

**Anatomy.** — *The Phylogenetic Development of the Substantia Gelatinosa Rolandi*. Part. II. *Amphibians, Reptiles, and Birds*. By E. KEENAN. M. B., National University of Ireland. (From the Central Dutch Institute for Brain Research, Amsterdam.) (Communicated by Prof. C. U. ARIËNS KAPPERS.)

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In the first contribution on this subject, published in these Proceedings (Vol. XXXI, 1928), I dealt with the posterior horn regions of fishes. My observations led me to conclude that the substantia gelatinosa Rolandi is general throughout the fishes. The vertebrates below the fishes (*Amphioxus* and the cyclostomes) do not admit of comparison with higher forms in this respect, owing to the absence of differentiated anterior and posterior horns. Among the fishes it was found that, with the appearance of posterior horns, substantia gelatinosa was recognizable. Lissauer's zone, however, as a separate and recognizable area, is absent, while the body of the horn proper of man is, in part at least, represented in the undivided mass of gray matter, the *corpus commune posterius*, situated behind the central canal.

Among the *amphibians* the following species were examined: —  
Urodèles: *Megalobatrachus maximus*, *Amblystoma tigrinum*, *Molge cristata*, *Proteus anguinus*, and *Necturus maculatus*.

Anures: *Pipa pipa*, *Bombinator pachypus*, *Bufo vulgaris*, *Rana esculenta*, and *Rana catesbyana*.

To COGHILL (1909, 1913, 1914, and 1915) and HERRICK (1915), we are indebted for our fuller knowledge of the nervous mechanism in *amphibian* larvae, where the appearance of the cord and its cellular and fascicular arrangements are quite different from those observed in the fully developed animal. The relations in these larvae resemble those of *Amphioxus* and the *cyclostomes* more closely than they do those of *fishes* or adult amphibians, consequently they do not lend themselves for comparison with higher forms in the present instance.

With the passage of the larval stage, and the approach to the adult condition of the animal, the cord undergoes marked changes; and a completely new nervous mechanism, consisting of extra-spinal ganglia, new intra-spinal tracts, and an intra-segmental reflex arc, appears.

The adult amphibian cord as represented by the *bull frog* (*Rana catesbyana*) is shown in figs. 1, 2 and 3, sections through the cervical swelling, the middle thoracic, and the sacral regions, respectively.

While the cord shows, in many respects, a low development, approaching

the selachians more closely than the teleosts, as has been pointed out by V. LENHOSSÉK (1895), and also has been demonstrated by KAPPERS (1918)

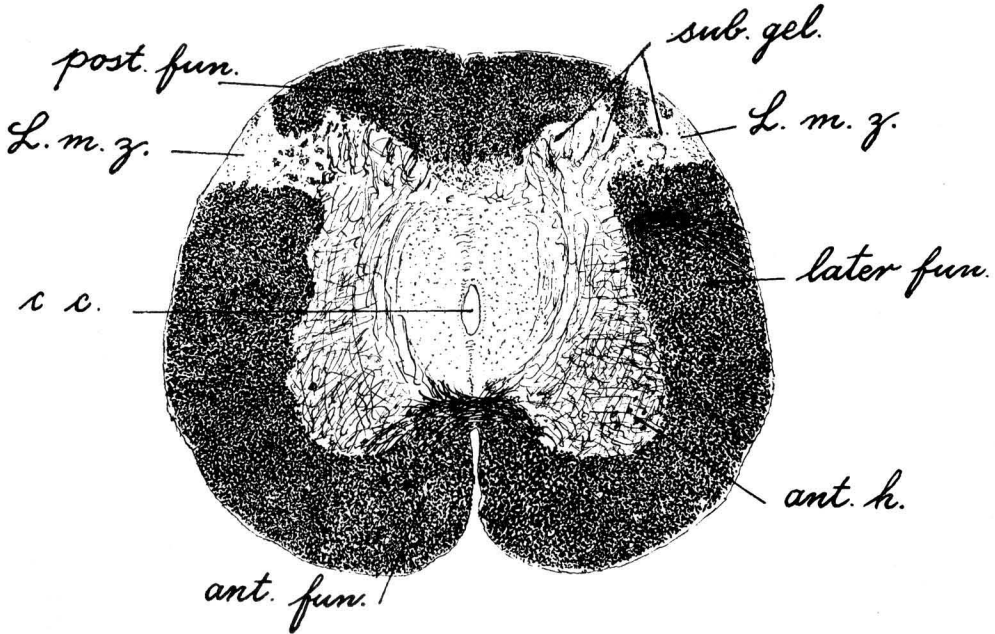


Fig. 1. Transverse section through the cervical enlargement of the spinal cord of *Rana catesbyana*  $\times 34$ .

