Anatomy. — *"The meninges in Cyclostomes, Selachians, and Teleosts, compared with those in man."* By Dr. C. U. ARIËNS KAPPERS.

The meninges in lower vertebrates are very different from those in mammals and man.

Though formerly — mislead by superficial resemblances — also in Cyclostomes and Plagiostomes, a dura mater, arachnoidea and pia were supposed to exist, at the present time this supposition is only maintained in the "Mikroskopische Anatomie der Wirbeltiere (Heft IV)", published in 1923, by R. KRAUSE, who however does not seem to have studied this subject very accurately.

Already in 1884 SAGEMEHL (l. c.) pointed out that a real arachnoidea does not occur in fishes, and that the widelymeshed tissue formerly considered as such, really lies between the so-called internal and external (periostal) dural membrane, and STERZI [1] (l. c. 1900—1901) in his comparative anatomy of the meninges emphasized that in Cyclostomes and Plagiostomes only one undifferentiated meninx is found, which he called *meninx primitiva*, and considered to be the origin of the dura, arachnoidea and pia in higher animals.

My own researches confirm STERZI's opinion regarding Cyclostomes and Selachians. It has however to be emphasized that only the internal dural membrane develops from the meninx primitiva, the external or periostal dural membrane originating from the endostal (or endochondral) connective tissue that generally in lower vertebrates lies at a great distance from the meninx primitiva, and consequently far from the origin of the internal membrane. In my opinion it is better (c. f. also GEGENBAUR [2]), POIRIER and CHARPY [3]), TESTUT [4]), STERZI [5]) and RAUBER [6])) not to

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[1] STERZI. Ricerche intorno all' anatomica comparata ed all' ontogenesi delle meningi. Atti del reale instituto veneto di scienze, lettere ed arti. Anno accademico 1900—01. Tomo 60. Parte II.

See also: STERZI. Recherches sur l'anatomie comparée et l'ontogénèse des meninges. Archives italiennes de biologie, Tomo 37, 1902.

[2] GEGENBAUR. (Lehrbuch der Anatomie des Menschen, 6te Auflage 1896, Bnd. II, Page 441) speaks of the „von der inneren Lamelle gebildete eigentliche Duralsack des Rückenmarkes".

[3] POIRIER et CHARPY. Traité d'anatomie humaine, Tome III, Iier fasc. Paris, 1901, p. 107.

[4] TESTUT speaks of the internal membrane as „dure mère propement dite". See: Traité d'anatomie humaine, 6ième Edition, Paris 1911, p. 1050—1061.

[5] STERZI. Intorno alla divisione della dura madre dell' endocranio. Monitore zoologico italiano, Anno XIII, 1902.

[6] Also RAUBER in his Lehrbuch der Anatomie des Menschen (1e Auflage 1903, Bnd. II,

C. U. ARIËNS KAPPERS: "The meninges in Cyclostomes, Selachians and Teleosts, compared with those in man".
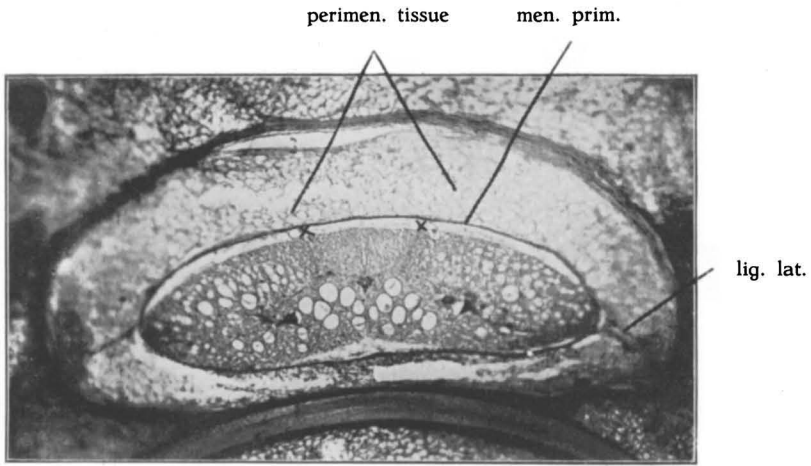

