

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

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When we examine a transverse section of the spinal cord of a higher vertebrate we can at once distinguish in the posterior horns certain well-marked areas. In man three subdivisions are described, the relations being as follows: the body of the posterior horn proper occupies the most central position, and is in direct continuity with the anterior horn ventrally; posterior to the body of the horn, and surrounding its extremity like a cap or cortex (KAPPERS, 1914) is the substantia gelatinosa Rolandi; extending from this region to the surface of the cord (the bottom of the postero-lateral sulcus) is Lissauer's marginal zone. This relationship exists throughout the cord, from the medulla oblongata above, where the gelatinous substance of the cord is continuous with a similar structure in relation to the descending root of the fifth cranial nerve, to the conus medullaris below.

The gelatinous substance has a closely massed homogeneous or jelly-like appearance, from which it derives its name. It is practically devoid of myelinated fibres, so that on treating by the Weigert-Pal method, especially if counterstained with paracarmine, it is clearly distinguishable from the rest of the gray matter.

Lissauer's marginal zone, with similar staining, is seen to contain widely separated fine and medium-sized medullated fibres. In addition, small nerve cells, and occasionally larger elements are present.

CAJAL (1909, 1911) attributes the gelatinous appearance of the substance to the rich network of dendrites of the small cells which crowd the area. These dendrites branch mainly in one level, parallel to the posterior surface of the cord. They rarely extend into the gray substance of the posterior horn proper.

The substantia gelatinosa, together with Lissauer's marginal zone, which is believed to be closely related to it functionally, has been extensively studied in higher vertebrates (HATSCHEK in the seal, 1896; DEXLER in the elephant, 1907; SANO in mammals, 1909; RANSON in man, Rhesus monkey, the cat, the rabbit, the albino rat and the guinea pig, 1913, 1914; etc.), and its form and position pretty well described. Researches in this direction in lower forms seem, however, to be almost entirely wanting, as substantia gelatinosa has not been recognised in the posterior horns, or, at any rate, has never been properly described as such.

In the following pages I set down the results of my observations in fishes, as part of a general phylogenetic survey.

The specimens used were from the large collection at the Central Dutch Institute for Brain Research, Amsterdam. The following is a list of the species examined during the progress of this section of the work :

- Amphioxus lanceolatus
- CYCLOSTOMES
 - Petromyzon fluviatilis
- GNATHOSTOMES
- SELACHIANS
- SHARKS
 - Hexanchus griseus
 - Acanthias vulgaris
 - Spinax niger
- RAYS
 - Raja clavata
- HOLOCEPHALIANS
 - Chimaera monstrosa
- GANOIDS
 - Calamoichthys calabaricus
 - Polyodon folium
 - Acipenser ruthenus
 - Amia calva
 - Lepidosteus osseus
- TELEOSTS
 - MALACOPTERYGII
 - Elops saurus
 - Megalops cyprinoides
 - Albula vulpes
 - Mormyrus cashive
 - Clupea harengus
 - Engraulis encrasicholus
 - Osmerus eperlanus
 - OSTARIOPHYSI
 - Erythrinus unitaeniatus
 - Cyprinus auratus
 - Blicca björkna
 - Leuciscus rutilus
 - Scardinius erythrophthalmus
 - Idus idus
 - Arius spec.
 - Malapterurus electricus

SYMBRANCHII

Symbranchus marmoratus

Monopterus javanensis

APODES

Anguilla vulgaris

HAPLOMI

Esox lucius

CATOSTEOMI

Gasterosteus aculeatus

Spinachia spinachia

Syngnathus acus

PERSECOCES

Scomber scomber

Thynnus alalonga

Belone belone

Exocoetus evolans

Ammodytes lanceolatus

Mugil chelo

Ophiocephalus spec.

ANACANTHINI

Motella mustela

ACANTHOPTERYGII

Perca fluviatilis

Osphromenus spec.

Pleuronectes limanda

Rhombus maximus

Solea vulgaris

Gobius minutus

Cyclopterus lumpus

Trachinus draco

Zoarces viviparus

PLEGTOGNATHI

Tetrodon spec.

DIPNOANS

Ceratodus forsteri

The cord of *Amphioxus*, the lowest vertebrate, is so primitive in character that a comparison of its parts with those of higher members of the phylum is not altogether possible. On cross section it is triangular in shape, with a concave base. The gray matter is massed around the central canal, and does not show any indication of anterior or posterior horn formations (cf. KAPPERS, 1920).

In *cyclostomes* the cord shows a higher development than in *Amphioxus*. It is flattened or ribbon-shaped. The gray matter extends laterally as a wing-like expansion on either side of the central canal. There is, thus, on each side but one mass of gray matter, so that the anterior and posterior horns of higher vertebrates are not marked out, but are combined in the undivided mass. Here, as in *Amphioxus*, owing to the absence of real posterior horns, conditions such as we have in the higher forms do not exist.

In *gnathostomes* there are certain broad general features which allow comparisons of its members to be made, notwithstanding great differences in the degree of development. The cord is rounded or oval, and the gray matter on either side shows anterior and posterior horns.

Among the *selachians*, the lowest fishes, we find in sharks an arrangement of the gray matter as shown in figs. 1 and 2.

In *Hexanchus griseus* (fig. 1) the well developed anterior horns run ventrally and laterally, in *Acanthias vulgaris* (fig. 2) chiefly laterally. The posterior horns pass backwards and laterally from an undivided mass of gray matter situated behind the central canal, which I shall call the *corpus commune posterius*, to within a short distance of the surface of the cord.

