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# EPENDYMAL NEUROSECRETION. I.
# GOMORI-POSITIVE SECRETION IN THE SUBCOMMISSURAL ORGAN OF DIFFERENT VERTEBRATES

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The posterior commissure in the vertebrates is situated caudally above the third cerebral ventricle. The ventricular portion underneath is lined by multiple ependymal cell-rows differing in structure from the surrounding epithelium, and by the hypendyma containing capillaries and fibres. Reissner's fibre, a threadlike structure, emanates from this ependymal cell surface and extends freely across the ventricular cavities to the termination of the central canal of the spinal cord. The structure underneath the posterior commissure has been described in the mouse by Stieda in 1870 and has been given the name subcommissural organ by Dendy and Nicols in 1910 (Figs. 1, 2, 3).

The physiological function of the subcommissural organ, in spite of numerous studies (Legait 17, Bargmann 5, Oksche 23, Steyn 28), is still not clear.

An important step was reached when in 1950 Stutinsky [29] succeeded in demonstrating the Gomori-positivity of the subcommissural ependyma in the Anura, thereby bringing the organ within the scope of neurosecretory investigations.

Adam [1], Barry [6], Mazzi [21, 22], Oksche [23, 24, 25], and Steyn [28] studied the subcommissural organ for its function in fish and amphibians and Bargmann and Schiebler [5] in birds and mammals. According to the results, in the vertebrates the organ is either rudimentary or actively secreting. The secreted substance is produced in the ependymal cells from where it is probably released either into the cerebrospinal fluid (apical secretion) or *via* the cell processes into the arachnoidal capillaries (basal secretion). The substance resembles the hypothalamic neurosecrete and is believed to play a significant role in the fluid household of the organism (Gilbert 11, 12, 13).

The present paper reports on our studies concerning the ependymal cells of the subcommissural organ and their comparison in different vertebrates.

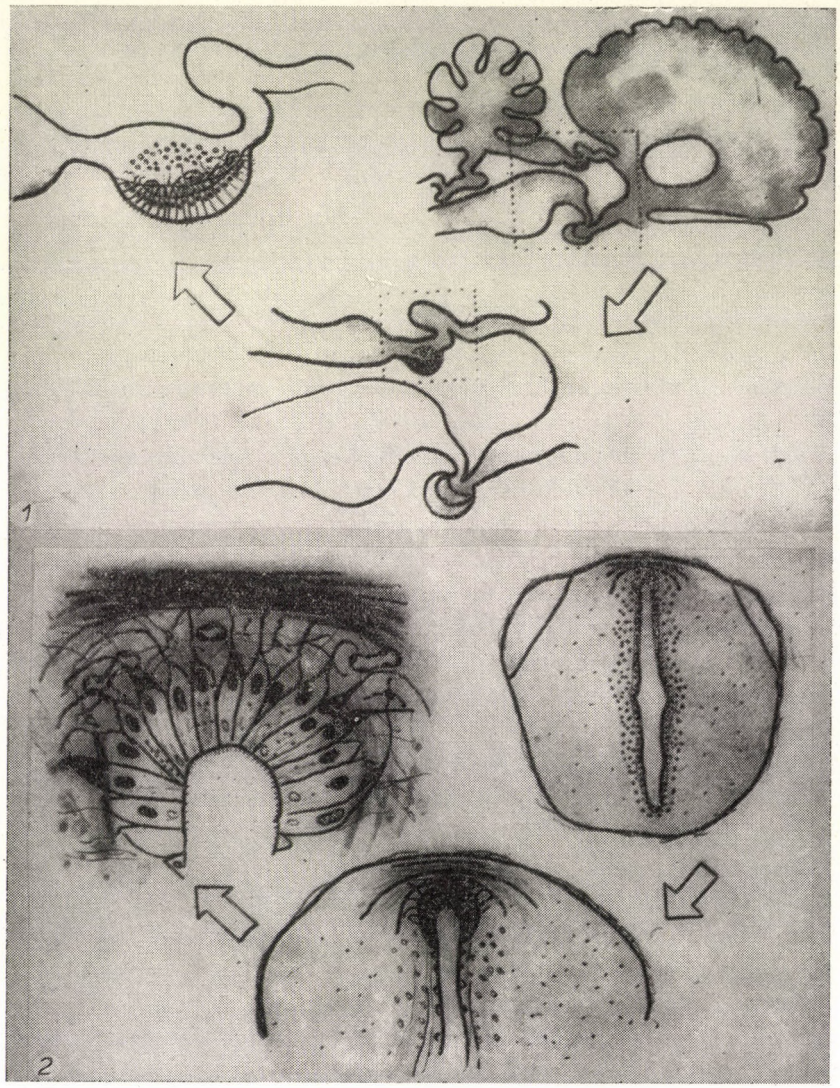


*Fig. 1.* Variously magnified schematic representation of the subcommissural organ in a sagittal section of the mammalian brain

*Fig. 2.* Transversal sections in various scales demonstrating situation of the subcommissural organ