Fig. 1. Spinal cord of Petromyzon in situ
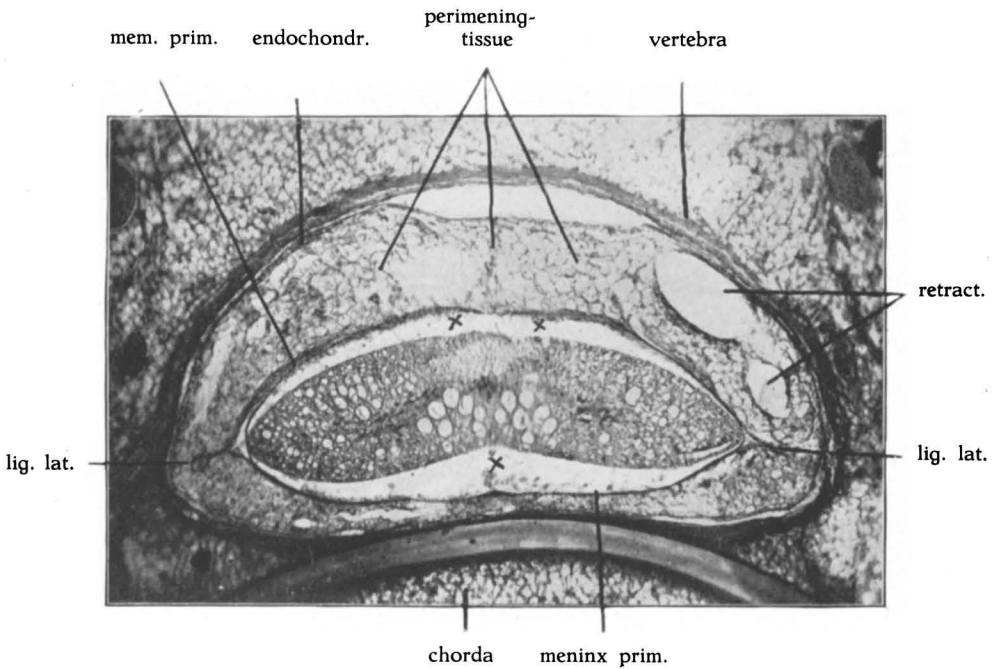x x Space between meninx primitiva and cord, caused by retraction.

Fig. 2. Spinal cord of Petromyzon in situ.
x x x Spaces caused by retraction.

consider the so-called external or periostal membrane of the (spinal) dura (which follows all the sinuosities of the bone) as a part of the dura proper, though it fuses with it in the cranial cavity in the adult (after an embryonic condition in which it may be distinguished from it).

The distinction of a periostal and an internal layer in the dura mater spinalis only leads to confusion and to the idea of an ambiguous membrane, which ambiguity disappears by leaving the so-called periostal dural membrane there, where it belongs after its nature and origin, viz. to the connective tissue of the endochondrium or endost and not to the dura.

Concerning the Cyclostomes, I found in Petromyzon fluv. (fig. 1 and 2) relations, as described by STERZI.

The medulla spinalis is surrounded by a single membrane in which no differentiation into separate layers is visible. I call this membrane, with STERZI, meninx primitiva. It is continuous with the sheath of the roots.

This membrane, which shows strong lateral ligaments extending far laterally into the perimeningeal tissue (fig. 1, 2) does not yet penetrate with septa into the substance of the spinal chord, so that the membrane easily detaches (XX) from the cord. The nutrition of the spinal cord has to pass everywhere through the superficial glious layer (limitans superficialis) [1]), there being no intramedullary septa and intramedullary vessels.

Outside this meninx primitiva, which, as I shall show later on, also contains the anlage of the dura mater (in the sense of the word mentioned above) lies a broad layer of large cells, which is to be considered as a filling-tissue and reaches as far as the endochondrium of the vertebrae.

This perimeningeal tissue consists of round and oval mucous cells.

In some of my preparations spaces occur, that look like epidural sinusses, which also in human embryos (v. GELDEREN l.c.) are found between the so-called interior layer of the dura and the so-called periostal layer. I could not find however traces of blood here. They are also more or less local spaces that do not spread over a great length. As I could not find any connection with the venae invertebrales, they probably are retraction cavities (caused by the fixation).

The relations in Plagiostomes do not show much difference herewith.

p. 337) speaks of "Lamina interna oder Dura spinalis in engerem Sinne". A similar opinion is given in CUNNINGHAM's Textbook of Anatomy (3d Ed. 1909, page 600).

[1]) Already in Selachians, meningeal septa with bloodvessels grow into the spinal cord, causing a closer relation between the nervous substance and the vascular system. As however the limitans gliosa superficialis grows at the same time with those septa, a real penetration of meningeal tissue into the nervous substance itself does not occur. In fact the septal spaces are to be considered as the fissures in the forebrain, with this difference that they are much smaller and for the greater part filled up with pia tissue, while the arachnoidal cavities in the brain fissures are much wider and go further downwards. They also resemble each other by the fact that the dura remains outside them, in the brain, as well as in the spinal cord.

In Scyllium I also found only one meninx, to be called meninx primitiva, in which no differentiation in separate layers is visible. It contains small blood vessels, that penetrate with meningeal septa into the spinal cord.

Moreover the sharks show the four spinal ligaments already described by STERZI: the rather strongly pronounced lateral ligaments (fig. 3 and 4), and the thinner, often scarcely developed, dorsal and ventral ligament. Only the lateral ligament extends for some distance through the perimeningeal tissue. The others are merely thickenings of the meninx primitiva. Besides this meninx primitiva which just as in Cyclostomes, continues in the rootsheath, a large amount of peri-meningeal tissue is found which reaches as far as the endochondrium and shows much more widely spread meshes than in Cyclostomes.

Only here and there — especially in the neighbourhood of the endochondrium — it is a little more compact (fig. 4).

Large thinwalled veins (without muscular coat) are seen in the perimeningeal tissue, especially on the dorsal and lateral side. There is no doubt as far as concerns their homology with the so-called epidural veins in mammals and man, though they are relatively much larger and therefore resemble sinusses. [1])

The relations in Ganoids (Acipenser and Polyodon) are similar to those in Selachians: so I shall not describe them again.

My researches concerning the relations in the most specialized group of fishes, the *Teleosts*, show that there are in this subdivision large differences in meningeal structure that *might* explain the rather different descriptions present in litterature, if the chief and rather different descriptions — those of SAGEMEHL and STERZI — were not both based partly on the same material.