While the general shape of the posterior horns in these two sharks is practically similar, namely somewhat cone-shaped with the blunt apex separated from the surface by a narrow band of fibres, the arrangement of the details is slightly different. In both forms a small triangular band of fibres separates the diverging posterior horns from each other. This mass of fibres consists of the posterior funiculi of these animals, which are very small in comparison with those of mammals (BROUWER, 1915),

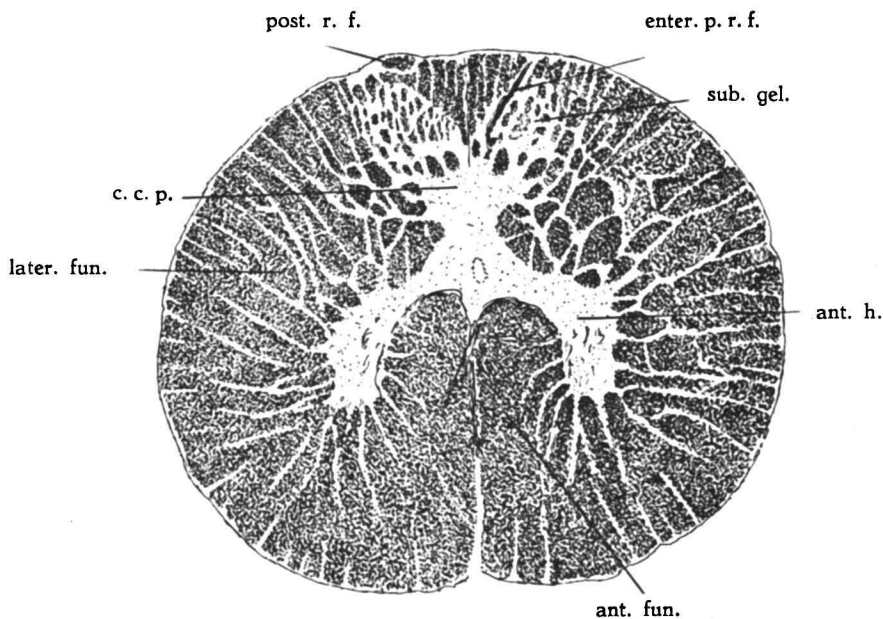


Fig. 1. Transverse section near the cranial end of the spinal cord of *Hexanchus griseus* $\times 17$.

ABBREVIATIONS FOR ALL FIGURES.

ant. fun., anterior funiculus.	interm. area, intermediate area.
ant. h., anterior horn.	later. fun., lateral funiculus.
ant. r. f., anterior root fibres.	Mauth. f., Mauthner's fibre.
c.c., central canal.	post. fun., posterior funiculus.
c.c.p., corpus commune posterius.	post. r. f., posterior root fibres.
enter. p. r. f., entering posterior root fibres.	sub. gel., substantia gelatinosa.
fasc. med., fasciculus medianus.	

and are not of the same nature. The columns of GOLL and BURDACH are either very small or are absent. The bulk of the posterior funiculi is formed

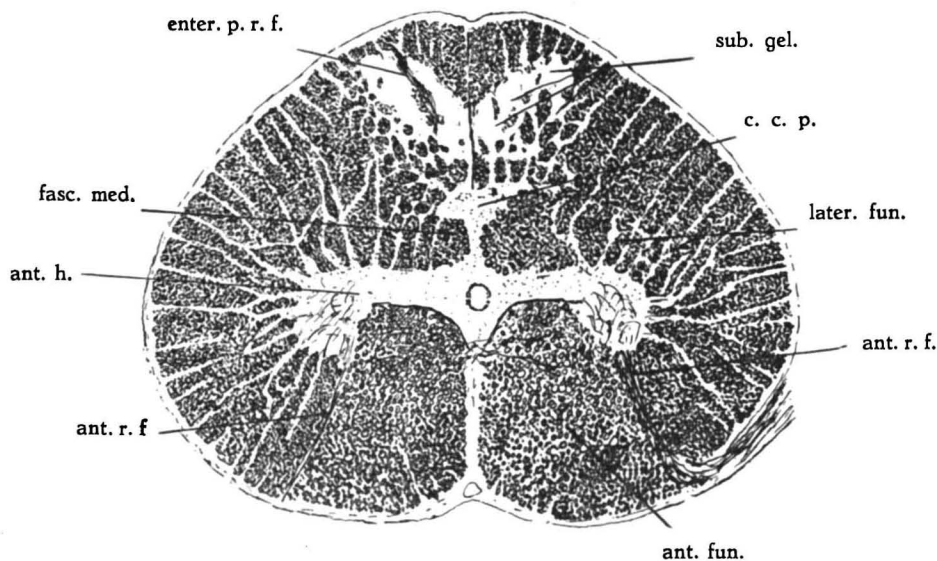


Fig. 2. Transverse section near the cranial end of the spinal cord of *Acanthias vulgaris* $\times 25$.

by descending axones of dorsal funicular cells (v. LENHOSSÉK, 1895), such as are still represented in man in the cornu-commisural bundle (cf. KAPPERS, 1920).

In *Hexanchus griseus* the most dorsal parts of both posterior horns are more separated, while the connection with the corpus commune posterius is broader than in *Acanthias vulgaris* (cf. figs. 1 and 2). In *Hexanchus* the corpus commune posterius is broad and prominent, and attached to the anterior horns by a wide stalk. In *Acanthias* this body is prominent behind, where it is continuous with the posterior horns. Ventrally it narrows until its connection with the anterior horns is drawn out into a slender stalk, on either side of which runs the fasciculus medianus, descending from the vestibular region of the oblongata. *Acanthias*, therefore, has an appearance as if the anterior and posterior horn regions were more pulled apart than in *Hexanchus*.

This is even more conspicuous in the case of *Spinax niger* where the stalk of connection is very much elongated.

