Zeitschrift für Zellforschung, Bd. 42, S. 229-246 (1955).

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A CYTOLOGICAL STUDY OF THE NEUROHYPOPHYSIS OF SCYLLIORHINUS CANICULUS.

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With 15 figures in the text. (Eingegangen am 11. Februar 1955.)

Introduction.

The details of the structure and the cytology of the neurohypophysis of the Selachii are not so well known as, for instance, those of the posterior lobe of mammals.

STENDELL (1914) describes the pars nervosa of Scylliorhinus as an undifferentiated thin plate in intimate connection with the intermediate lobe, in which no ganglion cells are present. According to DE BEER (1926) the organ is composed of neuroglia fibres, which extend from the border of the infundibular cavity and penetrate into the pars intermedia. SCHARRER (1952) states that the description which STENDELL gives of the pars nervosa does not refer to the pars nervosa sensu stricto, but only to the fibrous part of it. The real posterior lobe is composed of fibre endings which penetrate into the pars intermedia and which contain the neurosecretory substance. In SCHARRER'S own words (1954a, p. 238): "In the Selachian fishes there is a disseminated, not a consolidated posterior lobe, and the posterior lobe consists only of the sum total of nerve endings, with no other cells." The absence of cells makes it consequently difficult to interpret the pars nervosa of Scylliorhinus as a gland. According to BARGMANN and SCHARRER (BARGMANN 1951, 1953a; BARGMANN and SCHARRER 1951; SCHARRER 1953, 1954b), the posterior lobe of the hypophysis is not an endocrine gland at all, but on the contrary an organ of storage in which is gathered neurosecretory material formed in the nucleus praeopticus of the hypothalamus. SCHARRER'S description of the pars nervosa of Scylliorhinus (1952) is strongly in favour of this view.

However in Selachian fishes the pituicytes in the posterior lobe are usually not absent. For instance in *Raja clavata* Howes (1936) reports the presence of neuroglial cells with large nuclei surrounded by a thin layer of cytoplasm and long branching cytoplasmic processes. Among these cells isolated ovoid cells were found with granular oxyphil cytoplasm. ROMEIS (1940) describes also pituicytes in the pars nervosa

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of *Raja australis*. These cells are of different size but are all of regular form and possess either one or two short processes or none at all. The nucleus is relatively large and the cytoplasm granular. ROMEIS concludes in accordance with data derived from other Vertebrate species, that in the pars nervosa of all Vertebrates there are active secretory neuroglial cells.

The pars nervosa of *Scylliorhinus* consequently does not fit in this general conception. It must be regarded as an exception in respect of its microscopic-anatomical structure, and in view of the possible part played by the pituicytes in the series of Vertebrates. If this statement is sound, it is of great importance because from the work of MAZZI (1952) and SCHARRER (1952, 1954b) it is evident that in the dogfish neurosecretory material is transported to the pars nervosa, stored in the nerve endings, and passed into the blood capillaries without the cooperation of the pituicytes. Therefore in this hypothalamo-hypophyseal system it is not necessary to decide whether the pituicytes secrete one or more posterior lobe hormones themselves, or only transform the neurosecretory material in such a way that its passage into the blood capillaries is promoted.

From the work of HERRING (1908), CUSHING (1933) and others the view originates that part of the "Herring-bodies"-secretory material stored in the pars nervosa—is formed by the cells of the pars intermedia which penetrate into the posterior lobe and change into secretory granula. Bock (1928) confirmed these statements and described the passage of intermediate cells into the pars nervosa in Gasterosteus aculeatus and more recently COLLIN (1951, 1953a and b) and RACADOT (1953) observed the same phenomenon in mammals. HERRING (1911), who studied the elasmobranch pituitary especially for this purpose denies the presence of invading epithelial cells which are characteristic of the pars nervosa of the pituitaries of animals higher in the scale of Vertebrate life. Also in this sense the pars nervosa of the elasmobranch fishes would therefore be an exception. This conclusion is the more remarkable if we consider the fact that especially in the Selachii there is an intimate connection between the posterior and the intermediate lobe.