STERZI (l.c. I, page 1142) examined especially Tinca and further Cyprinius, Esox, *Barbus*, Muraena, Anguilla, Rhombus, Solea and Labrax, and found everywhere under the generally perimeningeal tissue only one meninx, which he calls meninx primitiva, just as in Cyclostomes and Plagiostomes.

He distinguishes therein two layers, an exterior and interior layer. The *exterior layer* is very thin and consists almost entirely of large flattened cells, more or less pigmented. Further there are star-shaped cells and some cells with long offshoots and connecting ramifications. Between them there are some pigmentcells. In this layer also some elastic fibres are seen. He does not speak of a fibrous thickening of this exterior layer which might indicate a dural development.

The interior layer is more developed. On this [2]) (in this ?) layer, the bloodvessels occur that supply the medulla. It consists of connective tissue fibrils and elastic fibres, crossing each other in different directions.

He further mentions the ligaments and remarks that the sheath of the meninx continues in the rootsheath.

Concerning the perimeningeal space, he remarks that the latter is well developed dorsally

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[1]) Similar large epidural veins occur in Carnivora, Edentates, Cetacea and Elephas, where the epidural space still prevails on the arachnoidea.

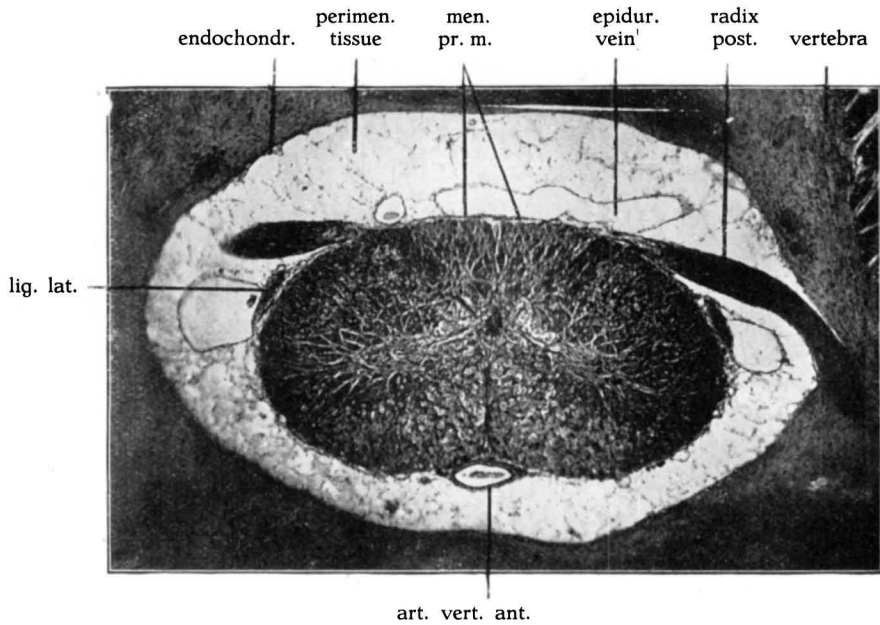[2]) The author (l.c. page 1143) says: "Su di esso poggiano i vasi."

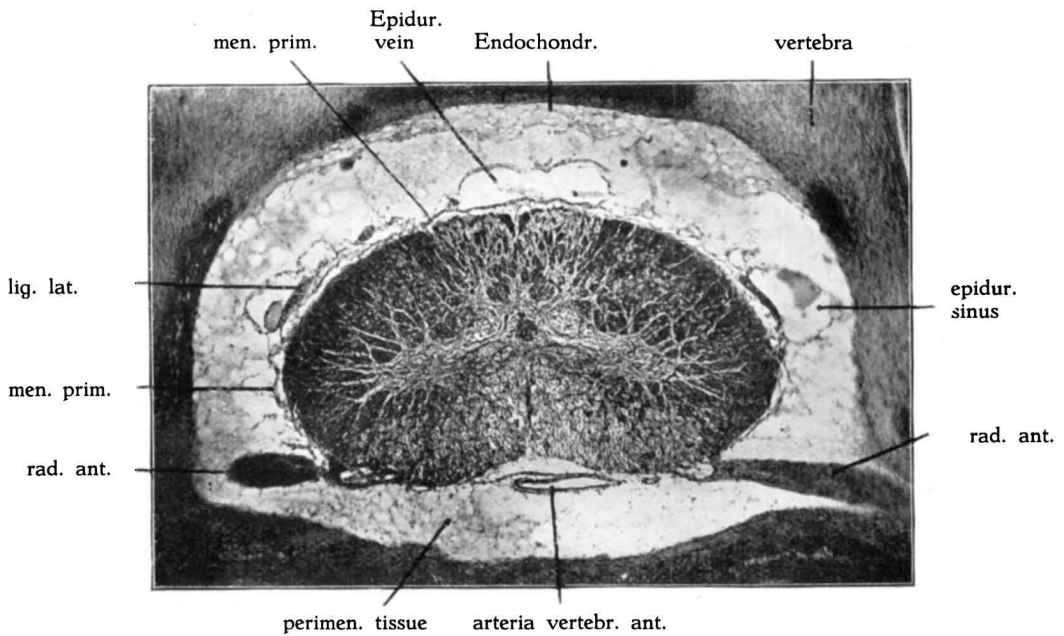Fig. 3. Spinal cord of Scyllium canicula in situ.

