enlargements the increase in area of the ventro-lateral funiculi is greater than that of the grey matter and dorsal funiculi. This is doubtless due to the large number of association fibres which form a field of fine fibres surrounding the anterior horns.

FIG. 4. Diagram showing the size of the various areas of the cord at different levels. The curves are drawn on a scale which shows the size in square mms. The spinal cord is drawn in below the diagram and represents the general size for the corresponding segments.

Between the curves which represent the grey matter and the dorsal funiculi there is a closer uniformity in size; although the former shows a greater increase in the regions corresponding to the wing and leg musculature.

Of all three curves on the diagram that of the dorsal funiculi indicates the smallest as well as the least variable area. It is smallest at the 44th segment, and presents practically no change as we proceed cephalad until the 36th segment. If we look at Fig. 2, b it is to be seen that the dorsal nerve roots from the 36th to 31st segment are enormously increased in size. Corresponding to the entrance of these large dorsal nerve roots, in the same segments in the diagram there is an abrupt ascent of the dorsal funiculi curve. Attention is called to the fact that the increase in the size of the dorsal funiculi extends cephalad from the point of increased dorsal root fibres. Therefore we may assume that the collaterals in the dorsal funiculi extending caudalward from the dorsal roots are either very few in number or very small in diameter, and that the general course of the entering impulses is in the cephalic direction.

The descent of the curve of the dorsal funiculi from the 30th to the 26th segment is as abrupt as the previous ascent. While in a space of six segments the area of the dorsal funiculi was increased nine times in size, this area, four segments higher up, has lost already more than three-fourths of this increase, and so the area at the 26th segment is only one-fourth of that at the 30th. If we take for granted that all the fibres that leave the dorsal funiculi enter the grey substance, and that there is very little variation in the size of the fibres from the 30th to 26th segment (both of which facts are confirmed by microscopical study of the cross-sections) then we may say that three-fourths of the fibres present in the dorsal funiculi at the 30th segment have entered the grey substance before the 26th segment. In other words *the course of the dorsal root fibres within the dorsal funiculi is a short one, and not more than a small proportion of these fibres ever reach the medulla by this tract.*

That which is apparent regarding the dorsal funiculi in the lumbosacral enlargement is seen again in the cervical enlargement, though in the latter it is less marked. Above the cervical enlargement the rate of accession and loss of fibres in the dorsal funiculi maintains a constant balance, and the curve of area runs as a horizontal line.

FINER STRUCTURE OF THE CORD.

By the usual methods of staining, the cord resolves itself into three elements: Neuroglia, which forms the general framework; Nerve-Cells

and Myelinated Axis-Cylinders, which form the fibre tracts and make up the bulk of the white substance. The histology of the cord will be discussed under these heads.

The *neuroglia* was studied in preparations stained by the iron hæmatoxylin picro-fuchsin method of Weigert. This method cannot be spoken of as a *glial* stain; on the contrary, the glia does not stain with fuchsin as in the original Van Gieson method, but remains a yellowish brown and is seen in sharp contrast to the brilliant red connective-tissue elements. By combining the original Van Gieson method and the Weigert modification we may study the glial distribution by a process of exclusion; this permits the following general description:

The glia fibres are more numerous in the grey substance than in the white, and are more numerous in the ventral horns than in the dorsal horns. They form an especially thick mass in the region of the central canal. In the white matter on the periphery, adjoining the pia, is a rather uniform layer of closely-lying fibres which forms a glial sheath to the cord, the *peripheral glia sheath*. This layer, at a point corresponding to Lissauer's fasciculus, is thickened and extends into the substance of the cord as a broad strand to meet the tip of the dorsal horn, which fails to reach the border of the cord. This strand spreads laterally to the dorsal horn and forms the web-like *formatio reticularis* situated in the median part of the lateral funiculus.

In most sections another glial process is seen extending from the sulcus longitudinalis dorsalis toward the central canal, the *septum longitudinale dorsale*, supporting a blood-vessel with its connective tissue sheath. Aside from the peripheral sheath and the processes as mentioned, the glia of the white substance forms a more or less uniform framework, supporting the nervous elements proper. There remains to be mentioned a special modification of the glial arrangement associated with the formation of the sinus rhomboideus.