In COLLIN's view (1951) the colloid from the posterior lobe that originates from intermediate cells, is transported partly to centres in the hypothalamus (neurocrinie), partly extruded through the ependymal layer—in accordance with HERRING (1908), CUSHING (1933) and others —into the ventricle of the brain (hydrencephalocrinie). Besides there are several statements in the literature (COLLIN 1928, 1953a; LEGAIT 1942; GOSLAR and TISCHENDORF 1953) which point to a secretory activity of the ependymal cells (ependymocrinie). The presence of such processes in the Selachian nervous system is still doubtful (ROMEIS). MAZZI (1952) alone describes the presence of neurosecretory material beneath the ventricular ependyma in *Scylliorhinus* and suggests with regard to the presence of neurosecrete granula on the ventricular side of the ependymal layer, its passage into the liquor.

In favour of the processes of neurocrinie and hydrencephalocrinie several authors point to the fact that the ependymal layer in the posterior part of the recessus infundibuli is partly lacking in mammals and birds (Collin 1929, 1947, 1947/48, 1951, 1953a; ROMEIS 1940; FARKAS 1940). In these places the fibrillar tissue borders immediately upon the ventricle, and the passage of interfibrillar substances into the liquor can take place easily. In Elasmobranchia, according to HERRING (1911), the wall of the infundibular cavity is composed of a continuous layer of columnar cells. In this respect too, therefore the situation in the hypothalamic region of *Scylliorhinus* is an exception.

Thus, the following data taken from the literature support the view that the neurohypophysis of the Selachii is different from that of other Vertebrates and greatly favour the idea of neurosecretion,

1. a disseminated posterior lobe consisting only of the sum total of nerve endings;

2. absence of pituicytes;

3. no signs of passage of intermediate cells and colloid into the posterior lobe;

4. no signs of hydrencephalocrinie and only suggestions for ependymocrinie;

5. a continuous ependymal lining of the infundibular cavity above the pituitary.

In studying the cytological structure of the saccus vasculosus and its adjacent parts in *Scylliorhinus* we became much interested in the structure and details of the neurohypophysis as being out of accord with the general view given above.

In order to obtain more data about the histological and cytological structure a more careful study was made of the neurohypophysis of *Scylliorhinus*, and the attempt was made to determine whether:

1. any pituicytes are present and, if their presence can be confirmed, to analyse their secretory activity;

2. whether there is any passage of intermediate cells and colloid into the pars nervosa;

3. whether there are signs of hydrencephalocrinic or ependymocrinic — and in relation with it —

4. whether the ependymal layer above the pituitary is discontinuous and thus support the idea of the transport of colloid into the ventricle.

Material and methods.

The material consisting of brains of adult dogfish (Scylliorhinus caniculus) was collected by the first author in the summer of 1950 during a stay in Naples for the purpose of studying the saccus vasculosus and its adjacent ependymal regions. The brain-case was therefore opened dorsally and laterally and cotton wool moistened with BOUIN's fixation fluid was placed on the roof of the brain. After some hours the brain was removed from its case and immersed in BOUIN's fluid. Finally the material was imbedded in paraffin, sectioned at 8μ and stained with HEIDENHAIN's iron-haematoxylin.

Results.

As stated already in a previous communication (VAN DE KAMER and VERHAGEN 1954) the neurohypophysis is built up mainly of nerve



Fig. 1. Diagrammatic drawing of a median section of the brain of Scylliorhinus caniculus. r.p. recessus posterior; s.v. saccus vasculosus.

fibres that form a narrow layer in intimate connection with the intermediate lobe and penetrate between the cells of this lobe in the form of strands (Fig. 1). It is therefore a disseminated and not a consolidated organ. There are capillaries and blood sinuses between the tissue of the pars nervosa and the pars intermedia.

Bordering the ventricle there is an ependymal layer that only in its most caudal part has the form of a continuous epithelium of columnar cells (Fig. 2). Dorsally this continuous part passes without interruption into the coronet-epithelium of the saccus vasculosus. This columnar epithelium loses its continuity rostrally towards the infundibular cavity, and the ependymal cells now form a discontinuous layer. In some places the ependymal structure has even completely disappeared and the fibres here border immediately upon the ventricle (Fig. 2).