Fig. 4. Spinal cord of Scyllium canicula in situ.

and ventrally but may be reduced laterally to a narrow fissure. The perimeningeal tissue [1]) in this cavity consists of fine trabecles between which lie large fatcells. Also many small vessels are found there. It has the function of a perimeningeal filling-tissue. Similar relations were found in the other bony-fishes which he examined.

Quite different was the description given before him (1884) by SAGEMEHL[2]) who in Siluroides and Cyprinoides (especially in Barbus and Perca) distinguishes two meninges, distinctly separated by a fissure, which he calls "pericerebraler Lymphraum" and which he considers to be the homologue of the subdural fissure in mammals.

The membrane lying interiorly to this fissure is, according to him, the origin of both the pia and arachnoidea[3]), although one cannot yet distinguish therein those two membranes. The only distinction to be made in this "vascular-membrane" ("Gefäszhaut" as he calls it) is that only the interior layer of this membrane continues into the fissure mediana anterior, while the exterior layer lies over it like a bridge. Thus far his description of the part lying under the subdural fissure.

Everything outside the "pericerebrale Lymphraum"[4]) SAGEMEHL considers as a dura mater in the old sense of the word, considering as such not only our fibrous dural membrane, but also our perimeningeal tissue and our periostal membrane (l.c. page 460—464).

Resuming we may say that there is a good deal of difference between the opinions of SAGEMEHL and STERZI. STERZI presumes that in fishes there is only one meninx which he calls meninx primitiva, which includes both the dura and the lepto-meninges in an undifferentiated state, while SAGEMEHL distinguishes a dural membrane and under it, separated by a fissure, a tissue which is the origin of pia and arachnoidea (a meninx secundaria as STERZI calls it in Reptiles and Birds). This meninx secundaria ("Gefäszhaut" of SAGEMEHL) shows only in some places a differentiation in an inner and outer membrane, which however has nothing in common with the differentiation in arachnoidea and pia.

The difference between these authors is the more striking as both, at least partly, examined the same material (Barbus).

Personal researches convinced me that the relations in Teleosts may be very different. I examined a very small Teleost, Girardinus, and compared it with a fish which may attain a very considerable size, Lophius piscatorius, and found very different relations.

In Girardinus no differentiation is visible in the meningeal tissue sur-

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[1]) He (and also SAGEMEHL) remarks that the perimeningeal tissue is mucous in Elasmobranchs and Ganoids, and adipose in Teleosts (l.c. page 1147). This is not always correct according to my experience. An Acipenser sturio in my collection has for instance a large quantity of perimeningeal fat tissue, and I found mucous tissue in several Teleosts. It seems that both these tissues are most fit to serve as an buffer substance in a movable enclosure.

[2]) SAGEMEHL. Beiträge zur vergleichenden Anatomie der Fische II. Einige Bemerkungen über die Hirnhäute der Knochenfische. Morphologisches Jahrbuch Bnd. IX, page 457, 1884.

[3]) For the Teleosts KRAUSE's description is practically in accordance with SAGEMEHL. He, however, does not mention SAGEMEHL's name and considers the interior layer entirely as a pia mater, (l.c. page 647). That the interior layer contains the origin of both pia and arachnoidea, is not mentioned by KRAUSE.

[4]) This word has nothing to do with the so-called epicerebral space of HIS, which this author abusively supposed to exist between membrana limitans gliae and the intima piae.

rounding the spinal cord (and the brain). So here with STERZI one may really speak of one meninx primitiva which also joins the periost, at least laterally where hardly any perimeningeal space is seen between vertebra and meninx (fig. 5).

Dorsally, where the space between the meninx and periost is wider, there occurs in this space a very thin, exceptionally widelymeshed perimeningeal tissue, in which, especially at its dorsal side, large veins appear. The same is found in the area of the oblongata and cranium, with this difference however, that there is a much larger quantity of perimeningeal tissue in the much larger cranial cavity. But neither here a differentiation is visible in the meninx primitiva. Consequently, with regard to this animal, STERZI's description is correct.

In Lophius piscatorius quite other relations were found. Here also a large quantity of widely meshed peri-meningeal tissue. The actual meningeal tissue lying under it however shows a vere distinct differentiation, in two membranes (fig. 7 and 8).

The outer part of the tissue lying under the widely meshed perimeningeal mucous tissue forms a dense fibrous layer which in some places is larger than in others, but which may be seen everywhere as a distinct layer. If this layer were separated from the underlying meningeal tissue by a continuous split, one would be right in speaking of a well differentiated dura mater. Such a *continuous* split as described by SAGEMEHL and called "pericerebraler Lymphraum" analogous to the subdural cavity in mammals, I cannot find in Lophius. The relations here are similar to those observed by VAN GELDEREN [1]) in early human embryos. This author found that the (interior layer of the) ectomeninx has become a denser tissue already in human embryos of 19.6 mm. (l.c. I page 2850), contrasting distinctly with the leptomeningeal tissue lying under it without being however separated from it by a fissure, which he even did not yet find in a stage of 25—30 mm., but only saw, occurring first as local dehiscentions, in an embryo of 35—40 mm.