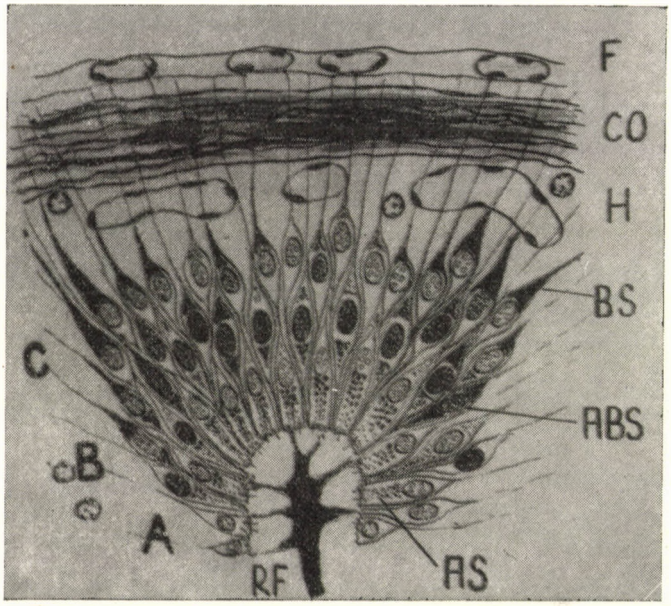


*Fig. 3.* Schematic frontal section of the subcommissural organ. A—B—C: Superficial, median and deep cell-rows. F: Brain surface; CO: Posterior commissure; H: Hypendyma; BS: Basal secrete in the deep layer; ABS: Apical and basal secretion in the median layer; AS: Apical secretion in the superficial cells; RF: Reissner's fibre

## Material and methods

The following species were studied:

| | |
|---|---|
| Fish. | Lebistes reticulatus. |
| | Brachydanio rerio. |
| Urodela. | Triturus vulgaris. |
| | Triturus cristatus. |
| | Pleurodeles waltlii. |
| | Amblystoma mexicanum. |
| Anura. | Rana esculenta. |
| | Bufo bufo. |
| | Bombina bombina. |
| | Pelobates fuscus. |
| Birds. | Passer domesticus. |
| | Columba domestica. |
| Mammals. | Myotis myotis. |
| | Rhynolophus hipposideros. |
| | Epimys norvegicus. |

A total of 165 animals of both sexes was used. All examinations were carried out in the autumn.

The animals were decapitated and the materials were fixed in Bouin's fluid, embedded in Péterfi's methylbenzoate-celloidin-paraffin, 6 microns thick serial frontal, sagittal and horizontal sections were prepared and stained with Gomori's chromhaematoxylin-phloxin modified according to Bargmann or with Gabe's paraldehyde-fuchsin.

## Results

The species studied were found to agree in the following points.

The subcommissural organ was not limited to the area underneath the posterior commissure but extended beyond it forward and backward in a measure varying from species to species. In view of certain structural dif-

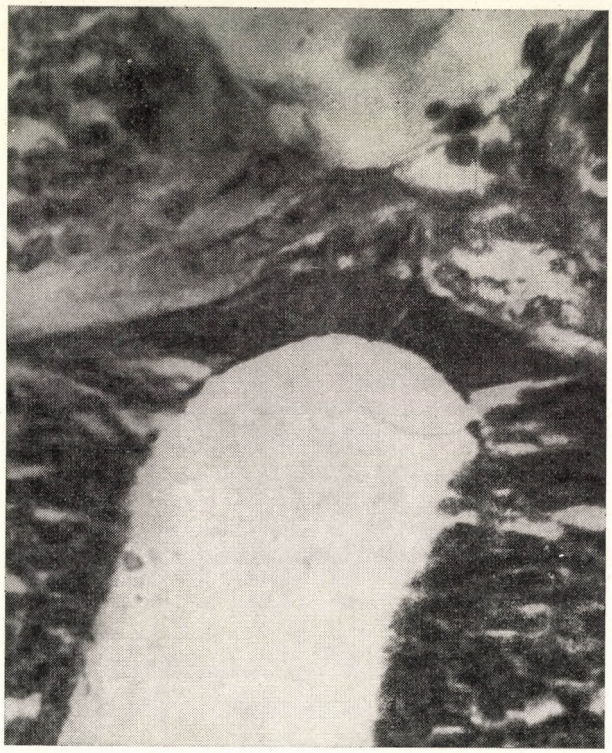

*Fig. 4. Lebistes reticulatus.* Frontal section through the subcommissural organ, stained with Gomori's chrome haematoxylin

ferences we divided the organ in species where it is considerably developed into three separate regions and described them as the rostral, commissural and caudal portions.

The ependymal part of the subcommissural organ in the more advanced forms of vertebrates upward of and including amphibians was found to be made up of three layers, each comprising cells arranged in rows and peculiar in shape to the layer they occur in. The superficial and the deep layers consisted of one or two rows, the intermediate in birds and mammals of five to ten. The

conical cells of the superficial layer (Fig. 3/A) were seen to terminate each in an ependymal process which traversed the superimposed layers, the majority extending across the hypendyma and the posterior commissure as far as to the outer brain surface, the rest ending in the neighbourhood of the hypendymal capillaries. The symmetrical spindle-like cells in the intermediate layer (Fig. 3/B) whose nuclei frequently stained with Orange G had a process at both ends, extending to the ventricle and to the outer brain surface. The spindle-like cells of the deep layer (Fig. 3/C) were asymmetrical in shape, with the longer portion pointing towards the hypendyma and the shorter towards the intermediate cell rows.