ABBREVIATIONS FOR ALL FIGURES

*a* = tract of finely myelinated fibres.  
*b* = bundle of coarse fibres.  
*c* = posterior region of the gray matter.  
*ant. fun.* = anterior funiculus.  
*ant. h.* = anterior horn.  
*ant. r.* = anterior root.  
*ant. r. f.* = anterior root fibres.  
*ant. sept.* = anterior septum.  
*b. of p. h.* = body of the posterior horn.  
*c. c.* = central canal.

*later. fun.* = lateral funiculus.  
*L. m. z.* = Lissauer's marginal zone.  
*margin. nuc.* = marginal nucleus of Gaskell.  
*med. nuc.* = median nucleus of Schwann.  
*nuc. Burd.* = nucleus of Burdach.  
*post. fun.* = posterior funiculus.  
*post. r.* = posterior root.  
*post. sept.* = posterior septum.  
*sub. gel.* = substantia gelatinosa.

for the medulla oblongata and the fore-brain, we find many points indicating the more advanced position of the animal in phylogenetic status. The contrast between *Rana catesbyana* and the teleosts in the size of the posterior funiculi is very marked. In the former, the accumulation of fibres in the posterior funiculi forces the posterior horns far apart, so that they form with each other a very obtuse angle. BROUWER (1915) estimates that, in the ordinary frog, the proportion of the posterior funiculi to the total white matter in the cervical region of the cord is about 13 %, while in fishes it is only about 5 %. The percentage is much higher in the bull frog. As pointed out by WALLENBERG (1907) for *Rana temporaria*, this high percentage is, in part, due to descending fibres of the fifth, eighth, ninth,

and tenth cranial nerves, which descend to a very low level in frogs, the trigeminal reaching as far as the lumbar swelling.

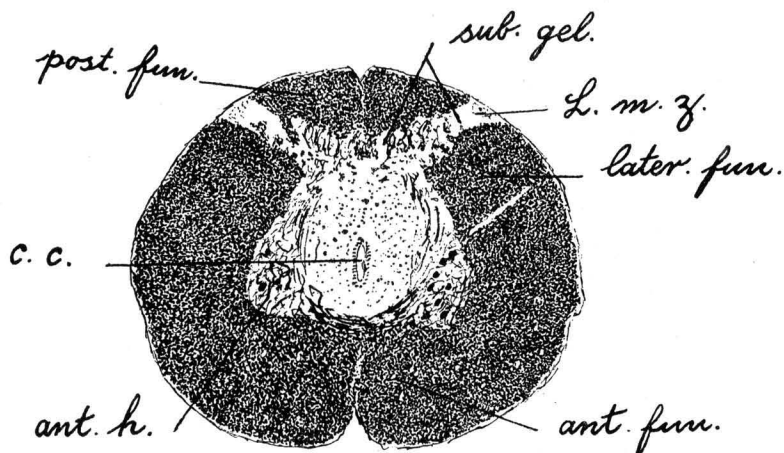


Fig. 2. Transverse section through the thoracic region of the spinal cord of *Rana catesbyana*  $\times 34$ .

The posterior horn reaches the surface of the cord, and, at its apex, there is an area containing widely-separated finely-medullated fibres, the rudiment of Lissauer's marginal zone of mammals. It is not so clearly defined in amphibians as in reptiles (figs. 4, 5, and 6). The remainder of the posterior horn consists chiefly of substantia gelatinosa, which stretches medially almost as far as the posterior septum, and is broken up into smaller masses by the passage of fibres between the posterior funiculi and the more ventral gray matter of the cord.

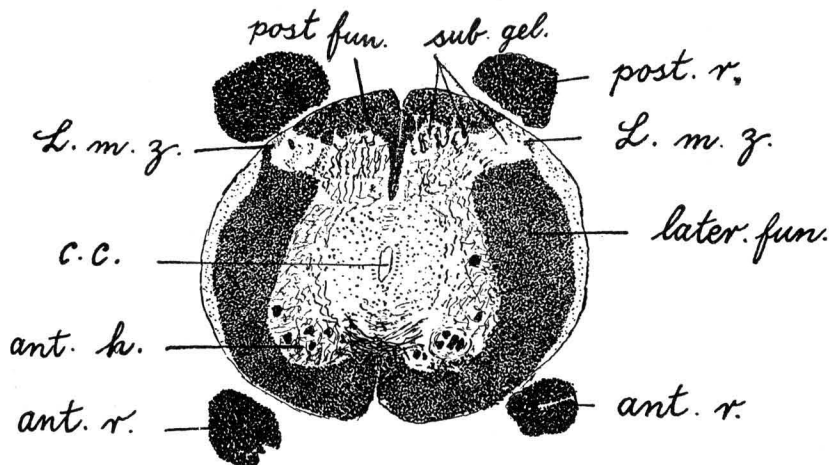


Fig. 3. Transverse section through the lumbo-sacral region of the spinal cord of *Rana catesbyana*  $\times 34$ .