The same condition I found in Lophius, where I could not perceive a continuous split, but only local dehiscentions between the dural membrane and the tissue of the meninx secundaria lying under it. (see fig. 8).

Yet I do not hesitate to consider the fibrous exterior membrane of the meninx primitiva in Lophius as dural tissue, as the fibrous condensation proves that it is developing into the direction of the strongly fibrous dura mater and not into the direction of the arachnoidea, which is becoming much more widelymeshed. If there were a continuous fissure, then it would not be correct to speak of an exterior dural membrane of the

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[1]) v. GELDEREN. De ontwikkeling der sinus durae matris bij den mensch.

Ned. Tijdsch. v. Geneeskunde, Vol. 68, 1924, Iste Helft, N⁰. 25, Pag. 2850, and Vol. 58 of the Anatom. Anzeiger, 1924, "Zur vergleichenden Anatomie der Sinus durae matris".

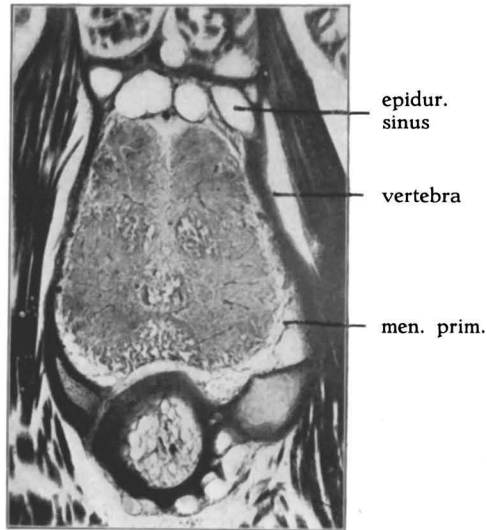**C. U. ARIËNS KAPPERS:** "The meninges in Cyclostomes, Selachians and Teleosts, compared with those in man".

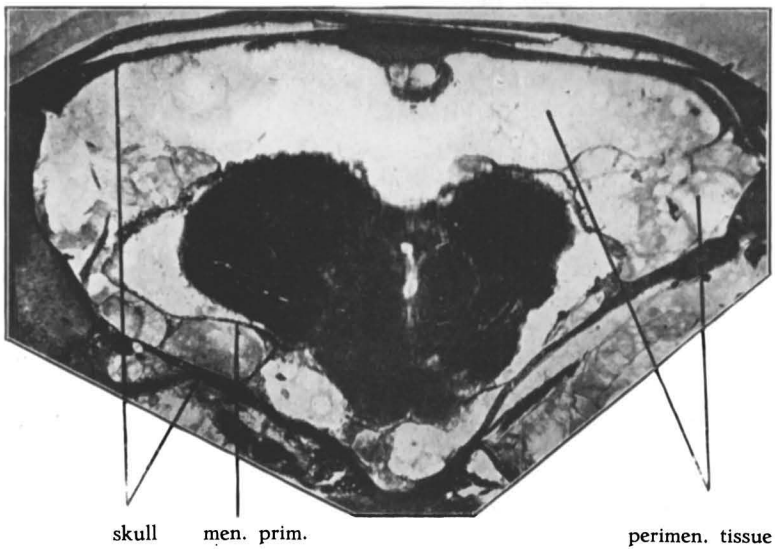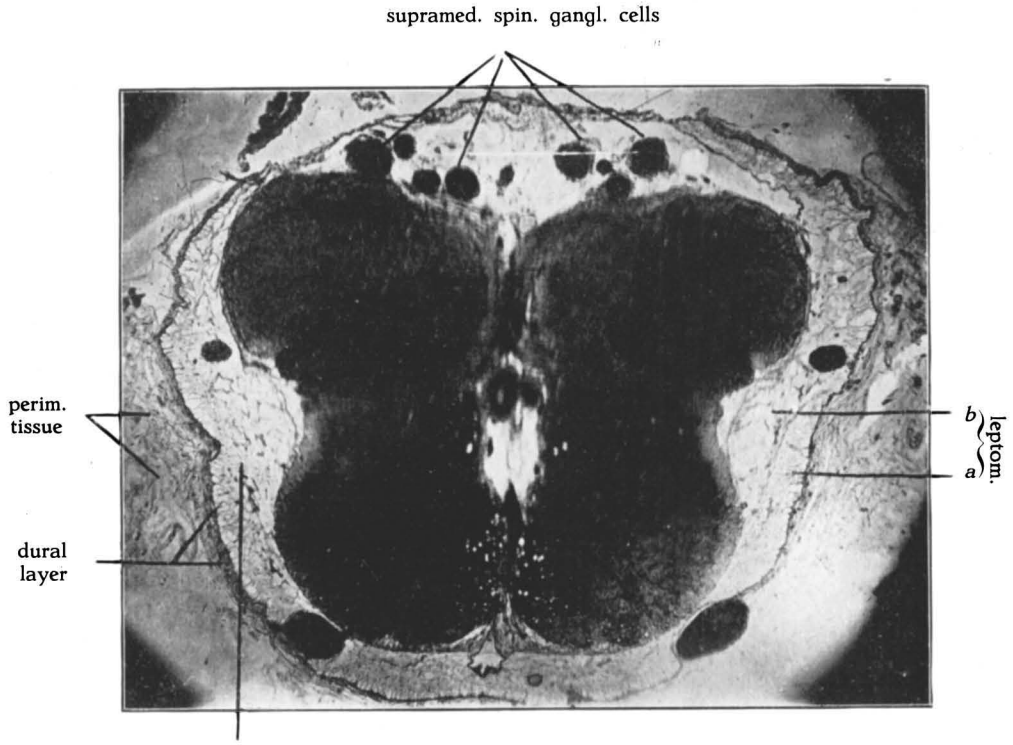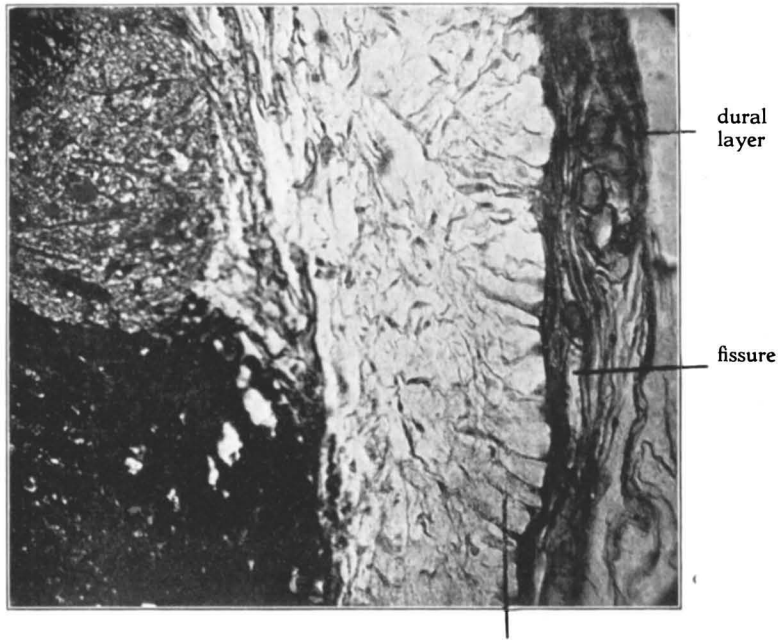Fig. 5. Spinal cord of Girardinus (cervical).
In situ.