SINUS RHOMBOIDEUS.

A macroscopic description of this structure has already been given, and we have spoken of the delicate gelatinous tissue with which it is filled. From the study of a series of transverse sections through this region it is our conclusion that this tissue is not a new structure, but is identical with the peripheral glia sheath and the septum dorsale which have become modified in their histological character.

In sections through the 29th segment there is a marked increase in the size of the sulcus longitudinalis dorsalis, which penetrates ventrally one-half the length of the septum dorsale and splits it in wedge-shape

fashion. In the 30th segment the sulcus extends the entire distance to the grey commissure completely separating the dorsal funiculi and forming the cephalic end of the sinus rhomboideus. At this level a change in the character of the glia shows itself in that part of the peripheral sheath between the ventral and dorsal nerve roots, as well as in the grey commissure and the adjoining divided septum dorsale. In these places instead of a compact mass of fibres the glia shows a looser and more sponge-like appearance. In the succeeding sections this glial modification rapidly increases in extent, coincident with the increase in the size of the sinus, and reaches its maximal development between the 30th and 36th segments. A drawing from this region is reproduced in Fig. 5, and a portion of the glial web is shown under higher magnification. It is thus seen that the peripheral glia sheath throughout the circumference of the cord, except at the attachment of the ligamenta denticulata, is changed into, or replaced by, a tissue consisting of enormous cells (.003 to .004 mm. in diameter), the body of each of which is filled with a transparent fluid of undetermined nature which crowds the small nucleus to one side, or the nucleus is suspended in the fluid supported by a slender stalk of cell tissue. It resembles fat tissue to some extent. It however fails in frozen section to stain with Herxheimer's solution of *Fettponceau*. In iron-hæmatoxylin picro-fuchsin preparations there is no trace seen of connective tissue fibres. The cells remained unstained like the neuroglia cells of other parts of the section. By exclusion, then, we are led to consider them as modified neuroglia cells, though we unfortunately lack the definite evidence of a selective stain.

The sinus rhomboideus of birds has always been an object of interest to investigators, especially as to the character and significance of the gelatinous material with which it is filled. Of the earlier writers the work of *Duval*¹¹ may be referred to, the results of which were more or less confirmed recently by *Kölliker*.¹² Both of these authors from embryological evidence agree as to the glial nature of the tissue filling the sinus. They, however, do not make mention of the presence of this web-like material around almost the entire circumference of the cord.

The grey commissure and the septum dorsale are entirely changed into this tissue, which thus fills the sinus as a broad network separating the blunt ends of grey substance and the dorsal funiculi and extending ventralward to the commissura ventralis. In the ventral part lies the

¹¹ Duval, L. c.

¹² Kölliker, Ueber die oberflächlichen Nervenkerne im Marke der Vögel und Reptilien. Zeitschrift f. wiss. Zool., LXXII, 1.

central canal held in suspension by a few coarser strands of glia fibres which lie among the cells and bridge over the space separating the grey matter. This meshwork formation of these modified glia cells extends somewhat into the territory of the white substance along the borders of the dorsal, lateral and ventral funiculi. Under low power this ragged edge of white substance gives the deceptive appearance of an artifact.

From the 38th segment caudalward there is a gradual retrogression of neuroglia to the form as previously described.

FIG. 5. Cross-section of the lumbo-sacral enlargement of the ostrich spinal cord, at the 36th segment, enlarged 12 $\times$. A portion of the sinus rhomboideus tissue is shown above with an enlargement of 270 $\times$.

CENTRAL CANAL.

The cylindrical epithelial cells lining the central canal form a layer .007 to .015 mm. thick which is supported by a thick mass of glial tissue,

the *substantia gelatinosa centralis*, in the middle of the grey commissure. Where the grey commissure is lacking, in the region of the sinus rhomboideus, the central canal is supported just dorsal to the commissura ventralis by the loose strands of glial fibres which bridge over the space between the blunt ends of grey substance.