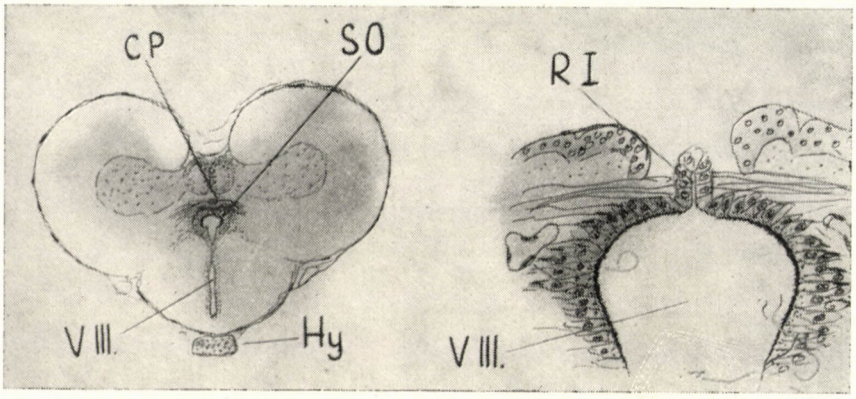


*Fig. 5. Lebistes reticulatus*

Left: Section at the level of the posterior commissure. CP: Posterior commissure; SO: Subcommissural organ; V III: Third ventricle; Hy: Hypophysis
Right: The subcommissural organ in the area of the intrapineal recess. RI: Intrapineal recess; V III: 3rd ventricle

In each of the three layers the Gomori positive granules may be present either in the apical portion at the ventricular side of the cells or in the basal portion at the side facing the exterior brain surface (Fig. 3). Each of these areas presented a different amount of the secreted substance, but the quantity appearing at one and the same place was invariably the same and could be regarded as a distinctive feature of the particular species.

Investigated separately, the individual species gave the following results.

In *Lebistes reticulatus* the subcommissural organ consisted of a thin hypendymal and a thicker ependymal portion (Fig. 4). The latter was made up of a superficial and a deep layer, with the constituent cells differing in shape (Fig. 5).

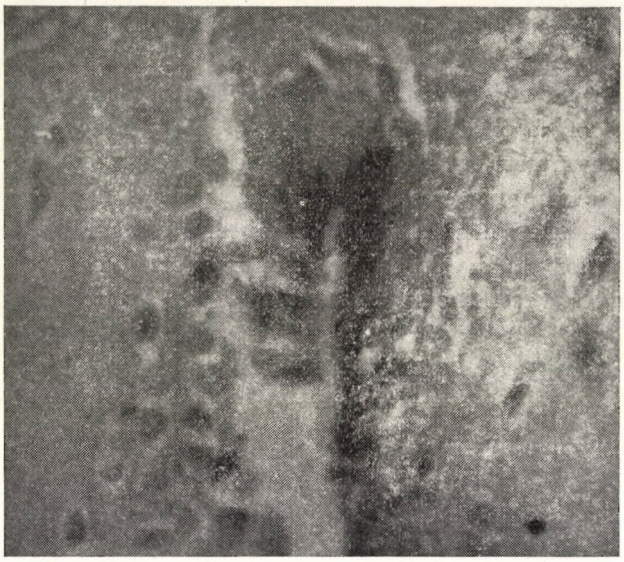

*Fig. 6. Rana esculenta.* Rostral portion of the subcommissural organ. Abundant apical secretion. Stained with paraldehyde-fuchsin

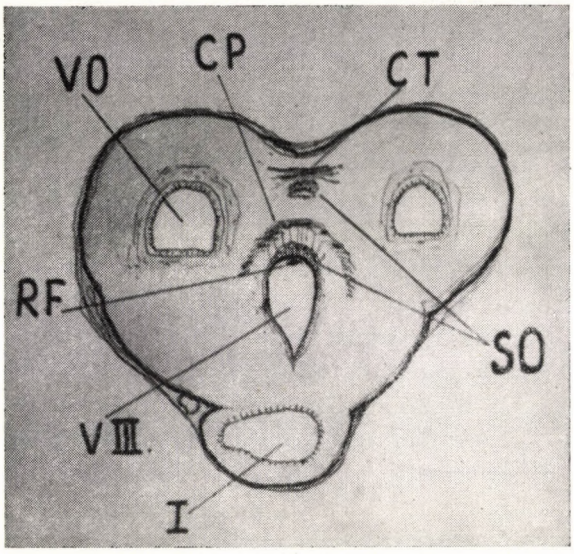


*Fig. 7. Rana esculenta.* Section at the level of the subcommissural organ. VO: Ventriculus opticus; CP: Posterior commissure: CT: Commissura tecti: SO: Subcommissural organ; RF: Reissner's fibre; V III: 3rd ventricle; I: Infundibulum

The superficial cells were conical, their broad ciliated sides facing the ventricle. Their ends facing the cerebral substance tapered off and terminated in thin processes which passed among the cells of the superimposed row and approached the posterior commissure. The oval nuclei were situated in the narrowing conical cell portions.