The corpus commune posterius of fishes is still represented in the amphibian cord, though it is not such a well-defined and separate body as in sharks, but is continuous with the general mass of gray matter surrounding the central canal, from which the anterior horns project ventrolaterally as short conical protuberances. This relationship exists throughout the entire length of the cord. Cranially, the substantia gelatinosa is continuous with the Rolandic substance of the descending fifth root. It is reduced in amount in the mid-dorsal region, and there is a slight relative increase again towards the caudal end of the cord. It is not so well developed in amphibians as in most members of the teleosts, resembling, in fact, more closely the condition seen in sharks.

The posterior roots cross the apex of the posterior horns in the region designated Lissauer's marginal zone, and pass towards the posterior funiculi. The massing of the root fibres in Lissauer's zone renders it difficult to say, with certainty, whether the roots contribute fibres to this region.

Of *reptiles*, the following species were examined: — *Chelonia*: *Dammonia subtrijuga*, and *Chelone mydas*.

*Crocodylia*: *Crocodylus porosus*, and *Caiman sclerops*.

*Lacertilia*: *Varanus salvator*, and *Lacerta agilis*.

*Rhoptoglossa*: *Chamaeleon vulgaris*.

*Ophidia*: *Boa constrictor*, and *Python reticulatus*.

In the *reptilian* cord, the three subdivisions of the posterior horn regions are well marked and easily recognised. The posterior funiculi are strongly developed, and the posterior horns are definitely separated from each other. It is interesting to note, in this connection, that reptiles are the lowest animals in which posterior funicular nuclei have been definitely recognised.

At the upper end of the cervical cord, the relations are as follows: the body of the posterior horn projects backwards and laterally from its junction with the anterior horn; the substantia gelatinosa is massive, and presents a wide border peripherally, where the marginal zone of Lissauer lies at the surface as a transversely-placed flattened, or triangular band, with the narrow base directed laterally. Between Lissauer's marginal zone and the underlying substantia gelatinosa is a layer of coarsely myelinated fibres, of varying depth and compactness in the different species, but always showing strands of gray matter connecting the superficial part of the substantia gelatinosa with the deeper part of Lissauer's zone. SINN (1913) believes this layer to consist, in birds, of descending root fibres of the fifth cranial nerve. Lower down the cord, its existence can probably be explained by the presence of spinal root fibres, ascending and descending. It occurs also, though less marked, in man.

In general, on closer examination, five layers can be distinguished, on passing from the surface of the cord to the body of the horn. At the surface, Lissauer's zone contains a very thin layer of finely myelinated fibres: deep to this is a more open layer in which the fibres are fewer, and with

which there is a considerable mixture of gray matter. This gray matter is continuous, through the layer of coarse fibres, with the underlying substantia gelatinosa. The coarsely myelinated fibres can be divided into two zones, the more superficial, in general, being closely packed, though in some species (crocodile, fig. 4) more closely than in others (*Dammonia*). The fourth layer consists of an admixture of isolated bundles of coarse fibres and substantia gelatinosa. The deeper part of the substantia gelatinosa, which constitutes the fifth layer, is practically devoid of myelination, and resembles the substance in mammals.

The subdivision into five layers is well illustrated in the case of the crocodile (fig. 4).