The lumen of the canal varies in irregular manner from round to oval, and where it lacks the support of the grey commissure it is no more than a narrow slit. Where it is round or oval it has a diameter averaging from .035 to .04 mm. In both cross and longitudinal stained preparations there is seen within the lumen the so-called *Reissner'sche Centralfaden*. *Kölliker*¹³ in a recent contribution gives the opinion that it is a "natürliche Bildung beim Vögel, Reptilien, und Amphibia," and also finds in it "eine überraschende Aehnlichkeit mit einem Achsencylinder." This is contrary to *Gadow*¹⁴ who considers it a product of shrunken cerebro-spinal fluid and lymph corpuscles. In favor of the view as held by *Gadow* may be stated the three following facts: The structure shows a marked and irregular variation in form and size in different sections; in some transverse sections it was seen as multiple "Centralfäden"; in sections stained with toluidin blue it retains a deep blue stain while the axis-cylinders in all other parts of the section are unstained.

NERVE-CELL GROUPS.

The majority of the nerve-cells of the spinal cord of the ostrich are situated in the grey matter of the ventral horn. There are, however, many cells in the grey commissure and the dorsal horn, and there are still other cells among the fibres of the white substance, especially near the periphery. These cells vary at different levels in their form, size, and manner of grouping. For their descriptions the following classification has been found advantageous:

1. Lateral Group—	a. Lateral cells.
	b. Dorso-lateral cells.
	c. Ventro-lateral cells.
2. Central Group—	a. Small mixed cells.
	b. Giant cells.
3. Commissural Group—	
4. Dorsal Group—	a. Clarke cells.
	b. Dorsal horn-cells.
5. Peripheral Group—	a. Nuclei marginales majores.
	b. Nuclei marginales minores.
	c. Scattered cells.

¹³ Kölliker, L. c., p. 159.

¹⁴ Gadow, L. c., p. 338.

The *lateral group* consists of more or less uniformly large multipolar cells, which in finer histology closely resemble the motor cells of the ventral horns of the higher vertebrates. Their distribution in typical sections is shown in Fig. 6. They are seen in every section, but vary in number, being most numerous in the lumbo-sacral region and least numerous in the cervical segments. Corresponding with the number there is some variation in the size; those in the cervical segments average .02 mm. in diameter, while in the lumbo-sacral region there are many cells over .04 mm. This group may be further subdivided into cells having lateral, dorso-lateral, and ventro-lateral positions. A particularly well-defined group of the ventro-lateral cells occurs in the region of the sinus rhomboideus (Fig. 6, segm. XXXVI).

If we compare this lateral group with the cells of the human cord as classified by *Waldeyer*,¹⁵ it is apparent that it corresponds to his median and lateral groups, each of which he subdivides into anterior, middle and posterior subgroups. The cells of the lateral group in segment XXXVI could have been separated in a similar manner into a median and a lateral group; the ventro-lateral cells would then well correspond to Waldeyer's median group, and the lateral group could be further subdivided into anterior, middle and posterior groups. Such a classification in the ostrich however serves only irregularly and for isolated segments, and therefore this distinction between the cell groups was not attempted; but all the large multipolar cells of the ventral horns, the so-called motor cells, were put under the one general class, the lateral group, as described above.

Most of the cells of the lateral group apparently send their axis-cylinders into the ventral nerve-roots. The axis-cylinders of the ventro-lateral cells, however, seem to enter the commissura ventralis. No attempt to establish such relations could be made without Golgi preparations, and these unfortunately were not to be had from our material.

The *central group* occupies the area of junction of the ventral and dorsal horns, and invades the territory of the horns proper. It consists of loosely-scattered cells which vary greatly in size and average a third smaller than the cells of the lateral group. They also stain less intensely and have fewer processes, consequently having less tendency to a multipolar form.

In the lumbo-sacral enlargement there appear cells among this group which from their size we may speak of as *giant cells*. They are quadrilateral or rounded in shape, and vary from .03 to .09 mm. in diameter.

¹⁵ Waldeyer, *Das Gorillärückenmark*, Abhandl. der kgl. preuss. Akad. der Wissensch. zu Berlin, von Jahre 1888.