Scattered between the fibre bundles there are two types of cells. The first type consists of cells of irregular form, rather poor in cyto-

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plasm, with thin branching processes and small elongated nuclei. Evidently this type of cell corresponds to the normal pituicyte of the posterior lobe of other Vertebrates. The second type consists of fairly large cells, with a dense homogeneous cytoplasm without processes and a characteristically large, deeply stainable, round nucleus, situated eccentrically. Close to the nucleus there are small vacuoles in the cytoplasm that may clearly fuse and give rise to a large vacuole situated in the upper part of the cell (Fig. 3). In some cases we could observe



Fig. 2. Parts of the wall of the saccus vasculosus (*s.v.*) and of the lobus intermedius (*l.i.*). Below, on the right, columnar epithelium (*c.e.*), on the left a discontinuous epithelial layer (d.e.l.), in the centre absence of epithelium. Magnif. 200 \times .

vacuoles which have burst and poured out into the surrounding tissue. These cells obviously possess secretory activity. The formation of the smallest vacuoles close to the nucleus and also the presence in some cases of small vacuoles inside the nucleus, point to a possible process of nuclear secretion. This process must be a highly active one, for in some special cases more than twelve of these vacuoles could be observed in the cytoplasm of one cell. Such cells represent the parenchymatous pituicytes. They certainly do pertain to the group of pituicytes, as they originate from the ependymal layer and are therefore true neuro-ectodermal cells.

The discontinuous ependymal layer is also built up of two cell types. There are large, long columnar cells with homogeneous cytoplasm and a round, deeply staining nucleus and some smaller supporting cells between them. These large cells distinctly resemble the parenchymatous pituicytes. In the otherwise homogeneous cytoplasm small vacuoles are visible close to the nucleus. In other cells these vacuoles are clearly



Fig. 3. On the left cells of the intermediate lobe (l.i.) and a blood capillary; on the right the fibres of the posterior lobe with a group of four invaded parenchymatous pituicytes and some smaller normal pituicytes. The parenchymatous pituicyte (p.p.) in the middle of the upper part of the photograph has a large vacuole in its upper part. Magnif. 1015 \times .



Fig. 4. Part of discontinuous epithelium. The cell on the right with a large vacuole in its upper part. The cell on the left with a spiral in the vacuole. Magnif, 1450 \times .

fused and form large vacuoles in the upper part of the cell. Their content is quite transparent and probably contains proteins, for in these Bouin-fixed cells, spiral threads are visible in the vacuoles. The vacuoles A cytological study of the neurohypophysis of Scylliorhinus caniculus. 235

are finally extruded into the ventricle. These ependymal cells evidently possess a secretory activity and represent therefore a good example of the process of ependymocrinie (Fig. 4).

The resemblance of the ependymocytes with the large parenchymatous pituicytes is not merely superficial, but very real, for we were able to observe the penetration of the ependymal cells into the fibrillar



Fig. 5. Four invading epithelial cells (e.c.), in the centre of the photograph. The middle cell is still an epithelial one. The left cell already in intimate contact with the intermediate tissue (*i.t.*). The cells on the right have just started their invasion. Magnif. $1085 \times$.

it

tissue beneath it, and their transformation into the parenchymatous pituicytes (Figs. 5 and 6). Consequently the number of cells in the ependymal layer decreases and the epithelium appears discontinuous. In such places, however, there is still a separation between the fibrillar tissue and the ventricle, as the smaller pituicytes act as substitutes. Together with the large ependymocytes their processes form a thin closing layer. It seems as if in this situation the ependymocytes try to cover the surface as far as possible. Instead of being placed with the long axis of the cell perpendicular to the surface, as in the continuous layer, the long cell-axis is now parallel with the surface (Figs. 7 and 8). In these epithelial parts we also occasionally found some mitotic figures in these large ependymocytes, which observation points to the same conclusion.

The discontinuity of the epithelium is found especially in those parts of the neurohypophysis where, immediately beneath its fibrous part, the blood sinuses are situated (Fig. 7).



Fig. 6. Invading epithelial cells (e.c.). The two cells in the middle have just started. The cell on the left is already invaded. Below on the left an other invaded epithelial cell. Magnif. $1085 \times$.

In other places the intermediate cells border immediately upon the fibrillar tissue and here the ependymal layer is entirely absent locally. Occasionally there are still some ependymal cells and also smaller pituicytes but their processes no longer form a continuous layer. Here the fibrous part of the neurohypophysis is clearly in immediate contact with the ventricle (Fig. 8).

The parenchymatous pituicytes are to be found not only in the superficial fibrous layer of the neurohypophysis, but also in deeper layers, as for instance in the fibrous strands between the cells of the intermediate lobe (Fig. 3), and close to the walls of the blood sinuses.