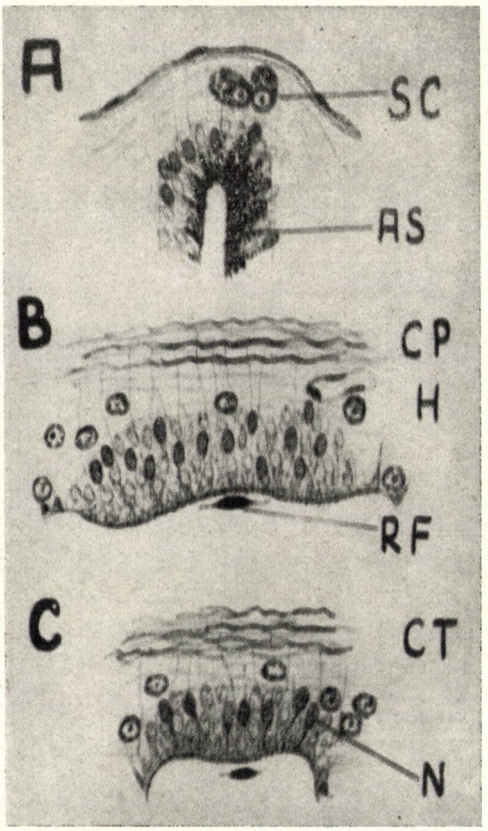


*Fig. 8.* Schematic representation of the subcommissural organ in the frog. A—B—C: Portions before and below the posterior commissure and below the commissura tecti; SC: Secretory nerve cells; AS: Apical secrete; CP: Posterior commissure; H: Hypendyma; RF: Reissner's fibre; CT: Commissura tecti; N: Median cell nuclei staining orange, with Orange G

The deeper situated spindle-like cells were connected with the ventricle by a cytoplasmic processe which passed through the superficial layer. Their opposite end tapered off to form the processes which extended, along with the homologous threads of the superficial cells, partly to the hypendymal blood vessels and partly across the fibres of the posterior commissure to the exterior brain surface. The oval nuclei, considerable in size as compared with

the cytoplasm, occupied the centre of the cells, dividing them into apical and basal portions.

Not only the cell forms were different but also the appearance of the secrete in the different rows. In the superficial layer, the Gomori-positive granules appeared as a fine powder settled apically between the cell nucleus and the ventricular surface, whereas in the basal thread-like process of the cytoplasm they had a wedge-like appearance. In the deeper rows the granules appeared apically and basally as a homogeneous wedge-shaped aggregation situated on either side of the nucleus. The amount of the secrete was everywhere less than in the corresponding parts of the other species.

*Fig. 9. Triturus vulgaris.* Section through the subcommissural organ. Paraldehyde-fuchsin stain. Arrows indicate massive cuneiform basal secrete traceable far into the ependymal process

The picture in *Branchydanio rerio* showed much resemblance to the one just described.

In *Triturus vulgaris* (Figs. 9 and 10) the subcommissural organ, reaching beyond the superposed posterior commissure, was traceable rostrally beyond the intrapineal recess and caudally a long way into the cerebral aqueduct.

The ependymal cells were arranged in several rows forming a superficial, a median and a deep layer (Fig. 11). In structure the superficial layer resembled that in the subcommissural organ of *Lebistes reticulatus* with the difference that at the basal side its cells were more abruptly tapering towards the process. The median layer consisted of several rows of symmetrical spindle-like cells in the commissural portion of the organ; the nuclei frequently stained red

with Orange G. In the deep layer the apical portions of the symmetrical spindle-like cells were rounded off, with rapidly tapering processes extending to the ventricle.

There were considerable differences in the intensity of the secretion between the cell-rows themselves and the rostral, commissural and caudal portions of the organ.

*a)* The rostral part (Fig. 11/A) was poor in cells. The superficial layer presented little apical granules, the intermediate and deep ones hardly any.

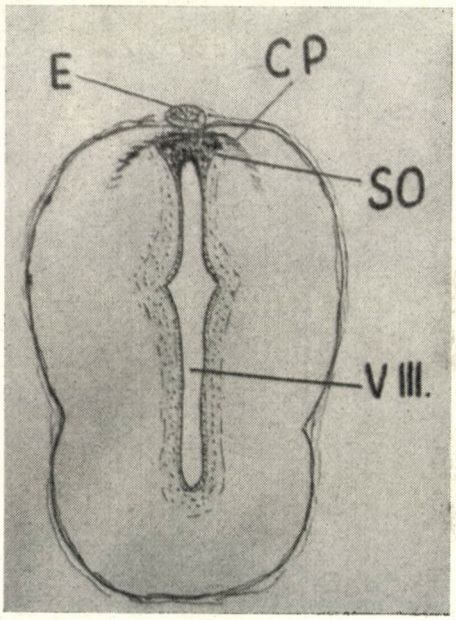


*Fig. 10. Triturus vulgaris.* Section at the level of the posterior commissure. E: Epiphyseal stalk; CP: Posterior commissure; SO: Subcommissural organ; V III: 3rd ventricle