They are distinguished from the Clarke cells and cells of the lateral group by having fewer processes, by their tendency to easy disintegration, staining less intensely and having finer granules in the cell body. These cells are present throughout the whole enlargement, but are more numerous in the upper part (27th to 31st segments). A

FIG. 6. Cell-groups in the grey substance of the spinal cord of the ostrich.

few are also seen in the 13th to 16th segments, just above the cervical enlargement. As can be seen in Fig. 6, segm. XXIX, they are scattered over the entire area of the central group. Very often they are seen on the extreme ventral or dorsal border of the grey matter. The largest number seen in any one section ($20\ \mu$ thick) was eight. These giant cells present a striking similarity to the large cells seen in the lateral group of the nucleus funiculi gracilis of the human medulla.

The *commissural group* is made up of a compact group of small intensely-staining multipolar cells, which are found in the grey commissure in the thoracic division of the cord, from the 20th to 27th segments. It suggests, by its position, a possible relation with the viscera.

The *dorsal group* includes in sections through the 26th to 31st segments a small group of cells on the median border of the grey matter at the junction of the two dorsal horns. The cells of this group resemble those of the lateral group, though slightly smaller. From their similarity, in position and appearance, to the group in the mammalian cord these are classed as Clarke cells (see Fig. 6, segm. XXIX). Otherwise as noteworthy are classed under the dorsal group the occasional small multipolar or spindle-shaped cells, which are seen on the periphery of the **dorsal horn both median and lateral, and frequently on the tip of the horn near the entrance of the dorsal root.**

PERIPHERAL GROUP.

In 1889 *Lachi*¹⁶ described a peripheral group of nerve-cells forming a series of segmental projecting nuclei, occurring in the lumbo-sacral enlargement of the spinal cord of doves. This nucleus was seen later by *Gaskell* and *Schafer* but attracted little attention until *Kölliker*,¹⁷ originally unaware of Lachi's work, published the results of a most complete study of this structure, both in the embryo and the adult bird. Kölliker finds three varieties of peripheral cell-groups, namely: *Hofmann'sche Grosskerne*, so named after his Präparator P. Hofmann, who had called his attention to them; *Hofmann'sche Kleinkerne*; and a scattered group.

In the embryonal cord, 4½- to 5-day chick, Kölliker describes a group of cells separating itself from the superficial cells of the ventral horn. This group in the 10-day chick is completely separated and forms a definite peripheral nucleus, the *Hofmann'sche Kerne*. There are 28 of these nuclei on each side of the cord, segmentally arranged according to the 28 spinal nerves and ganglia. Of these nuclei the 5 or 6 pairs, corresponding to the level of the sinus rhomboideus, undergo a marked development, and in the 15-day chick can be seen bulging from the periphery of the cord just dorsal to the ventral nerve roots, *Hofmann'sche Grosskerne*. The nuclei in the other regions of the cord do not share this development, but remain more or less

¹⁶ P. Lachi, *Alcune particolarità anatomiche del ringonfiamento sacrale nel midollo degli uccelli*, Memorie della Società Toscana di Scienze Naturali. Vol. X, Pisa, 1889.

¹⁷ Kölliker, a.—Ueber einen noch unbekannten Nervenzellenkern in Rückenmark der Vögel, *Akad. Anzeiger* (Wien), Nr. XXV, 1901. b.—Weitere Beobachtungen über die Hofmann'schen Kerne am Mark der Vögel, *Anatom. Anzeiger*, Bd. XXI, Nr. 3, 1902. c.—L. c.

rudimentary, the Hofmann'sche Kleinkerne. The third or scattered group is made up of cells similar to the lateral group cells of the ventral horns, and occurring at irregular points on the periphery of the ventro-lateral funiculi, more especially near the exit of the ventral nerve roots and near the Hofmann'sche Grosskerne. Kölliker considers these cells to be detached elements from the ventral horns.

In the ostrich the occurrence and arrangement of peripheral cells is similar to that found by Kölliker and Lachi in the dove and hen. In describing them we follow Kölliker's classification, but would substitute more descriptive names.