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Fig. 7. Detail of the left part of Fig. 2. Part of the discontinuous epithelial layer (d.e.l.) Magnif. 420 \times .



Fig. 8. Part of the discontinuous epithelium (*d.e.l.*) of the neurohypophysis. The ependymal layer is locally entirely lacking. Below intermediate cells and blood capillaries. In the middle of the photograph a part of an intermediate cell filled with colloid droplets (*c.d.*). Magnif. 420 \times .



Fig. 9. Large intermediate cell filled with colloid, penetrating into the fibrillar tissue of the posterior lobe. On the right part of the pars intermedia, on the left part of the posterior lobe. Magnif. $1450 \times .$



Fig. 10. Migration of an intermediate cell filled with colloid droplets into the norillar tissue of the posterior lobe. On the left intermediate cells. On the right fibres of the posterior lobe. Detail of Fig. 11. Magnif. 1375 ×.

In all these cases the cells are easily recognizable by their form and the stainability of their nuclei and by the appearance of the cytoplasm with the formation of vacuoles. The cells situated in the fibrous strands extrude their contents into the spaces between the different fibres, and for those close to the wall of the sinuses it is suggested that their contents pass over into the blood sinus.

Not only ependymocytes, but also intermediate cells penetrate into the fibrous part of the neurohypophysis (Fig. 9). The intermediate cells are large with a densely granulated cytoplasm and possess a rather large nucleus. Sometimes the whole contents of the cell change into colloid droplets which stain very deeply with iron-haematoxylin. Sometimes the nucleus is not changed during this process and remains in the cell, but more often the nucleus disappears also and the whole cell-contents pass over into droplets. We found these cells in the intermediate lobe and also especially, where the cells of the intermediate lobe border immediately upon the fibrillar tissue of the pars nervosa. These cells migrate into the pars nervosa and extrude their colloid content between the fibres (Fig. 10). No doubt this represents a form of holocrine secretion. Correlated with this process of holocrine secretion several intermediate cells are in mitotic division (Fig. 11).

There are also invading intermediate cells, with a normal appearance and without a colloid content. Perhaps these cells represent an earlier functional phase and will afterwards change and pass into colloid. It looks as though the intermediate cells, when becoming active, increase considerably in size and at the same time the cytoplasm becomes more and more stainable and finally changes into colloid droplets (Fig. 11). In some places a large part of the intermediate tissue penetrates into the pars nervosa. There the intermediate cells tend to make an extensive surface of contact with the fibrillar tissue of the neurohypophysis. In one case even, a part of the intermediate tissue projects between two blood sinuses into the pars nervosa, and the intermediate cells which have penetrated have dispersed horizontally between the fibrillar tissue and the sinus wall, thus forming a very remarkable mushroom-like structure of intermediate cells (Fig. 12).

A real ependymal structure bordering the ventricle is absent exactly above the surface where intermediate cells and the tissue of the posterior lobe make contact (Figs. 11 and 12). This relation suggests a direct passage into the ventricle of substances formed by the intermediate cells. It is also possible that the products of the intermediate cells influence the fibres, or the parenchymatous pituicytes, resulting in a secretion of substances from the posterior lobe into the ventricle. In both cases, however, it points to a process of hydrencephalocrinie.



Fig. 11. Below the groups of intermediate cells (*i.e.*). On the right in the middle an intermediate cell in mitosis (*m.*). Bordering the fibrillar tissue of the posterior lobe several considerably increased granulated intermediate cells (*g.i.e.*). On the left an invading intermediate cell (*i.e.*) filled with colloid droplets. Magnif. $450 \times .$



Fig. 12. Intermediate tissue penetrating between two blood sinuses into the pars nervosa. The invaded intermediate cells (*i.c.*) have dispersed horizontally, thus forming an extensive surface of contact with the fibrillar tissue of the pars nervosa (*p.n.*). Note the increase in size of several intermediate cells, their increasing granula content and the colloid droplets (*c.d.*) in the centre of the upper part of the tissue of the intermediate lobe. Magnif. $570 \times .$

p.p. - i.t.

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Fig. 13. Parenchymatous pituleyte (p.p.) with a vacuole in the upper part of the cell, in intimate contact with the intermediate tissue (i.t.). Detail of the left part of Fig. 12. Magnif. 1665 \times .