The *posterior roots* enter the cord near the apex of the posterior horn, and run for some distance cranially, lying between the tip of the horn and the surface (the region corresponding to Lissauer's zone in higher vertebrates), where they are easily recognized because of their coarse appearance. They remain as a quite distinct bundle here, especially in *Hexanchus* (fig. 1). In *Acanthias* the root fibres spread out in a somewhat semi-lunar manner. They are more intimately mixed with the fibres at the

apex of the posterior horn. Further cranially, these root fibres pass ventrally through the substance of the horn towards its base. I have traced fine fibres from the posterior roots to the corpus commune posterius in *Spinax niger* and to the corresponding area in the ray *Raja clavata*, this animal being especially favourable because of the root entering through the lateral part of the horn, and of the fan-like expansion of the fibres towards their terminations so that the ventral expansion to the intermediate area is easy to follow (fig. 3). The coarse fibres could be traced to the longitudinal bundles which traverse the posterior horn where the greater part of them enter as ascending and descending fibres. These ascending and descending bundles are very small in comparison with the posterior columns of higher vertebrates (BROUWER, 1915).

In *Hexanchus* these intra-cornual longitudinal bundles are more numerous than in *Acanthias*. The posterior horns are completely broken up by small bundles, and at the base of the horn, at its junction with the corpus commune posterius, are a few larger ones; the latter are also well marked in *Acanthias*. The gray matter is continuous around the fibres as connecting strands, and on closer examination shows the characteristics of *substantia gelatinosa*. The entire gray matter of these horns is of this character.

In *Acanthias* the fibre-bundles are more compact and less numerous, so that the gray matter is collected into larger masses, and the gelatinous nature of the substance is easier to recognize, acquiring a greater similarity to the *substantia gelatinosa* of mammals. It is present in much larger quantities than in *Hexanchus griseus* or *Spinax niger*.

As far as could be ascertained there is no variation in amount at the point of entrance of the root fibres, but it approaches nearer the surface, probably on account of neurobiotactic influences. This is especially noticeable in *Acanthias vulgaris*.

It is clear, therefore, that these posterior horns differ in character from those of higher vertebrates, where the *substantia gelatinosa* forms merely a cap for the body of the posterior horn proper. We are led to the conclusion that the body of the posterior horn, so large in mammals, is very small in sharks, and chiefly represented in the undivided intermediate mass of gray matter, the corpus commune posterius. On tracing this intermediate mass of gray matter cranially it is found to divide, in the lower region of the medulla oblongata, into two parts, which become separated from each other by the opening out of the central canal to form the fourth ventricle. Each subdivision becomes continuous with the commissural nucleus of the vagus on its own side. This would seem to indicate a visceral association for the column, which assumption is further strengthened by the fact that in several species (*Spinax niger*, *Chimaera monstrosa*, *Raja clavata*) fine fibres from the posterior roots could be traced into it.

The fibres at the apex of the posterior horns do not show the characteristics of those of Lissauer's marginal tract as described for mammals. They are coarser, more heavily myelinated, and more closely packed together.

That they are not of the same nature is probable. At any rate the posterior roots do not contribute fine medullated fibres to this region, as can be seen to occur in higher animals.

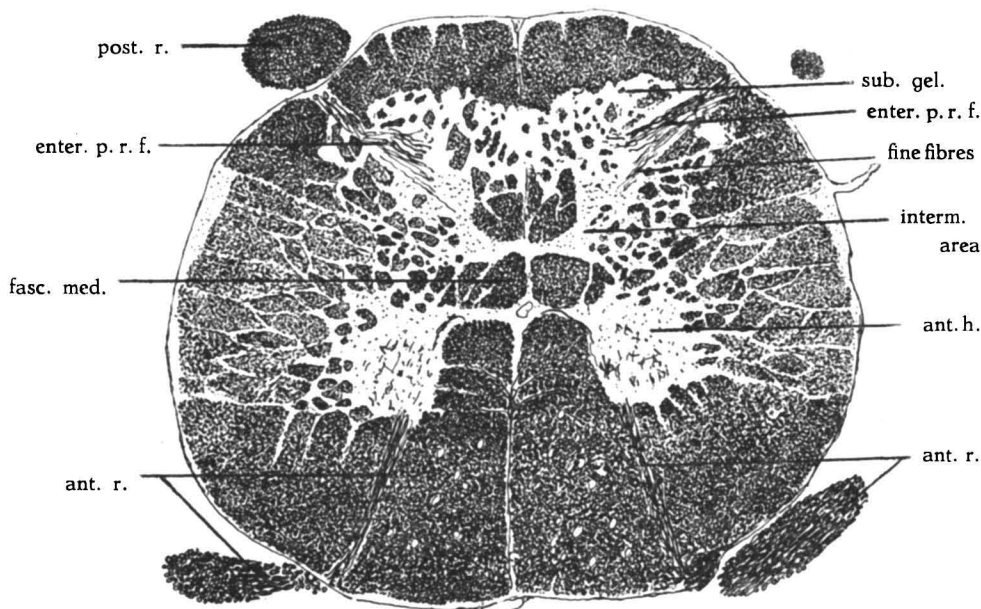


Fig. 3. Transverse section near the cranial end of the spinal cord of *Raja clavata* $\times 18$.

In the ray, *Raja clavata*, the substantia gelatinosa is well developed (fig. 3). The intermediate mass has become drawn apart into the lateral wing-like expansions which are continuous with the substantia gelatinosa on either side, so that a greater resemblance to the posterior horn of higher animals is produced, the more so, as each intermediate wing also connects with the anterior horn. The fasciculi mediani are closely approximated between this region and the anterior horns, and in consequence the connecting gray matter is reduced, as in *Acanthias vulgaris* and *Spinax niger*, to a narrow strand.