The *nuclei marginales majores* (Lobi accessori.—Lachi; Hofmann'sche Grosskerne.—Kölliker) lie on each side of the cord just dorsal to the ligamenta longitudinalia lateralia at levels marked off by the sulci transversi ventrales. Of these nuclei 6 pairs could be readily seen with the naked eye. They appear as elongated oval greyish semi-translucent elevations measuring macroscopically 1.0 to 1.4 mm. long. The interval between successive nuclei averages 6.0 mm. Each segment of the lumbo-sacral region was cut in transverse or longitudinal series, mostly the former. In studying these sections this nucleus was identified in the 30th, 31st (32d injured in removing the cord), 33d, 34th, 35th, and 36th segments. Thus the nucleus occurs in the region of the sinus rhomboideus, extending a little cephalad as well as somewhat caudad to it. Microscopically in the preparations the nucleus is seen projecting from the lateral border of the cord just dorsal to the attachment of the ligamentum denticulatum, as is represented in Fig. 5.

The size of the nuclei averages among the larger ones .10 to .18 mm. antero-ventral diameter, and .08 to .12 mm. lateral diameter. In a continuous series of sections 20 μ thick the nucleus is present in 62; that is the nucleus is 1.24 mm. long. These dimensions are somewhat smaller than the macroscopic, as could be expected from shrinkage associated with the embedding process, and possibly partly due to greater accuracy in measuring, the boundaries of the nuclei being more definite in the prepared and stained specimen.

The free border of the nucleus is overlapped by pia, and the inner border merges gradually into the white substance of the cord. It consists of a network of glia tissue, somewhat looser and more vascular than the adjoining cord. In this sponge-like framework lie a number of multipolar nerve-cells and myelinated axis-cylinders. The cells resemble those forming the lateral group of the ventral horn, but are not more than one-fourth to one-sixth as large. In one nucleus 10 of these were seen in which the cell nucleus was cut through. In the

majority of sections there are not more than 5 such cells present. The myelinated axis-cylinders have mostly a longitudinal course, and are about the same size as those in the neighboring periphery of the cord. Throughout the greater part of the nucleus they are uniform in number, 112 were counted in one section, but such a count is subject to error as it is often difficult to say whether the fibres belong to the lateral funiculus or to the nucleus owing to the indistinct inner border of the latter. In studying a complete series of transverse sections through the nucleus, prepared after Weigert's myelin-sheath method, one gets the impression that these large axis-cylinders belong properly to the lateral funiculus. In such sections near its caudal and cephalic ends the nucleus appears as a small island of increased glia tissue lying in the midst of the axis-cylinders near the border of the cord. In the succeeding sections this glia tissue rapidly increases in amount and envelops and carries with it the surrounding nerve-fibres, until finally it bulges from the side of the cord as an exuberant overgrowth. The large size of the nerve-fibres compared to the cells of the nucleus, and their uniformity in number at different levels, would also lend support to the view that they are independent of the cells and not properly a part of the nucleus. There are, however, a certain number of fine axis-cylinders seen in the sections, both with longitudinal and oblique course, which may be related to the cells embedded in the nucleus.

The *nuclei marginales minores* (Hofmann'sche Kleinkerne) are seen in sections taken from the cervical region at levels where the nerve roots make their exit from the dural sheath and vertebral canal. Their size and general position are indicated in Fig. 1. They do not project from the periphery of the cord and have no appearance of activity. The cells are small and are not definitely multipolar. The glia in which they lie is only slightly increased over that present in other regions of the periphery of the cord.

The *scattered group* includes multipolar cells similar to those of the ventral horn, both in shape and size. One or two of these are found in nearly all sections of the lumbo-sacral enlargement, lying among the fibres of the periphery of the ventro-lateral funiculi. They are found most often near the nuclei marginales majores, or among the fibres leaving the cord as the ventral root. It is this group that Kölliker regards as detached elements from the ventral horns.