Fig. 6. Frontal part of the midbrain of Girardinus in the skull.

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Fig. 7. Cervical cord of Lophius in the meninges.

Fig. 8. Enlarged photograph of the meninges in Lophius.

meninx primitiva, but of a real dura mater and a meninx secundaria, as they occur in Reptiles.

Concerning the condition of the inner layer of the meninx, its much more widely meshed character is striking (fig. 8—10). In many places we may distinguish in it an exterior layer *a* from an interior layer *b* (see fig. 7—9). In the former, lying directly underneath the mesothelial layer by which it is covered, the cells often stand almost perpendicularly (like palisades) on the external layer of flat cells (fig. 8 : *a*), while the meshes of the interior part are much less regular. Another difference is that only the interior layer follows the fissures and the septa and moreover it contains more small bloodvessels, running in that part that lies immediately on the limitans gliae.

Though there is here a fairly widely meshed tissue, especially in the palisade-part, according to my opinion we may not compare this with the trabecular tissue of the arachnoidea since real "trabecles", that is to say fibrillar threads of connective tissue covered with mesothelial cells, do not occur here. The pseudo-trabecles are ramifications of single cells and consequently might be called *monocellular trabecles* similarly as those occurring in the widely meshed reticular tissue of lymph glands. Moreover in real arachnoid tissue the meshes are much wider and the trabecles far less numerous.

Another argument pleads for this. In mammals the arachnoidea has very wide spaces just at the dorsal side of the oblongata on the choroid of the fourth ventricle (cisterna posterior cerebelli) and communicating with the ventricle by means of the foramen Magendi (where this occurs). In Lophius, however, the widely meshed leptomeningeal tissue surrounding the whole surface area of the spinal cord (fig. 7) on all sides, in the area of the calamus (fig. 9) is dorsally a little less developed, and on the choroid roof still less so, being especially developed at the lateral and ventral sides of the oblongata [1]) (see fig. 10).

This seems to be in favor of my opinion that this tissue does not yet perform an important function as a receptaculum of ventricular fluid, running into it in higher animals and forming most of the liquor cerebrospinalis externus, but here performs chiefly the same function as widely meshed reticular connective tissue does in other places, f. i. in the intestina and lymph glands.

That this differentiation occurred in Lophius and not in Girardinus may perhaps be partly due to the much larger space of the vertebral canal in the latter. In larger fishes the skull and vertebral canal increase much more than the nervous system itself, and owing to that the tissue lying between them also increases considerably. That this increase which is very obvious in the perimeningeal tissue in Lophius, does not only

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[1]) Ontogenetically WEED (Anat. Rec. Vol. 10, 1916, p. 479) found the meningeal differentiation also occurring first in the basal parts.

concern the perimeningnal tissue (as happens in the cranial cavity of Girardinus, which also is much larger than the vertebral canal of this animal, fig. 6) but in Lophius also holds good for the meningeal tissue itself, points however to a higher differentiation [1]) to a stage immediately preceding an arachnoidal development.