The substantia gelatinosa occupies a somewhat quadrilateral area, and is well pronounced, though broken up by groups of fibres as in lower forms. The long axis of this mass is placed transversely, and extends from the posterior septum medially to within a short distance of the cord laterally. The posterior border is slightly convex. At the posterior septum the mass comes into contact with that of the opposite side. In many places the septum is absent, and there is a structural continuity.

A wide band of fibres separates the horn from the dorsal surface of the cord. This narrows laterally where the postero-lateral angle of the gelatinous substance comes nearer the surface, and at this point the root fibres enter. These as stated above spread out fan-like in the posterior horn, the most ventral fine fibres running towards the lateral wing of the

intermediate mass, while the remainder becomes associated with the longitudinal bundles which traverse the horn.

Chimaera monstrosa, which exemplifies the condition in the *holocephalians*, resembles the sharks more closely than the rays (fig. 4). The corpus commune posterius approaches closer in type to that of *Hexanchus* than of *Acanthias*.

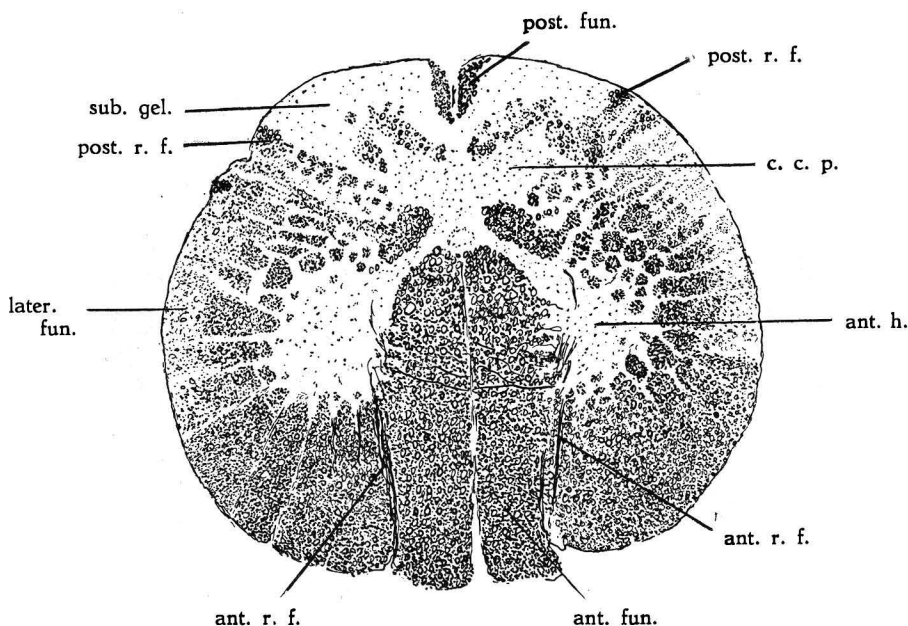


Fig. 4. Transverse section near the cranial end of the spinal cord of *Chimaera monstrosa* $\times 25$.

The limits of the area of substantia gelatinosa are somewhat hard to define owing to the slight staining of the specimen. The fibre bundles which in other species are scattered irregularly through the horn are here more compact. The posterior root fibres enter at the lateral angle of the area, and pass through the lateral part of the horn towards the region of the fibre bundles.

In view of the demonstration by RANSON (1911, 1913) of unmyelinated fibres in the peripheral nerves and posterior roots of mammals, and the importance he attaches to them as being the chief supply to the substantia gelatinosa, I examined a specimen of *Chimaera monstrosa* stained by Cajal's silver method to determine if similar relations exist here.

In the cat, RANSON (1913) points out that the posterior root on entering the cord divides into two parts; a lateral, consisting mainly of unmyelinated fibres but having also a few finely myelinated, which passes through Lissauer's zone and enters and ends in the substantia gelatinosa, and a medial which enters the posterior funiculus and is distributed in the manner generally described for the posterior root.

I was unable to find a similar state of affairs in this specimen. In the Weigert-Pal preparation the cord is very poorly stained, especially laterally and dorsally, and this applies also to the posterior roots where only a few lightly stained fibres can be seen

(fig. 4). In the silver preparation these lightly stained areas take on a dark colour owing to the number of closely packed axones present. The posterior root shows a great increase in fibres and on tracing these into the cord they traverse the lateral part of the horn, remaining a compact bundle until they reach the fibre bundles which run longitudinally through the base of the substantia gelatinosa, with which the majority of them becomes associated. Some fibres pass ventrally towards the corpus posterius. There is no separation into distinct myelinated and unmyelinated parts.

The *ganoids* present even greater differences among themselves in the structure of the cord than the selachians. Generally speaking, they approach more closely in development to that of higher forms, but many members of the group present features characteristic of selachians. *Acipenser ruthenus*, especially, resembles *Hexanchus* in the structure of the corpus commune posterius.

The posterior horns are somewhat quadrangular on section. The substantia gelatinosa is easily identified from the surrounding gray matter, and occupies the entire posterior projection or horn. It is in contact with the white matter along a very irregular line, especially towards the periphery where it sends expansions dorsally, thus presenting a dentated appearance. It is separated from the posterior septum by a small accumulation of fibres. Within this posterior horn the gelatinous substance has a closer relation to that of higher forms than is the case with selachians. It is massed into irregular accumulations practically devoid of myelinated fibres. Between these nuclear-like masses and in linear arrangement are bundles of myelinated fibres.