Fig. 14. Parenchymatous pituicyte (p.p.), with a spiral thread in its vacuole, in intimate contact with the intermediate tissue (i.t.). Detail of the left part of Fig. 12. The same picture as Fig. 13, but in other focus. Magnif. 1665 \times .

The intimate contact between the intermediate cells and the parenchymatous pituicytes is in favour of such an influence. Moreover, the secretory activity of the parenchymatous pituicytes is most distinctly visible in these regions of contact (Figs. 13 and 14).

Discussion.

From the foregoing data it is concluded that there are two types of cells in the neurohypophysis of the dogfish. The first type corresponds to the normal pituicyte of the posterior lobe of other Vertebrates. The second type is very probably homologous with the parenchymatous pituicyte of GEBSH (1939) and is distinctly a secretory cell. This statement is in complete contradiction to SCHARRER's data (1952, 1954a), which deny the presence of cells in the pars nervosa in Scylliorhinus. Perhaps this contradiction can be explained if we take into consideration the description which SCHARRER gives of the Herring-bodies. SCHARRER (1952, p. 200) states: "Im Verlaufe der vom Infundibularboden in die Pars intermedia eindringenden Faserbündel liegen runde oder ovale, aus körnigem Material bestehende Gebilde, die sich wie die an den Nervenfasern aufgereihten neurosekretorischen Granula mit Chromhaematoxylin-Phloxin tiefblau färben. Diese Körper wurden erstmals von HERRING (1908) in der Pars nervosa von Säugern beobachtet und in der Folge von anderen Untersuchern beschrieben und in verschiedener Weise gedeutet" and "Es handelt sich offenbar bei Scyllium um vergleichbare Gebilde, d. h. um außerordentlich vergrößerte Nervenendigungen, die vielleicht ebenso wie bei den höheren Wirbeltieren der Aufspeicherung von Neurosekret dienen."

It seems to us that the parenchymatous pituicytes described above are interpreted by SCHARRER as Herring-bodies. As these cells stain very deeply with chrome-haematoxylin-phloxin their structure was strongly masked and their cellular nature overlooked. In support of our view is the figure which SCHARRER has given of "ein doppelter großer Herring-Körper" (Fig. 4, 1952). This body is conspicuously divided in two parts—a quite unusual situation for this substance—and shows two light spots in eccentric position, whereas the surrounding parts are darkly stained. In our opinion it consists of two parenchymatous cells with their nuclei in eccentric position. With respect to the stainability of the cytoplasm and of the nucleus our figures are the reverse of SCHAR-RER'S drawing. Our method (iron-haematoxylin) was used to stain especially the nuclei, while SCHARRER'S method (chrome-haematoxylinphloxin) was applied to stain particularly the neurosecretory substance in the cytoplasm (Fig. 15).

The secretory activity of the parenchymatous pituicytes raises the question of the possible function of the secretory product. In the views of BARGMANN (1954), SCHARRER (1954a), LEVEQUE and SCHARRER (1953), HILD (1954) and others, the pituicytes do not produce hormones themselves. LEVEQUE and SCHARRER state: "The possibility that glia elements in general are potential sources of hormones cannot be excluded,

but at present no experimental evidence is available in support of such a hypothesis."

In agreement with this view several authors [HILD (1952), HILD and ZETLER (1953), BARGMANN (1953b), SCHIEBLER (1954)] have put forward the idea of the formation of a substance by the pituicytes which is responsible for the liberation of the posterior lobe hormones from the nerve endings and promotes their passage into the blood

capillaries. In our preliminary communication (VAN DE KAMER and VERHAGEN 1954) we supported this hypothesis without definitely excluding the possibility that the secreted substance is itself a hormone.

If the above given interpretation of the identity of some of the Herring-bodies described by SCHARRER with the parenchymatous pituicytes is sound, there is the remarkable fact that the parenchymatous pituicytes of the posterior lobe contain a large quantity of neurosecretory material. It is possible that these cells store this material but since the secretory activity of these cells could be demonstrated, the conclusion is arrived at that the parenchymatous pituicytes produce the neurosecretory substance themselves.



Fig. 15. On the left intermediate cells, on the right fibrillar tissue of the pars nervosa and a parenchymatous pituicyte (p.p.)with a large vacuole in its upper part.