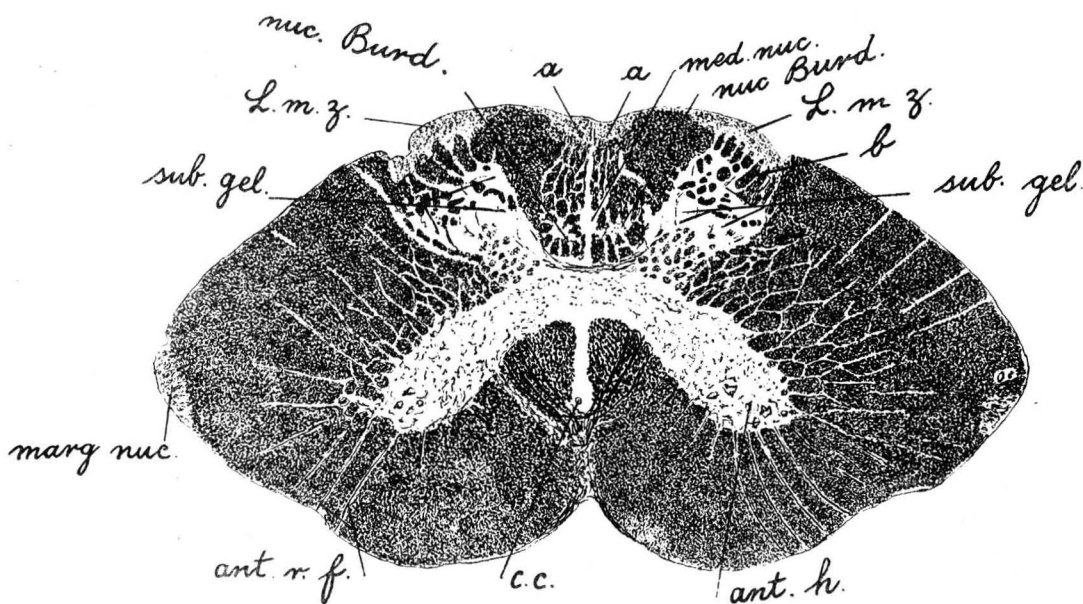


Fig. 4. Transverse section through the upper cervical region of the spinal cord of *Crocodilus porosus*  $\times 18$ .

Regarding the recognition of two distinct areas in Lissauer's zone, SINN (1913) has described what I term the deeper layer of Lissauer's zone under the name "promontorium" in birds, and shows a close postural relation between its medial narrow extremity and the lateral nucleus of the posterior funiculus. ZEEHANDELAAR (1920) associates it in function with the posterior horn, and I think it more correct to regard it as part of Lissauer's zone, owing to the number of scattered, finely myelinated fibres it contains.

On tracing the series lower down the cord, the above relationship persists, but the entire horn narrows very much. Lissauer's zone becomes deeper and somewhat triangular, with the apex directed towards the centre of the cord. The zone of coarse fibres also narrows and deepens.

In fig. 4, at the surface of the cord, on either side of the posterior septum,

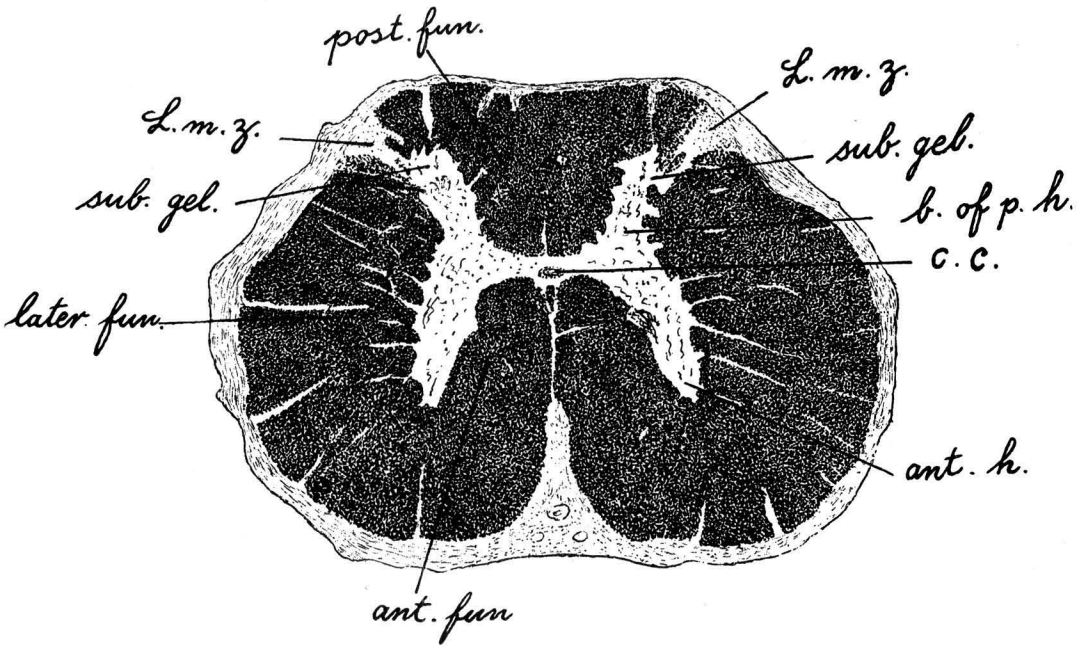


Fig. 5. Transverse section through the 2nd cervical segment of the spinal cord of *Dammonia subtrijuga*  $\times 48$ .