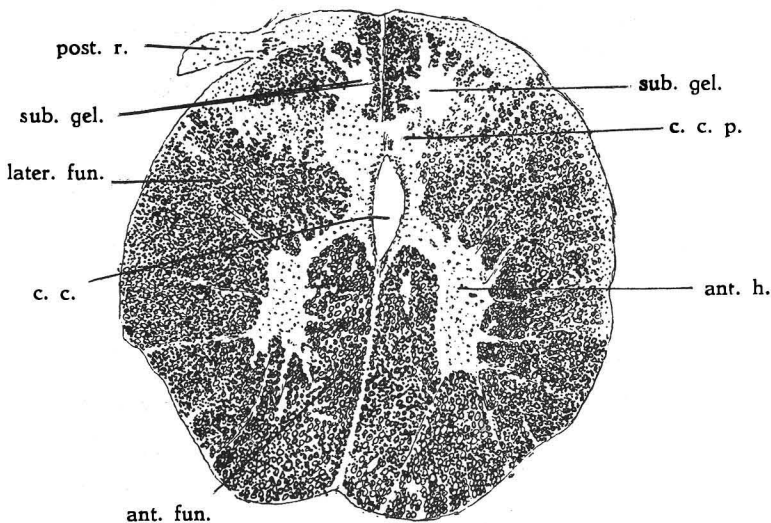


Fig. 5. Transverse section near the cranial end of the spinal cord of *Polyodon folium* $\times 90$.

Polyodon folium resembles the last mentioned very closely (fig. 5). The substantia gelatinosa is easily delimited because of its flowing together to form a single mass devoid of myelination. It is very irregular in outline

especially towards the periphery, and here also the dorsal projections are marked. It is not so abundant in *Polyodon* as in *Acipenser*. In *Amia calva* it approaches very closely in arrangement to that of the teleosts. The gray matter is arranged in a *H*-shaped manner as in higher forms (fig. 6), so that the corpus commune posterius of lower forms has disappeared as such, and merges with the surrounding gray matter. The posterior horns are very large pear-shaped structures, with the wide end directed dorsally and slightly laterally, and the narrow end or stem continuous with the anterior horns on either side of the central canal. As in the types already described they consist of gelatinous substance, merely a small area at the central end being of different structure, so that the substance in this animal reaches very great development. Medially a triangular mass of fibres, with the base directed ventrally, separates the horn from the posterior septum. The narrow apex is continuous with the fibres which cover the horns dorsally. The great massing of substantia gelatinosa within the horn produces a bulging on the surface and causes a distinct posterior fissure. Laterally a depression is formed between this bulging mass and the ventrolateral part of the cord, from the bottom of which a small septum projects inwards.

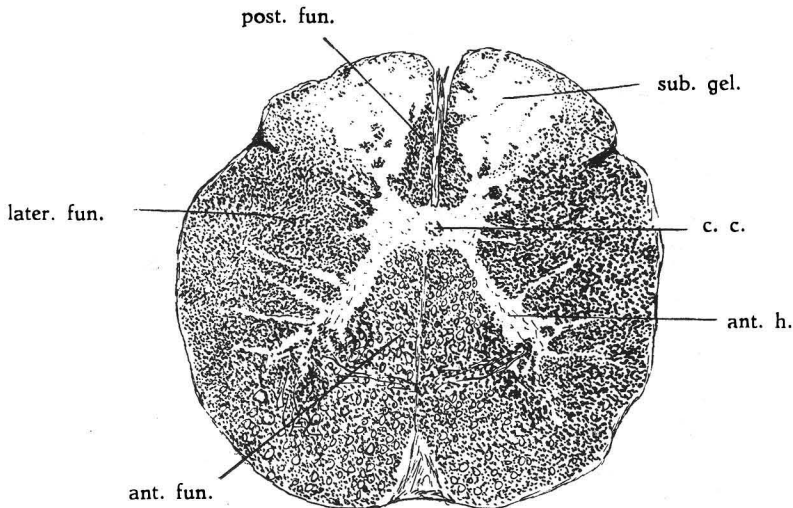


Fig. 6. Transverse section near the cranial end of the spinal cord of *Amia calva* $\times 37$.

The arrangement of the substantia gelatinosa within the horns, as in many teleosts, is in small masses, which may be partly or completely surrounded by myelinated fibres, the whole arrangement presenting the appearance of an accumulation of several "nuclei". The fibres may surround these in a concentric manner, and in many cases, especially in certain teleosts, a hilum-like arrangement is present through which fibres can be seen to pass. In other cases the substantia gelatinosa is folded around a

central core of fibres ("internal cortical lamination" of KAPPERS, 1914). In this species masses are indicated as forming clumps but are not surrounded by fibres.

The posterior roots enter the cord near the lateral edge of the posterior horns, where they divide into ascending and descending branches, and become indistinguishable from the covering fibres.

In two other species of this group examined, *Calamoichthys calabaricus* and *Lepidosteus osseus*, the substantia gelatinosa is present in medium quantity and development. *Lepidosteus* deserves special mention because of its resemblance to *Spinax niger* and *Acanthias vulgaris* in the arrangement of the corpus commune posterius, its attachment to the anterior horns being reduced to a narrow strip.

The great class, *teleosts* including, as it does, animals of such varied appearances, sizes and modes of life, presents many differences in the structure of the cords, some of which, indeed are so marked as scarcely to allow of a typical description (cf. *Albula vulpes* and *Osmerus eperlanus*). Looked at from the point of view of the presence or absence of gelatinous substance and its relations to the posterior horns such a typical description will perhaps suffice.

The teleosts are sometimes described in common with the ganoids under the heading Teleostomi, but, owing to the primitiveness in arrangement of the substantia gelatinosa in most members of the ganoids and the general resemblance to sharks, I have described them under separate headings.