Thusfar the results of my microscopic research on the meninges in fishes, where the large quantity of perimeningeal, mucous or adipose tissue stands prominent: its quality of a buffer tissue being of great use to the large flexibility of fishes [2]). We know that traces of a thin perimeningeal adipose tissue still occur in man, in the space between the actual dural membrane and the endost of the vertebrae, while it disappears in the cranial cavity, which is much less subject to changes in form [3]).

The comparison of the relations between fishes and man, however, asks for a further explanation as far as concerns the development of the arachnoidal spaces and the liquor cerebro-spinalis externus.

There is no doubt that the lowest vertebrates as Cyclostomes, Plagiostomes and Ganoids do not have actual arachnoidal cavities and consequenty no liquor cerebro-spinalis externus which in mammals fills the subarachnoidal cavities and whose total volume in man considerably surpasses the volume of the liquor cerebro-spinalis internus (ventricular fluid).

Together with the want of liquor cerebro-spinalis externus, we see the striking fact that the liquor cerebro-spinalis internus — the ventricular liquor — is not seldom very richly developed in lower fishes.

This relative large volume of liquor cerebro-spinalis internus, is not only proved by the wide ventricles in Plagiostomes (especially sharks) and Cyclostomes, but also by the fact that, where these ventricles are covered at the surface by a choroidal membrane, this membrane generally bulges outward considerably, as is shown e.g. in the fourth ventricle and the roof of the midbrain of Petromyzon (fig. 11). Also other primitive fishes — f. i. Ceratodus (V. D. HORST) — have similar protruding choroid membranes, and with some fishes (Lepidosteus and Amia), the choroid roof of the third ventricle (the so-called parencephalon) even evaginates in such a degree to all sides that choroidal sacks are formed filled with liquor internus, extending outside alongside the brainwall, far frontally as well as caudally [4]) (fig. 12).

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[1]) Girardinus belongs to the Haplomi, that are considered to stand at a lower level than the group of the Pediculati, to which Lophius belongs.

[2]) The fact that the flexions made by fishes in swimming are chiefly lateral may perhaps explain the preponderance in the size and development of the lateral ligaments.

[3]) Compare also POIRIER et CHARPY, l.c. page 107.

[4]) ARIËNS KAPPERS. Untersuchungen über das Gehirn der Knochganoïden, Amia calva und Lepidosteus osseus. Abhandlungen der Senckenbergischen Naturf. Gesellschaft, Frankfurt a/Main, 1907.
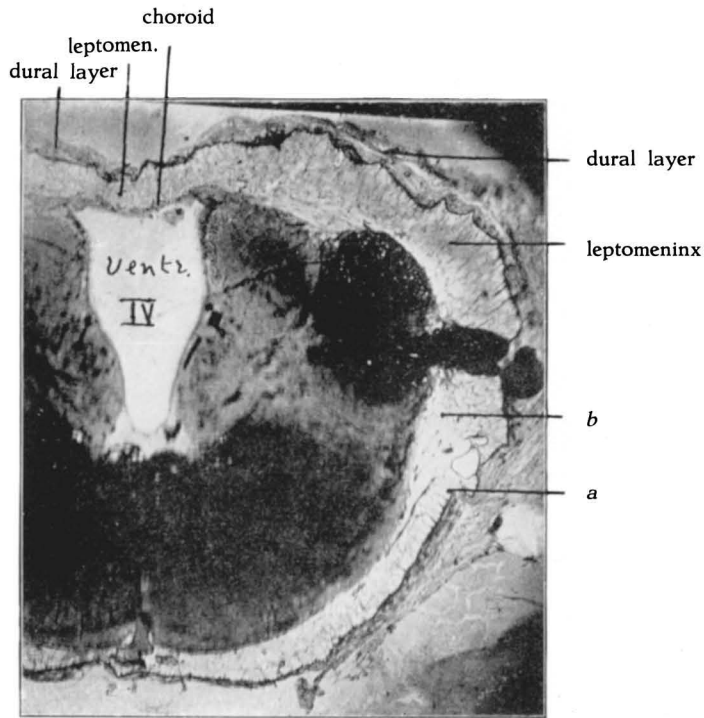
Fig. 9.   Lophius. Oblongata on the level of the Calamus.
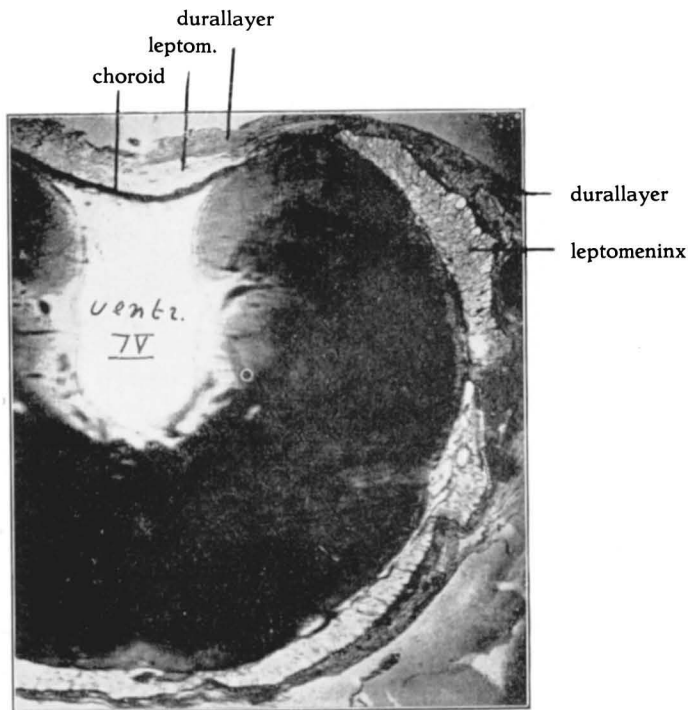
Fig. 10.   Meninges of Lophius immediately behind the cerebellum.