*b)* The portion situated below the posterior commissure (Fig. 11/B) was unique for an abundance of secrete in each layer. The secrete appeared apically and in explicitly diffuse form in the superficial layer, apically and basally in the intermediate layer where it assumed a conical shape, and again basally in conical shape in the innermost layer which exceeded the other two in respect of secretory activity. Basal granules were traceable a fairly long distance inside the fibrils spreading across the hypendyma in which there were cells reminiscent of ganglion cells, similar to those observed in *Rana esculanta* (see further). Ependymal processes leading towards the brain surface and replete with secretory substance were seen to pass between these

cells. The colloid particles about the ganglion cell nuclei gave a strong Gomori-positivity.

Additional features of the commissural portion were that the median layer was made up of three to four cell-rows and that most of the cell nuclei stained an orange red with paraldehyde-fuchsin.

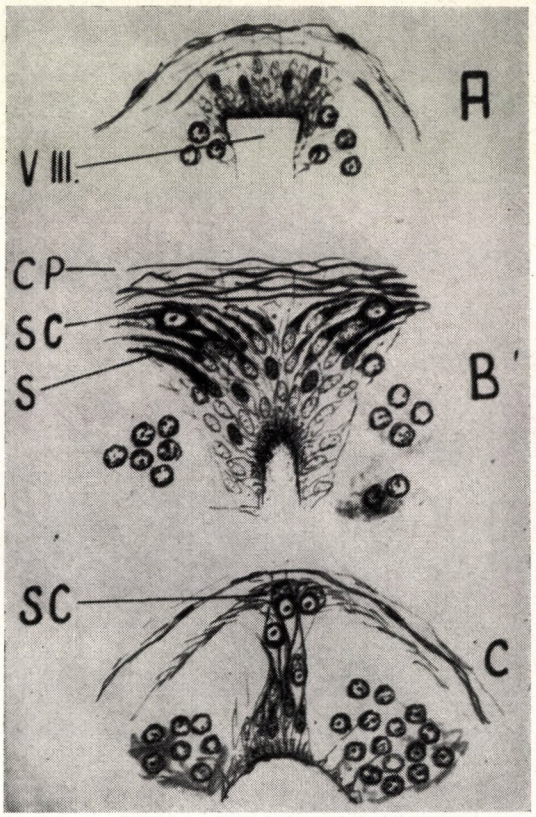


*Fig. 11. Triturus vulgaris.* Schematic illustration of the subcommissural organ in the rostral commissural and caudal portions. V III: 3rd ventricle; CP: Posterior commissure; SC: Secretory nerve cells; S: Basal secrete

*c)* In the caudal portion, the apical secretion of the superficial, and the basal secretion of the lowermost, cells were the most intensive.

The subcommissural organ of *Triturus cristatus* essentially agreed with that of *Triturus vulgaris*.

Different from the preceding were the pictures of all the three portions in the subcommissural organ of *Pleurodeles waltlii*, presenting a finely powdered

apical secrete stronger even than observed in the *Triturus* genus, in fact exceeding in intensity all the other examined species (Fig. 12).

In the caudal portion underneath the ependyma there was a ganglion consisting of a few cells with Gomori-positive granules in them (Fig. 13). The ependymal cell processes filled with secrete and extending towards the brain surface were observed to entwine the ganglion cells very closely.

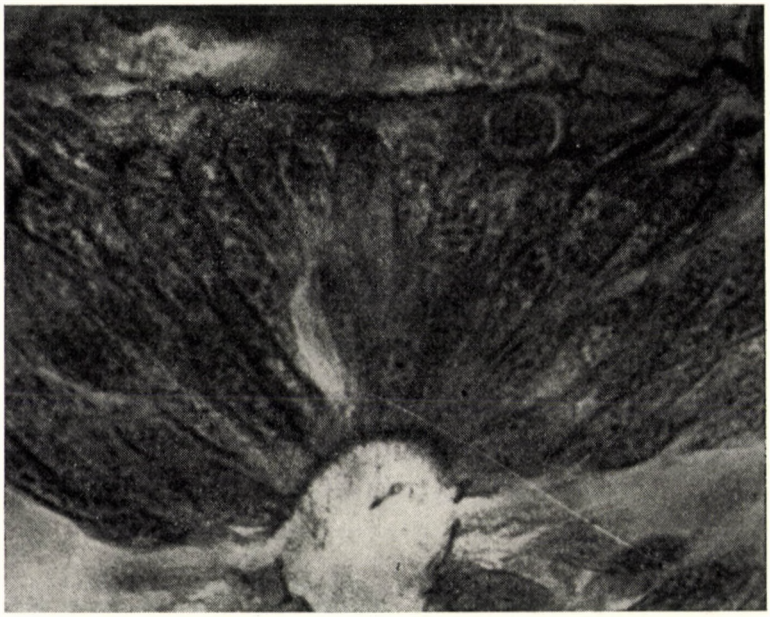

*Fig. 12. Pleurodeles waltlii.* Subcommissural organ in cross-section. Paraldehyde-fuchsin stain. Abundant basal secrete

The subcommissural organ in *Amblystoma mexicanum* was similar to that of *Pleurodeles waltlii.*

*Rana esculenta* (Figs. 6 and 7) agreed with the Urodela in the triple stratification of the subcommissural organ but differed in the behaviour of the individual layers. In view of these differences as also of the size of the organ we again summarized our findings in three groups separately for the portions in front of, underneath and behind, the posterior commissure.