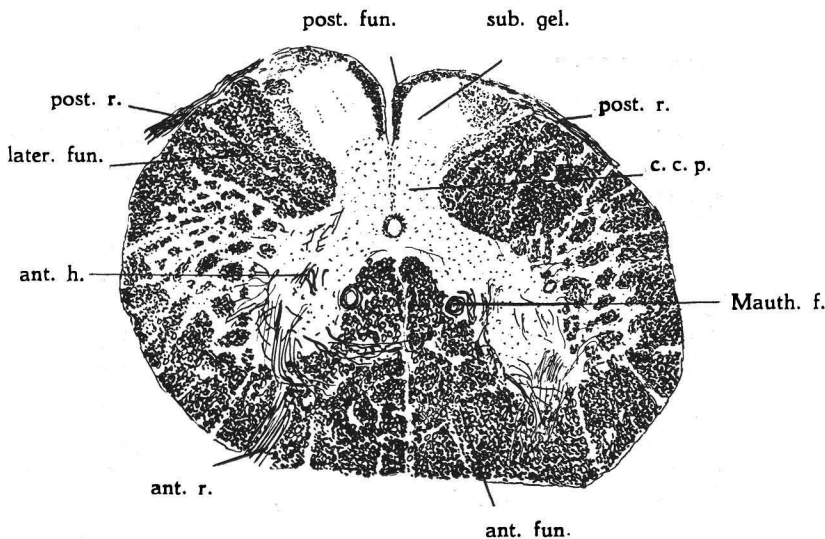


Fig. 7. Transverse section near the cranial end of the spinal cord of *Esox lucius* $\times 76$.

The teleost cord as represented by *Esox lucius* is shown in fig. 7. The gray matter has not reached the typical H-shaped arrangement seen in higher animals. In fact in regard to this character it appears more

rudimentary than *Amia calva*. The anterior horns are (as in still lower forms) separate structures, though much broken up at their ends. The dorsal region of the gray matter is made up of two oval masses (the posterior horns) united ventrally by a single mass of gray matter (the intermediate area or corpus commune posterius). The latter area in many cases shows an indication of division by means of a septum, represented in some places by a few indifferent cells. The corpus commune posterius is continuous, around the central canal, with the anterior horns.

The posterior horns diverge slightly from each other. They are covered medially by a narrow layer of myelinated fibres which is continuous round the posterior surface to the point of entry of the posterior roots. Laterally the horn is ill defined, being broken up by scattered coarse and fine fibres. It consists chiefly of gelatinous substance which is arranged in one large mass traversed here and there by fibres, coarse and fine. The posterior roots approach the cord laterally and run dorsally to the lateral angle of the posterior horn, where the greater part of the fibres continue towards the posterior funiculus; a small part, however, enters lateral to the substantia gelatinosa (cf. HERRICK, 1907; KAPPERS, 1920; and VAN DER HORST, 1927).

In many teleosts the arrangement of the gelatinous substance is not so simple as in *Esox lucius*. VAN DER HORST (1927) in describing this area in *Albula* says "Here the nucleus exhibits the peculiarity that it does not form a more or less compact mass as is usually the case in teleosts, but has the form of a rather thin curved lamella. Thus, it assumes a form similar to the lower olive and other, especially sensory, areas that enlarge their surface by making folds."

This curving of the mass and even isolation of parts by fibre masses occurs in many teleosts. In *Erythrinus unitaeniatus* the condition is well marked. In *Osphromenus* the isolated masses are partly or completely surrounded by fibres, many of which run circularly.

These foldings occur especially in animals in which the substance is well developed. The phenomenon also occurs amongst the mammals, especially the ungulates.

It is worthy of note that in teleosts as in lower fishes, the gelatinous substance practically fills the posterior horns. The body of the horn in mammals, therefore, in so far as it is present in fishes is very small, and seems to be represented only in the corpus commune posterius.

The relation between these parts in fishes and mammals demonstrates the great preponderance of substantia gelatinosa in the lower forms. *Albula vulpes* is a particularly good example of this relation, as here it reaches a development not approached by any other species examined, while the corpus commune posterius is reduced to a small area dorsal to the central canal.

Whereas part of the body of the posterior horn in mammals is probably represented in this undivided mass in fishes, still this part is very small.

This probably has to do with the small amount of projection fibres to the cerebellum and mesencephalon that arise in posterior horn cells. To this may be added that the epicritic (HEAD, 1905) or gnostic (KAPPERS, 1920) sense, that in mammals is connected with the posterior horns by collaterals of the posterior funiculi, is poorly developed in fishes.

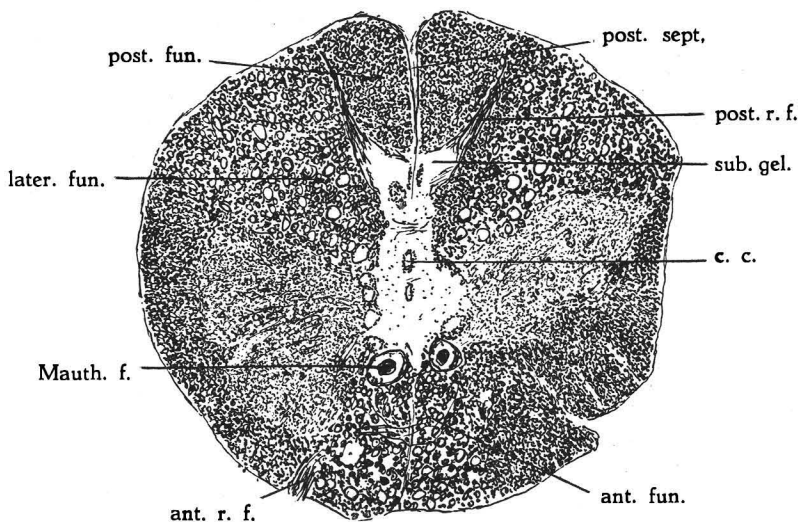


Fig. 8. Transverse section near the cranial end of the spinal cord of *Osmerus eperlanus* $\times 76$.