In regard to Kölliker's¹⁸ suggestion of a relation between the Hofmann'sche Grosskerne and the enormous size of the commissura ven-

¹⁸ Kölliker, L. c. (c.), p. 176.

tralis we may state the fact that a longitudinal ventro-dorsal section cut through the commissura ventralis, from the 32nd to 34th segment, shows that the commissure here is practically uniform in the ventro-dorsal diameter. It presents no segmental increase in size at the levels of the Hofmann'sche Kerne which would be expected if the size of the commissure in the lumbo-sacral enlargement were due to the presence of these nuclei.

FIBRE TRACTS.

Myelinated fibres are present both in the grey and white substance of the cord. In the former they are seen in the preparations in cross and longitudinal section, and form a network which cannot be resolved into definite fibre tracts.

The great bulk of the spinal cord fibres make up the white matter, and form a thick envelope surrounding the grey substance. This envelope may be separated into ventral, lateral and dorsal funiculi. The boundary between the first two is an artificial one, produced by the fibres of origin of the ventral nerve roots. At levels where those fibres are few or absent there is no point of division between the two funiculi.

The *dorsal funiculi* are more sharply defined. They are separated from each other by the septum posterior, and separated from the lateral funiculi by the dorsal horns and the glial processes which extend from the tip of the horns to the peripheral sheath of the cord.

The general variation in size and shape of the dorsal funiculi occurring at different levels of the cord can be seen in Fig. 3. The definite area is recorded by a table and by Fig. 4, in which a diagram gives the area in a curve indicating square mms. Thus a further mention of the shape and size of these funiculi is here not necessary.

In their finer structure the dorsal funiculi consist of fibres of entrance and departure, and fibres having a longitudinal course. The bundles of fibres entering as the dorsal nerve roots vary greatly in size, as is seen macroscopically. Those in the lumbo-sacral enlargement are two or three times larger than those in the cervical enlargement, and about five times larger than those of the upper cervical region. These fibres enter obliquely as a compact bundle at the dorso-lateral border of the funiculi. The bundle then breaks up into loose strands, disappearing among the longitudinal fibres. No fibres could be seen to enter the grey matter directly. In longitudinal sections most of the fibres could be seen to bend upwards, and could be traced a short distance in the longitudinal direction. A few fibres were seen which, on entering, turned caudalwards. In neither Van Gieson nor Weigert preparations, how-

ever, was a "Y" form seen, where the entering fibre had both a cephalad and caudad collateral. That so few fibres take a downward course accounts for the fact that in the 35th and 36th segments, where there is a pronounced increase in the size of the dorsal nerve roots, the corresponding increase in the size of the dorsal funiculi is in the cephalic direction. Furthermore, the course of these fibres in the dorsal funiculi cannot be a long one, and this is shown by the rapid decrease in the size of the funiculi coincident with the decrease in the number of entering fibres, a fact which we have already referred to in the consideration of the diagram, Fig. 4.

The collaterals from the dorsal funiculi to the grey matter vary in number in correspondence to the number of fibres from the dorsal nerve roots. In the lumbo-sacral enlargement these fibres enter the dorsal horn as a large strand of fibres which could be traced to the region at the base of the horn. In the cervical region fibres entering the grey matter are found only as single separate collaterals.

No definite subdivision of these funiculi into separate fasciculi or tracts could be made. In general, however, the fibres of the ventral one-third are smaller and form a triangular field of fine fibres, averaging $.2\ \mu$. These are apparently association fibres. This field is not present in the lumbo-sacral enlargement; here the grey commissure is absent, and the dorsal funiculi are separated by the sinus rhomboideus and lie further dorsal. The size of the fibres of this enlargement is uniformly large, the myeline ring in Weigert preparations averaging 1.0 to $1.5\ \mu$. We have already seen that the majority of the fibres of this region do not remain in the dorsal funiculi for a course of more than 3 to 4 segments, and that a small proportion of them reach the medulla through this tract. *It would seem, then, that large fibres do not necessarily indicate long fibres;* because in the lumbo-sacral enlargement the fibres are uniformly large and it is right here that we have shown that at least three-fourths of the fibres have a course in the dorsal funiculi shorter than 4 segments.