*a)* In the rostral portion (Figs. 6 and 8/A) intensive apical secretory activity of the superficial and median rows gave rise on the ventricular surface to a multitude of massive, colloidal Gomori-positive granules. Basal secretion was feeble in every layer. A further conspicuous feature of this portion was the presence of ganglion cells with copious cytoplasm underneath the ependy-

mal layer and exhibiting, as a sign of their neurosecretory activity, intensely staining Gomori-positive granules interspersed with vacuoles.

*b)* In the commissural portion (Fig. 8/B) the secretory activity seemed to have greatly diminished. The intermediate layer consisted here of three to four rows, with a moderate amount of secrete present at the apical sides of the cells. It was at this level that Reissner's fibre appeared, giving Gomori-positivity.

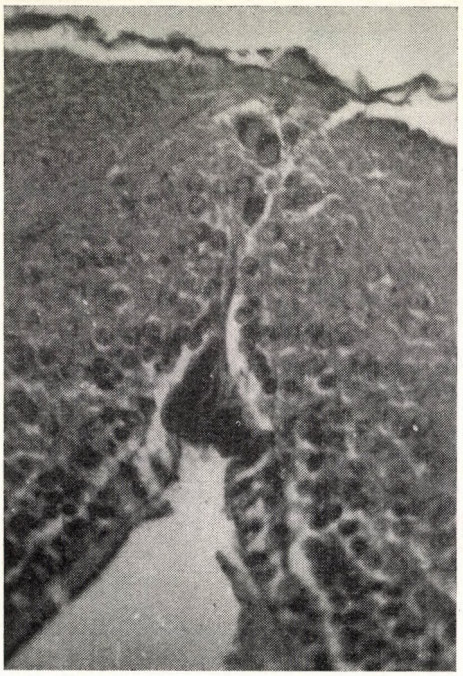

*Fig. 13. Pleurodeles waltlii.* Caudal portion of subcommissural organ. Paraldehyde-fuchsin stain

*c)* The caudal portion of the organ, situated below the commissura tecti (Fig. 8/C), contained less cells, with secretion apically, on the ventricular surfaces of the median and superficial rows.

Similar conditions were found in *Bufo bufo*, *Bombina bombina* and *Pelobates fuscus*.

In *Columba domestica* (Fig. 14) the organ was situated almost exactly under the posterior commissure, extending just a little beyond it front and rearwards. The intermediate layer consisted of five to ten rows (Fig. 15/*b*) with the cells closely compressed. There was little perinuclear cytoplasm;

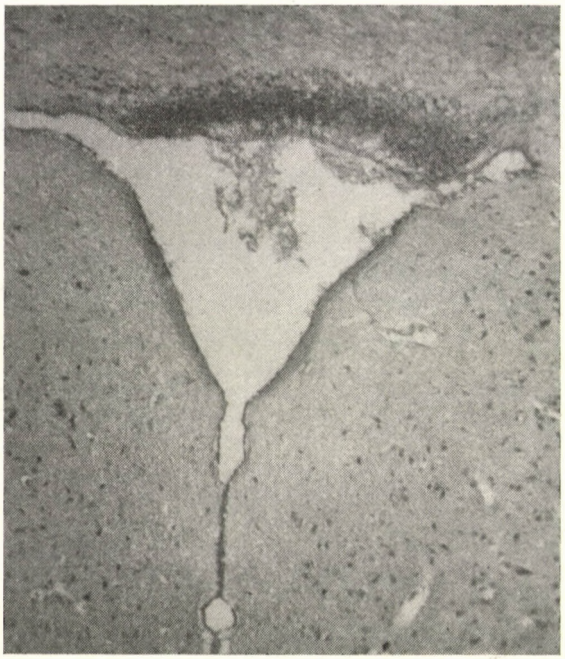

*Fig. 14. Columba domestica.* Subcommissural organ in cross-section. Gomori's chrome-haematoxylin-phloxin stain

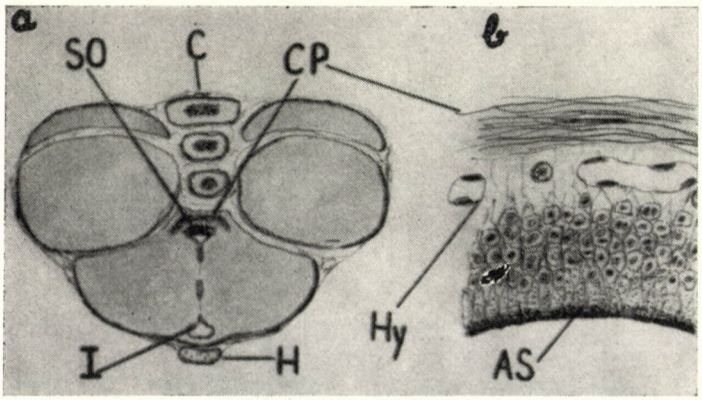


*Fig. 15. Columba domestica*

Left: Brain
Right: Enlarged schematic representation of subcommissural organ. SO: Subcommissural organ; C: Cerebellum; CP: Posterior commissure; I: Infundibulum; H: Hypophysis; Hy: Hypendyma; AS: Apical secrete