As a contrast to *Esox lucius* I figure the cord of *Osmerus eperlanus* (fig. 8).

The substantia gelatinosa is easy to recognize but is poorly developed, and separated from the surface of the cord by a wide band of fibres.

The posterior roots can be seen passing to it, and in the region of the posterior horns separate into dorsal and ventral divisions which enfold the gelatinous substance. The horns themselves are not well formed. They lie on either side of the posterior septum, and are free only in the apical regions. The corpus commune posterius is very conspicuous and has a quadrilateral outline.

Regarding the degree of development in the other teleosts I may say that a reliable standard of comparison is difficult to fix owing to the differences in size and general relations in some of these cords. SANO (1909) recognized the same difficulty in mammals, where he compiled tables of measurements of the area of transverse section of the cord, the entire gray matter, the posterior horns, and the substantia gelatinosa, and worked out the interrelations of these several parts. It is doubtful if even this is complete without an examination of the constituents of the posterior roots, and the skin areas they supply.

Albula vulpes is remarkable for the very great development of its substantia gelatinosa, and it is noteworthy that some form of cutaneous

sensibility seems to be especially developed, as appears from the fact that a large cutaneous branch of the facial nerve occurs in this fish (VAN DER HORST, 1927). *Albula* is the only teleost in which such a branch has been so far described. The presence may add to the great development of the substantia gelatinosa in the cervical cord of this animal. Perhaps in the sensory spinal roots a similar increase of analogous fibres occurs that may be responsible for the strong development of this substance throughout the cord.

After *Albula*, and somewhat in the following order with regard to development of the substantia gelatinosa come *Mormyrus cashive*, *Osphromenus spec.*, *Pleuronectes limanda*, *Mugil chelo*, *Gobius minutus*, *Ophiocephalus spec.*, *Perca fluviatilis*, *Esox lucius*, *Megalops cyprinoides*. All these show well-marked gelatinous substance. Those showing least development are *Zoarcas viviparus*, *Motella mustela*, *Idus idus*, *Osmerus eperlanus*, *Monopterus javanensis*, and *Malapterurus electricus*, while the general body may be described as intermediate in development.

A perusal of the list will show that this order is very irregular in regard to the classification given.

Most of my observations were made on sections of the cranial end of the spinal cords. In some teleosts a larger part of the cord was available, and in *Albula vulpes* I had an opportunity of studying the cord in its entire length. At the cranial end, where the descending fibres of the trigeminal, facial, and vagus nerves are still present, the substantia gelatinosa is very massive, occupying a little less than half the entire section (cf. also VAN DER HORST, 1927). It presents here two or more folds. Below the point of disappearance of trigeminal, facial, and vagal fibres it decreases considerably in size, and there is an accompanying simplification in the folding. Traced caudally, there is a gradual reduction of the gelatinous substance until the tail region is reached, where again a slight increase occurs. This is in accordance with what is generally known concerning the sensibility of the cord of fishes viz., that the head region is the most sensitive, after it the tail, the body being the least specialized. The cord of fishes is not complicated, as in higher forms, by cervical or lumbar enlargements. Notwithstanding the reduction, the development in the tail region is still considerable (fig. 9), exceeding in fact that of the cranial region of most forms. The arrangement in this region is, however, relatively simple, merely a single fold around a core of slightly myelinated fibers. The root fibres behave as in *Esox lucius*, dividing into two parts, the larger running dorsal and the smaller lateral to the horn. The dorsal passes round the substantia gelatinosa and some of its fibres reach the posterior funiculus which, in the interval between the roots, is an isolated bundle.

Finally in fig. 10 I give the condition in the *Dipnoi* as represented by *Ceratodus forsteri*. The cord appears fairly high in type though it still presents characteristics which betray its lowly connections. The gray

matter, however, shows a more typical H-shaped arrangement than in any other fish. The medial part of the corpus commune posterius is reduced in the region of the dorsal gray commissure. Its lateral parts are probably incorporated in the posterior horns which are very simply constituted. They

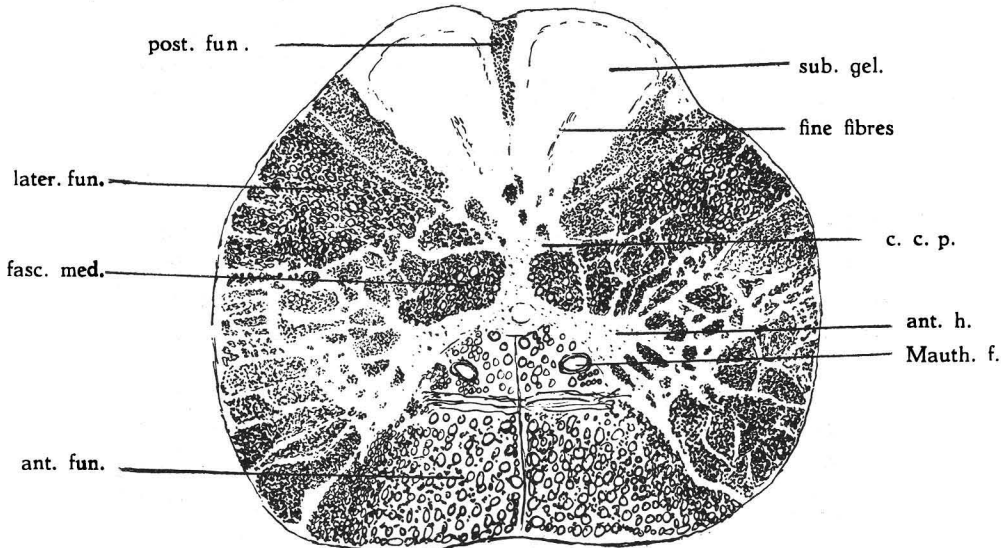


Fig. 9. Transverse section near the caudal end of the spinal cord of *Albula vulpes* $\times 51$.