The *lateral funiculi* present an inner zone of fine fibres and an outer zone of coarser fibres, the latter fibres averaging $1.0\ \mu$. The inner zone, or *formatio reticularis*, makes up a third to one-half the area. It is connected with the grey substance by numerous radiating strands of fibres, and apparently consists of association bundles. The outer field is connected with the central grey substance by less numerous strands of fibres. It is in this outer zone that *Friedländer*¹⁹ found ascending

¹⁹ Friedländer, L. c.

and descending cerebellar tracts by experimental secondary degeneration in doves.

The *ventral funiculi* have an inner zone which is a ventral extension of the inner zone of the lateral funiculi. The outer zone, *tractus cerebello-spinalis ventralis medialis* of Friedländer, is somewhat larger, and forms a more or less triangular field, of which the *fissura ventralis* forms one side. The fibres of this field are all large and average 1.5μ , many of them being over 2μ . In the lumbo-sacral enlargement the enormous increase in size of the ventral and lateral funiculi seems due to an accession of smaller fibres which are added to the inner zone, and this increase is more marked in the ventral than in the lateral funiculus.

A *commissura alba anterior* of obliquely crossing fibres is present at all levels of the cord, connecting the two ventral funiculi. It is greatly increased in size between the 28th and 36th segments. A sagittal section through the commissure in this region does not show any segmental grouping of these fibres. In Weigert preparations strands of fibres can be traced through the commissure coming from the outer zone of the ventral funiculus and extending to the opposite ventral horn. We have here doubtless a motor tract from higher centers, the fibres of which decussate before ending about the cells of origin of the motor nerve roots. The large number of ventral horn-cells in the lumbo-sacral enlargement would thus partly explain the large size of the commissure which here prevails. No trace of commissural fibres dorsal to the grey commissure was found in any of our sections. A posterior white commissure is apparently lacking.

RÉSUMÉ.

In looking back at the more important characteristics presented by the spinal cord of the ostrich, a feature to be first referred to is that in its mass the cord forms by far the largest part of the central nervous system. In other words, then, we have here an animal the various parts of whose body receive their principal innervation from the spinal cord, and the influence of the brain on these parts is secondary and remote—an animal that works chiefly with its primary apparatus.

This suggestion as to the important part played by the primary nervous complex is further confirmed by the fact that the grey substance and associating collaterals vary in amount at different levels according to the demands made by the parts supplied. Thus throughout the cervical cord where there is a small and uniform number of neck muscles to be supplied the primary apparatus presents a correspondingly small

and uniform size. It is increased in the region supplying the wing musculature. A relatively greater increase would be expected in flying birds, the comparison of the ostrich with one of the large birds of prey would be interesting. When we go farther caudalwards and come to the increase of the primary apparatus corresponding to the massive leg musculature we find a great tumor-like enlargement, or Locomotor Brain, which demonstrates, as perhaps nowhere else in the animal kingdom, the close interdependence between a section of the central nervous system and the area innervated.

An interesting feature of the lumbo-sacral enlargement is the manner in which the neuromeres are marked off on the ventral surface of the cord by the hill-like prominences, calling to mind the segmental appearance presented by the well-known *Trigla* cord.

The marked development of the sinus rhomboideus offers favorable conditions for the study of this characteristic feature of the bird cord. We are enabled to contribute some facts as to the nature of the peculiar tissue with which this sinus is filled.

In studying the finer structure of the cord, the grouping of the cells into defined columns could be followed, some of which extend throughout the length of the cord. Two particularly interesting groups were found, one limited to the thoracic region in the posterior grey commissure, the other a group of "giant" cells occurring in the lumbo-sacral and cervical enlargements. The segmental groups of cells or nuclei occurring on the periphery of the cord, which have recently been the subject of much attention, are found in the characteristic way, and moreover are here present as macroscopic structures.

Our material was not such as to allow us to say anything of especial importance concerning the fibre tracts that would be new for the bird spinal cord. In this direction we can only look for advancement from experimental work such as was begun by Friedländer in this laboratory. Attention, however, is to be called to the short course taken by the fibres in the dorsal funiculi, and to the small proportion of these fibres that eventually reach the higher centers through this path directly.