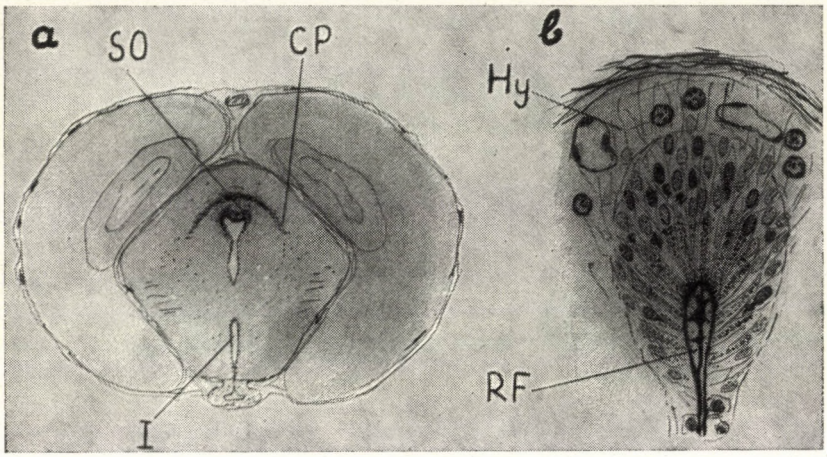


*Fig. 16.* Left: *Myotis myotis.* Section at the level of the posterior commissure. SO: Subcommissural organ; CP: Posterior commissure; I: Infundibulum
Right: *Epimys norvegicus.* Schematic representation of subcommissural organ. Hy: Hypendyma; RF: Reissner's fibre

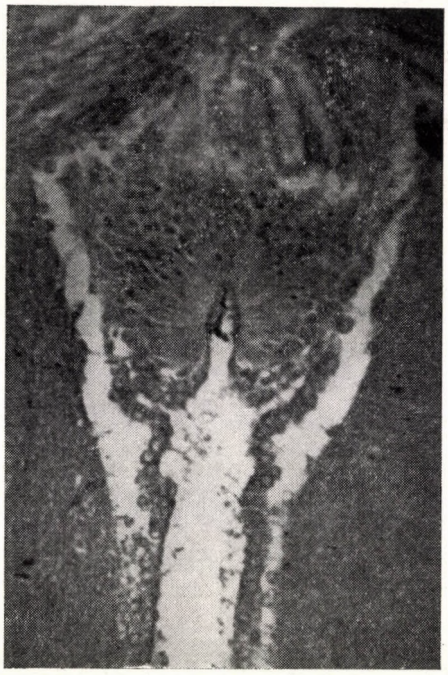

*Fig. 17. Epimys norvegicus.* Subcommissural organ in cross-section. Paraldehyde-fuchsin stain

processes were absent. Secrete was scanty around the nuclei but occurred in abundance in the apical part of the superficial layer.

Very similar were our findings concerning the organ in *Passer domesticus* which produced apical secretion apparently in the superficial layer only.

The subcommissural organ in *Myotis myotis* (Fig. 16/*a*) showed much resemblance to that of the albino rat. In the elongated cells of the superficial layer there was apical secretion. The majority of the intermediate cell nuclei stained with Orange G. The deep layer next to the hypendyma consisted of

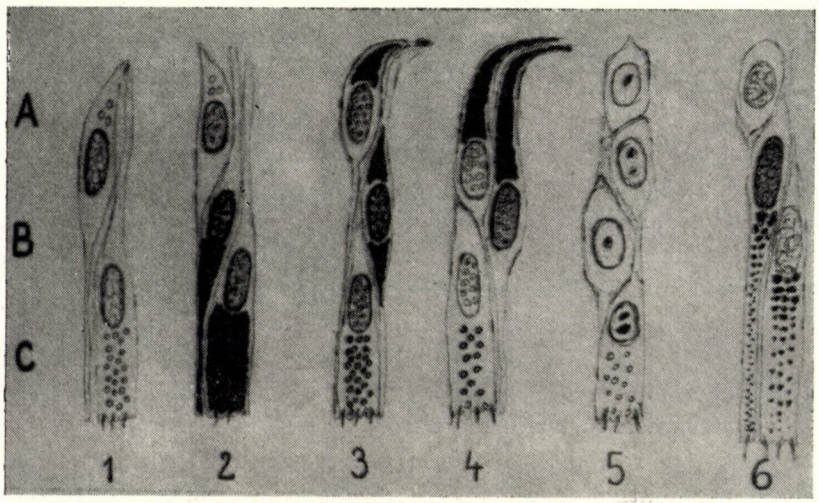


*Fig. 18.* Schematic representation of subcommissural secretion in various species. 1. *Lebistes reticulatus.* 2. *Rana esculenta.* 3. *Triturus cristatus.* 4. *Pleurodeles waltlii.* 5. *Columba domestica.* 6. *Epimsy norvegicus.* A: basal — B: median — C: apical region

but a few cells; their thin cytoplasmic processes with cuneiform incipient parts contained little secrete and extended between the intermediate cell rows towards the ventricle. Basal secretion occurred in none of the layers.