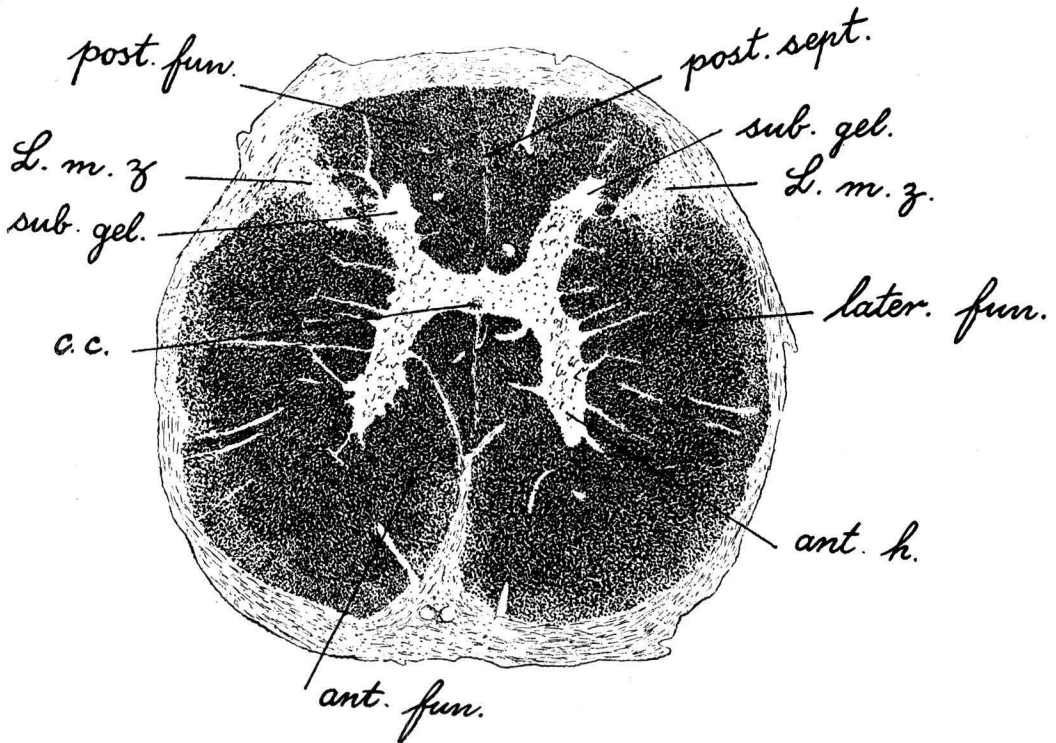


Fig. 6. Transverse section through the 4th thoracic segment of the spinal cord of *Dammonia subtrijuga*  $\times 48$ .

we see an area, poorer in myelination than the rest of the posterior funiculus, and resembling Lissauer's zone very much in appearance. It is connected with Lissauer's zone by a narrow sparsely-myelinated zone on the surface of the cord. It is probable, however, that this area is related in function with the underlying nuclei of the posterior funiculi, with which it is practically co-terminous.

In reptiles, there is a general tendency for Lissauer's zone to acquire a lateral position in relation to the rest of the posterior horn, and this is particularly marked in the case of *Dammonia subtrijuga*. At the upper end of the cord of *Dammonia*, Lissauer's zone is apical in position, but, lower down, it passes into a lateral position (figs. 5 and 6). In the mid-dorsal region, it becomes apical again, but gradually shifts laterally, and grows in size, as we approach the caudal end of the cord (fig. 7), until, in the lower sacral region, it lies in the concavity between the anterior and posterior horns. Intermingled with the fibres of this area are large nerve cells.

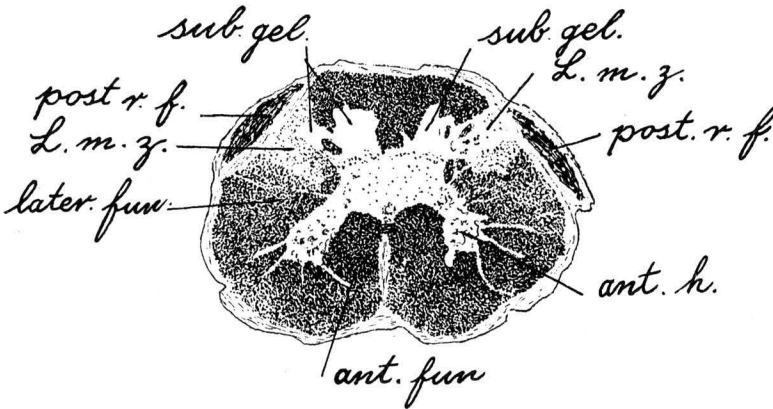


Fig. 7. Transverse section through the sacral region of the spinal cord of *Dammonia subtrijuga*  $\times 48$ .