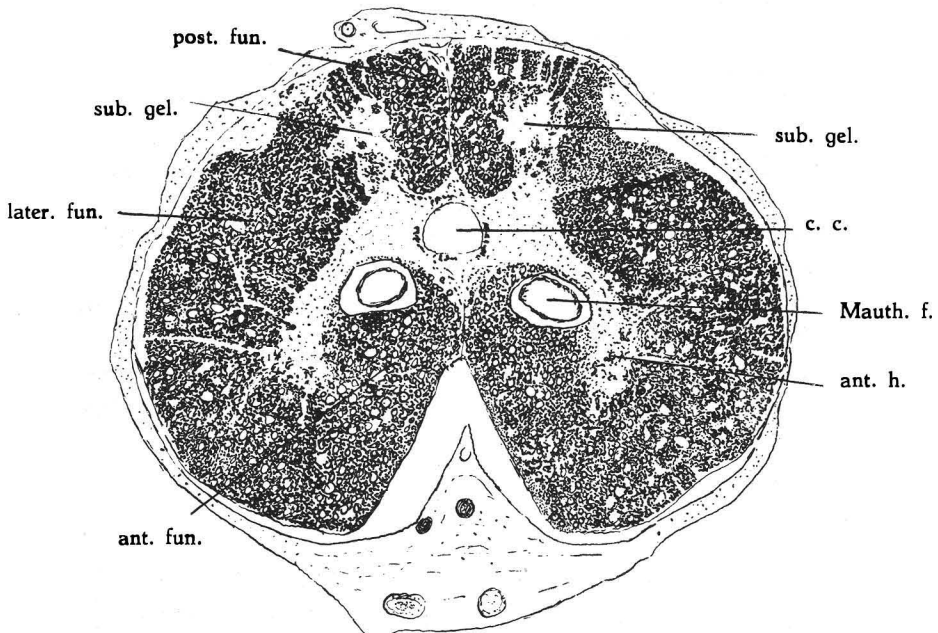


Fig. 10. Transverse section near the cranial end of the spinal cord of *Ceratodus forsteri* $\times 33$.

consist of an irregular mass of gelatinous substance on either side, which is almost isolated from the rest of the gray matter by a layer of medullated fibres situated at the neck.

The posterior funiculus is more massive than in teleosts, and reminds us of the condition in frogs (cf. KAPPERS, 1920, fig. 75). The horns are separated from the surface by a fairly wide band of fibres. Though the development of the substantia gelatinosa is not as extensive here as in most teleosts, it is still the ground-work of the posterior horns.

RESUMÉ.

A study of the posterior horn region of the cord of lower vertebrates gives us an idea of the principles on which that of higher forms is evolved. Beginning with *Amphioxus*, we find a very rudimentary condition, in which horn projections are not even indicated. In *cyclostomes* a single mass is present on either side.

The *fishes* show the beginning of the condition found in higher forms. The anterior horns are definitely indicated, though not sharply defined, and are usually broken up at their ends. The posterior horns are rudimentary projections from a single mass of gray matter which lies dorsal to the central canal. This body I have designated the *corpus commune posterius*. It is present throughout the different groups of fishes, though in various degrees of development. In *Raja clavata*, *Amia calva*, and *Ceratodus forsteri* it is much reduced, and replaced by bilateral structures, in which respect they resemble the higher forms. Still the posterior horns differ essentially in structure from that described for man. Whereas, in the latter, three areas may be distinguished from the centre to the periphery — body of the posterior horn, substantia gelatinosa Rolandi, marginal zone of Lissauer — the posterior horns of fishes mainly consist of substantia gelatinosa. The bodies of the horns of higher forms are (in part at least) represented in the corpus commune posterius. That this has chiefly a visceral function is probable from the facts (1) that cranially it becomes continuous with the commissural nucleus of the vagus in the medulla oblongata, and (2) that fine medullated fibres from the posterior roots can be traced to it.

A comparison of the relations between the body of the posterior horns and the substantia gelatinosa in mammals, and of the corresponding areas in fishes demonstrates the small size of the body of the horn and the great size of the gelatinous substance in the latter. In *Albula vulpes* this is especially striking. In the cranial end of the cord it almost fills the posterior horns, and occupies nearly half the total area of cross section. While according to SANO's tables, on the same level in man it occupies half the posterior horn, and about one-thirty sixth of the entire cross section.

Another difference between the posterior horns of fishes and mammals is that in the latter they are pushed far apart by the accumulation of fibres

to form the columns of GOLL and BURDACH in the posterior funiculi. In the former where these columns are small the horns lie close together; where the fibres are absent they are separated merely by the posterior septum, and even this may be wanting, so that they are structurally continuous.

What is the function of this nucleus, so prominent in lower forms but which loses in relative size in the higher animals? SANO (1909) concluded it could not have a wholly cutaneous sensory function because he found it best developed in mammals which were not at the top of the scale of sensitivity. He suggested a sympathetic function, but found little support, even in his own work for such an assumption.

In fishes which present well-developed substantia gelatinosa there is usually evidence of great cutaneous stimulation (Albula). Amongst those of poor development the reverse seems to be the case.

These results appear to support the view of RANSON (1915) that this substance is related to primitive sensation (protopathic of HEAD, 1905; vital of KAPPERS, 1920). As vital sensation is probably the only kind in fishes, we should expect variations in the nucleus in the same directions as skin sensibility. I intend, however, to discuss this subject more fully in a subsequent contribution.

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