Fig. 11. Fourth ventricle with high choroidal roof in Petromyzon fluviatilis; sagittal.
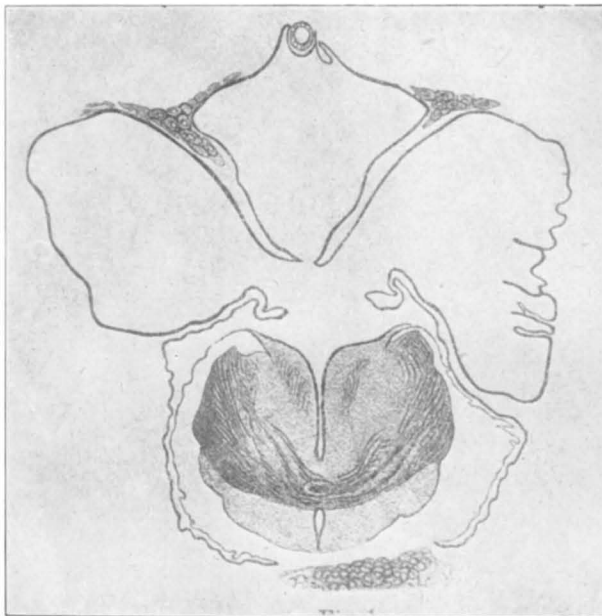

Fig. 12. Cross section through the frontal part of the thalamus with large recessus dorsalis, laterales and ventrales of the choroid of the third ventricle in Lepidosteus osseus.

Ii is evident by all this that the liquor internus has a relatively large volume in many lower animals, in strong contrast to the absence of arachnoidal cavities and liquor externus.

It is interesting that in higher animals, especially mammals — where the arachnoidal cavities with their liquor externus develop very strongly, [1]) and at last surpass the volume of the ventricular liquor — the choroid-membranes do no more ude as sacks, but (with few exceptions) [2]) grow inwards into the ventricles as ventricular draining organs.

In my handbook of comparative brain-anatomy (part II, page 820) I already stated that the coincidence of the accumulation arachnoidal liquor on one hand, and the growing of the choroid membranes into the ventricles on the other (secreting liquor into and at the same time draining the ventricles) is not accidental. It is sure that most of the liquor externus does not originate at the place where it later occurs, but — certainly for the greater part — originates from the ventricular fluid, which diffuses through the choroid-membranes (with or — in most mammals — without assistance of foramina of LUSCHKA or MAGENDI [3])).

This origin of liquor externus certainly is the most important one, though it may be added that in some places a slight diffusion of ventricular liquor takes place through the ependyma of the ventricles, and arrives into the Virchow-Robin spaces round the brain-vessels and so in the arachnoidal cavities.

In connection with this it is interesting that Dr. FREDERIKSE in the Institute for Brain-research could prove the existence of so-called „Kittsubstanz" (as also occurs between choroid cells and between intestinal epithelium) between the ependyma cells of the ventricles in the lizard.

In view of the fact that the liquor arachnoidalis originates certainly for the larger part by the diffusion of ventricular fluid through the choroid, it is not strange that the formation of the arachnoidal sacks in mammals arises at the same time with a more draining action and inversion of the choroid.

Of both choroidal functions, viz. the secretion of liquor into the ventricle [4]) at one side, and at the other the draining of ventricular fluid,

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[1]) Smaller arachnoidal cavities occur already in birds, as HANSEN PRUSS could show by injections. Journ. of Comp. Neur. Vol. 36, 1923.

[2]) The recessus laterales of the oblongata.

[3]) These foramina are seen for the first time in mammals and do not occur in all mammals. They are even sometimes (but rarely) failing in man.

[4]) The ependyma also takes some part here in, at least in some places (f.i. the infundibulum, see my book, Vol. II, page 821, fig. 437, and page 853, fig. 455 A and B) and the communications of WICLOCKI and PUTNAM. Note on the anatomy of the areae postremae, Anat. Record Vol. 19, 1920 and: Further observations on the anatomy and physiology of the areae postremae; Anat. Record, Vol. 27, 1924.

the first mentioned function occurs first [1]), and this explains as well the strong protrusion of the choroidal sacks in lower fishes, as the absence of proper arachnoidal cavities in these animals.

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[1]) That this process repeats itself in the same order in embryologic development is shown by the researches of LEWIS WEED, who proved that while the ventricular liquid appears in embryos already in the first stage of ventricular development, the liquor externus is found in the arachnoidal cavities of the pig for the first time in an embryo of 14 mM. See his researches: Development of the cerebro-spinal spaces in pig and man: Contributions to embryology, published by the Carnegie Institution, Vol. V, 1917.