The lateral position of the zone in these forms may be another manifestation of KAPPERS' law of neurobiotaxis, as the posterior roots, on entering the cord, split into two bundles, one of which passes into the lateral funiculus. This bundle is strongly marked in snakes (cf. KAPPERS, 1920).

As far as concerns the gelatinous substance, it may be remarked, that it is also largest in the sacral region of *Dammonia*.

In snakes, Lissauer's zone is difficult to recognize on account of the number of closely packed fibres it contains. It is triangular in shape, with the apex narrowed to a point, and attached to the lateral aspect of the club-shaped head of the posterior horn. The posterior horns are united to form a horseshoe shaped structure, attached by a narrow neck to the anterior horns, as in birds (cf. fig. 8), and contain scattered masses of gelatinous substance.

Of birds, the following species were examined : — *Ratites* : *Casuarius australis*, and *Struthio camelus*.

*Carinatae* : *Athene noctua*, *Cacatua roseicapilla*, *Catharistes urubu*, *Ciconia alba*, *Columba domestica*, *Colynbus septentrionalis*, *Cyanistes coerulea*, *Cygnus olor*, *Gallus domesticus*, *Grus japonensis*, *Geranoaetus melanoleucus*, *Larus argentatus*, *Pavo cristatus*, *Podiceps cristatus*, *Sturnus vulgaris*, and *Spheniscus demersus*.

In the upper cervical region of birds (fig. 8, *Gallus*), the same general relations as in reptiles exist. Lissauer's zone lies on the surface of the cord as a narrow triangular band, with the base turned laterally. The deeper part of the zone, to which SINN (1913) gave the name "promontorium", stretches medially almost as far as the posterior funicular nuclei, and consists of a mixture of gray matter and finely myelinated nerve fibres. Its lateral is wider than its medial end, and it communicates, around the lateral extremity of the layer of coarse fibres, with the gray matter of the posterior horn.

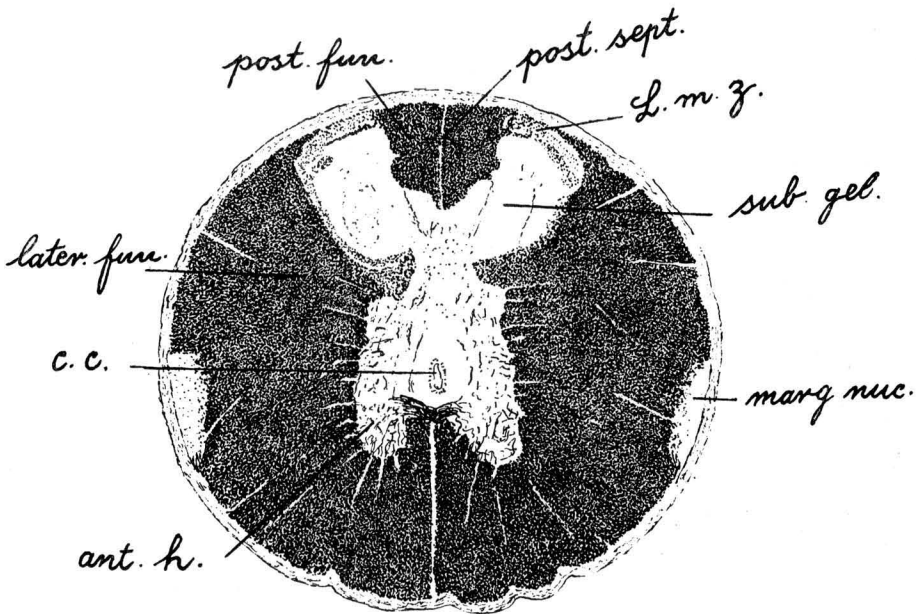


Fig. 8. Transverse section through the upper cervical region of the spinal cord of *Gallus domesticus*  $\times 43$ .

Lower down the cord, the substantia gelatinosa is still prominent. Lissauer's zone, in addition to its apical position, extends down on either side of the posterior horn, and especially on the lateral side in the case of the pigeon. In the cervical swelling of the pigeon, the posterior horn is spearhead-shaped. The body of the horn, ventral to the substantia gelatinosa, is constricted, but widens again somewhat at its attachment to the anterior horn. Lissauer's zone is triangular with its apex at the surface



of the cord, and its oblique base rests on the lateral side of the substantia gelatinosa.

In the thoracic region, the substantia gelatinosa forms a club-shaped mass at the extremity of the body of the posterior horn, while Lissauer's zone has a similar relation to that in the cervical swelling.