As is accepted generally, and was stated by SCHARRER (1954a, p. 190) "the neurosecretory substance consists of active polypeptides and a carrier or cement substance which can be extracted from unfixed tissues by organic solvents. After fixation with fluids such as Zenker or Bouin this substance is no longer soluble. It is this component which imparts to the neurosecretory material its stainability with chromehaematoxylin" and "Therefore, the GOMORI or other staining techniques do not stain the hormones, but a material with which these hormones are associated. The histological methods permit to ascertain the presence of hormones indirectly. Whether or not there are in the neurosecretory substance other still undefined components cannot be decided at present". If in accordance with this view the parenchymatous pituicytes contain a large quantity of neurosecretory material, this only indirectly indicates the presence of hormones. Therefore it is at present not possible to determine with certainty the part played by the secretory product of the pituicytes, but it seems as if they are also a source of hormones.

From the foregoing data it is concluded that in *Scylliorhinus* part of the neurosecretory material is formed in the pars nervosa by the pituicytes, and another part is according to SCHARRER and MAZZI formed in the hypothalamus and stored in the neurohypophysis. Accordingly the pars nervosa is neither exclusively an organ of storage nor simply the sum total of nerve endings.

There still remains the possibility that the functional condition of the experimental animals which SCHARRER used were different from our material and accordingly the phenomena of migration of ependymal cells less pronounced in his fishes.

In the view of HERRING there is no migration of intermediate cells into the pars nervosa of Selachii. In our *Scylliorhinus* material, on the other hand, there are several invading intermediate cells. In this respect the situation in the pars nervosa of the dogfish closely resembles that of *Gasterosteus aculeatus* as described by BOCK and that of mammals given by COLLIN and RACADOT.

The phenomenon of ependymocrinic stated for different species of animals was still unknown in Selachii. The secretory activity of the ependymocytes described above renders it desirable to study this process more in detail and to analyse the chemical nature of the secretory product that is extruded.

According to HERRING, the ependymal layer of the elasmobranch pars nervosa is a continuous epithelium. This statement is contradictory to that given for the posterior part of the recessus infundibuli in mammals and man. In *Scylliorhinus*, however, we have observed the discontinuity of the ependymal layer of the pars nervosa and its absence from several places. In these last cases the fibrous part of the neurohypophysis is therefore in immediate contact with the ventricle. Such a structure suggests a passage of substances from the pars nervosa into the liquor (hydrencephalocrinie). The migration of intermediate cells filled with colloid droplets into the pars nervosa, exactly beneath these surface structures, is, in our opinion, strongly in favour of such a passage. The data of MAZZI, who describes the passage of neurosecretory material into the ventricle, are in accordance with this hypothesis.

In conclusion we should like to say that apart from its diffuse structure the pars nervosa of *Scylliorhinus* is, according to these data, not exceptional in histological and cytological details when compared with other Vertebrates. The hypophysis of the dogfish is, on the other hand, a very favourable object for the analysis of the rôle of the parenchymatous pituicytes, for the study of the functional activity and cytological differentiation of the intermediate cells, and for the study of the processes of ependymocrinie and hydrencephalocrinie.

Summary.

1. In the pars nervosa of *Scylliorhinus* two types of pituicytes are described: relatively small irregular cells with thin branching cytoplasmic processes and large parenchymatous cells.

2. The parenchymatous pituicytes originate from the ependymal layer and possess secretory activity; their products are extruded into the spaces between the fibres of the pars nervosa.

3. A discussion is given concerning the identity of these cells with some special Herring-bodies, as described by SCHARRER, and of the probability of the formation of neurosecretory material by these cells.

4. Ependymocrinie is described for the cells of the ependymal layer of the pars nervosa.

5. Migration of isolated intermediate cells was observed and also of parts of the pars intermedia into the pars nervosa. The penetrating tissue tends to make an extensive surface of contact with the fibrillar tissue of the pars nervosa.

6. In correlation with this migration of intermediate cells, the absence of ependymal structures above the region of penetration is established, and the possibility of hydrencephalocrinie is discussed.

7. It is concluded that the pars nervosa of *Scylliorhinus* is not merely the sum total of nerve endings and therefore an exception in the series of Vertebrates, but an organ that in its histological and cytological details is in accordance with the data described for the pars nervosa of other Vertebrates.

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