In the sacral region the anterior horns greatly predominate in size over the posterior, which project laterally as narrow protuberances, in which gelatinous substance is still recognizable. As in amphibians there is no marked increase in the substance in this region of the cord, so typical of higher animals, and also indicated in *Dammonia* (fig. 7).

Fig. 8, taken from the upper cervical region of the chick, shows the great development of the substantia gelatinosa at this level, where it completely fills the posterior horns. Lissauer's zone shows the same structure as in reptiles, but the layer of coarse fibres is very small, and the gelatinous substance nearly touches Lissauer's zone. The horns are united to form a horse-shoe shaped mass attached, by a constricted area of gray matter, to the anterior horn region, and resembling very much, in this respect, the appearance in snakes.

The posterior funiculi of birds are small, according to BROUWER (1915), and confirmed by KAPPERS (1920), forming only 7% to 8% of the total area of the white matter in the cervical region. In the same region in reptiles, the percentage is 13%. BROUWER believed that the decrease in the posterior funiculi was only relative to the great increase in the ventro-lateral tracts, but KAPPERS found, on comparing the posterior funiculi with the gray matter, that the posterior funiculi of birds are actually small.

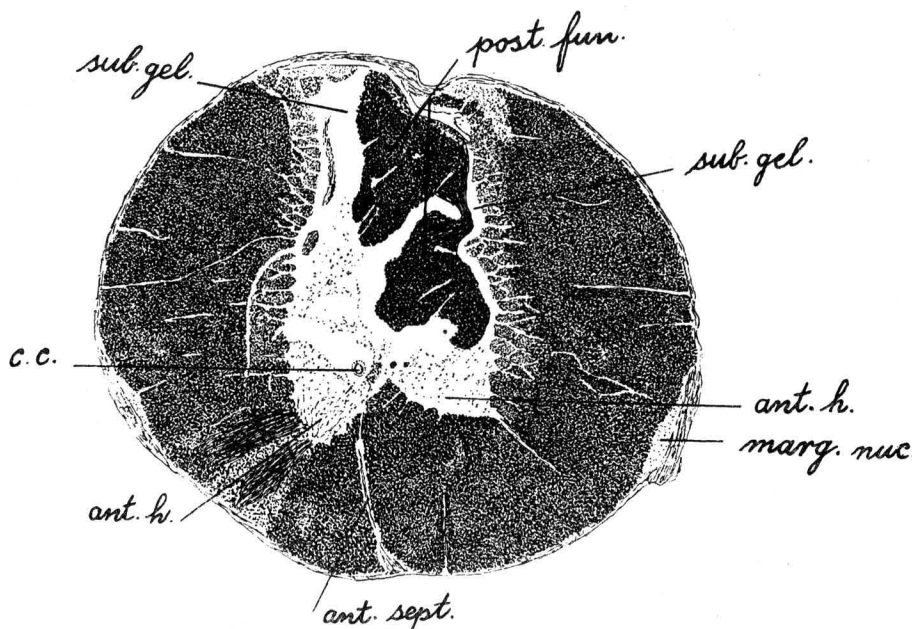


Fig. 9. Transverse section through the upper cervical region of the spinal cord of *Larus argentatus*  $\times 25$ .

Many of the species examined did not conform to the description given. Whether these irregularities are of the nature of heterotopies, or are, more or less, normal in these cords, I cannot, at the moment, say. In a specimen of the *swan* (*Cygnus olor*), as we pass from oblongata to cord, the gray matter resembles that of *Gallus domesticus* in appearance, but, on tracing the series downwards, the posterior horns unite to form a single backward projection, consisting mainly of gelatinous substance, and connected with the surface, on either side, by an ill-defined quadrilateral Lissauer's zone. The posterior funiculi are small and devoid of a posterior septum. Only some upper cervical segments were available for study.

In a specimen of *Larus argentatus* (figs. 9 and 10), I found a very marked irregularity of the posterior horn region, apparently not normal. In the lower end of the medulla oblongata, and in the first segment of the cord, the relations conform to the general description given. Below this, the posterior funiculi become very irregular. The posterior septum is indistinguishable, and masses of gray matter invade and surround the funiculi. The funiculi extend ventrally, in an irregular manner, into the anterior horn region, until an appearance like that in fig. 9 is produced. On tracing the sections caudally, the posterior funiculi become smaller and finally disappear, the gray matter having an arrangement more or less similar to that shown in fig. 10. Further caudally, in the gray matter at the periphery of the cord, there appears a bundle of fibres, which increases in size until it almost cuts off the club-shaped ends of the posterior horns from the rest of the gray matter. It diminishes in size again, and ultimately disappears (fig. 10).

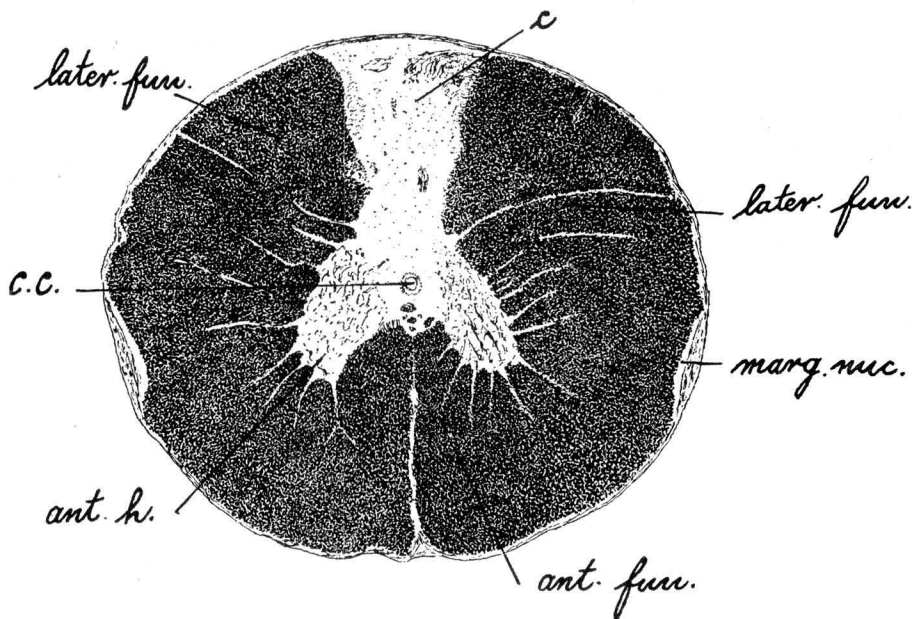


Fig. 10. Transverse section through the upper cervical region of the spinal cord of *Larus argentatus*, a short distance caudal to fig. 9,  $\times 25$ .

Just above the point of disappearance of the funiculi, a posterior root enters the cord.

A few sections caudally, two bundles of fibres appear in the gray matter at the surface of the cord, and grow in size and coalesce, continuing to grow until very slender, irregular posterior horns are produced. Here the available series ends. The greater part of the gray matter consists of irregularly-scattered gelatinous-looking material, fringed by finely myelinated fibres. The above changes take place over a range of about five hundred  $20\ \mu$  sections.

A somewhat similar phenomenon was observed in a specimen of the little owl (*Athene noctua*), and also in a specimen of *Geranoetus melanoleucus*.

### *Résumé.*

In *amphibians*, we find the first indication of a recognizable marginal zone of Lissauer. In fishes, fine and medium sized myelinated fibres are scattered through the gray substance of the posterior horn, and on either side of it, but their accumulation to form a single apical tract, such as exists in man, was not found. In the frog (*Rana catesbyana*), the fibres appear in the apical gray matter of the posterior horn as a widely separated but, nevertheless, recognizable tract. The substantia gelatinosa is on the whole poorly developed, but is present throughout the length of the cord, and extends from the apical area of fine fibres to the median septum in transverse sections, and is broken up into nuclear-like masses by coarse fibres. There is a gradual reduction in amount on tracing the sections caudally. The lumbo-sacral region of the cord does not show the marked increase in substantia gelatinosa which occurs in reptiles and mammals, or even so definite an increase as in *Albula vulpes*.

*Reptiles* show a marked increase in development of Lissauer's zone. The superficial part of the zone is more compact in structure than the deep part, which contains much gray matter and few, widely separated fibres. A layer of coarsely myelinated fibres intervenes between Lissauer's zone and the underlying substantia gelatinosa. This layer is incomplete in places, allowing a continuity between the gray matter of Lissauer's zone and that of the superficial part of the substantia gelatinosa. The deeper part of this layer of fibres pervades the superficial part of the substantia gelatinosa as small isolated bundles. This gives the appearance of a separate zone, consisting of small bundles of coarse fibres mixed with substantia gelatinosa. The deeper part of the substantia gelatinosa is more compact, and surrounds, posteriorly, the extremity of the body of the horn, as in mammals. In crocodiles, the substantia gelatinosa spreads down along the medial side of the horn, almost as far as the median septum. Caudally, in the sacral region, the substantia increases in amount as does also Lissauer's zone.

*Birds* show well developed substantia gelatinosa. Most species examined conform to the general type in reptiles, resembling, especially, the cord of snakes. They do not, however, show a marked increase in the sacral region.

Some irregularities were met with, the significance of which it was thought advisable not to attempt an explanation of at present.

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