Much the same was the picture in *Rhynolophus hipposideros.*

*Epimys norvegicus* (Fig. 16/*b*) presented extremely elongated conical cells in the superficial layer. The intermediate layer consisted of four to five rows, the cells situated closer to the surface emitted broad processes extending towards the ventricle. The deep layer was composed of round cells with barely traceable processes. Apical secrete comprising granules of different sizes was seen in the median and superficial layers (Fig. 17). Basal secretion was observed in neither of them.

## Discussion

Various qualities suggest themselves as a basis for the comparison of the subcommissural organs of the different animal species. The organ presenting basal and apical secretion of various intensity, has been described to contain cylindrical ependymal cells, a statement which our findings did not corroborate. In the species examined by us the cells were conical or spindle-shaped, occasionally polygonal, but never cylindrical and were always seen to have one or two processes.

Our examinations revealed the organ in most species to comprise three layers, each including a different type of cells (Fig. 3) viz.

1. a superficial layer,
2. an intermediate layer,
3. a deep layer.

The cells of the superficial layer have oval nuclei and are conical or triangular, their bases constituting the ventricular wall and their apices tapering off to form ependymal processes.

The spindlelike cells of the intermediate layer have one process at each end, the one extending to the ventricle and the other to the external face of the brain. The elongated nuclei are oval and stain frequently with Orange G.

The third layer consists of basally situated spindle-like cells, asymmetrical or sometimes polygonal, and characterized, especially in amphibians, by long cytoplasmic basal and thin apical processes.

There are two regions for the secrete to present itself in the cells of each layer: the basal and the apical parts. Four of the resulting six different places of appearance, namely, the apical region in the superficial, the apical and the basal in the intermediate and the basal in the deep layer were seen to display a more intense secretory activity than the rest. The apical secretion usually goes hand in hand with a multiplication of the Gomori-positive granules and with an intensive staining of Reissner's fibre. The basal secretory substance is traceable a fairly long way in the ependyma processes extending towards the posterior commissure.

The distribution of the secreted substance over the various regions differs from species to species and is characteristic of each of them. These changes are presumably due to functional differences. Discrimination between the three cell types and between basal and apical forms of secretion within each furnishes a proper ground for exact comparison and for determining changes in the state of the organ.

Neither is the secretory activity identical in the rostral, commissural and caudal portions, as has been observed by LEGAIT [17]. Since neither the median-sagittal nor the horizontal section proved adequate for the purpose of our study, the former because the secretory ependymal cells are frequently

situated symmetrically on both sides and the latter because it is impossible to obtain a true image of the location of the secretion granules in the cells by cutting them across, serially prepared frontal sections were the only ones amenable to comparison.

The examined groups showed the following typical forms of secretory activity, as illustrated in Fig. 18.

1. Fish: apical in the superficial cells, mildly basal in the deeper ones.
2. Anura: extremely strong apical in the median and the superficial cells.
3. Triturus genus: moderate apical in the superficial, strong apical and strong basal in the intermediate, strong basal in the deeply situated cells.
4. Pleurodeles: moderate apical in the superficial, very intensive basal in the intermediate and deep layers.
5. Birds: weak apical in the superficial cell-row.
6. Mammals: moderate in the superficial and median rows.

A comparison of the subcommissural organs in the various species revealed the most intensive secretory activity in the amphibians: a phenomenon which in our opinion is quite compatible with their life conditions. Histochemical and physiological investigations (Wislocki and Leduc 32, 33, Bargmann and Schiebler 5, Olsson 26, Gilbert 11, 12, 13 and others) revealed a similarity between the subcommissural and hypothalamic secretions. It seems justifiable to attribute them a significant functional role in species of partly aquatic partly terrestrial habitat.

In the fish the organ usually consists of one or two cell-rows. In amphibians, caudate or non-caudate, there are two or three of them and the spindle-like-cells of the second layer appear to represent a more differentiated form of the superficial integumentary conical cells, as can be inferred from the intermediate transitory forms. The spindle-cells of asymmetrical design in the deepest row show differentiation to a still higher stage of development.

A remarkable feature observed in the subcommissural organ was the presence of ganglion cells (Fig. 13) situated below the ependymal cells in the rostral and median portions and between the ependymal processes in the caudal portion. Those in front displayed neurosecretory activity, presenting a varying number of intensely staining Gomori-positive granules interspersed with vacuoles, and nuclei enlarged in different degrees. The cells situated caudally between the basal ependymal processes replete with secrete are rich in cytoplasm and form an elongated nucleus reaching in the mesencephalon.

Recent electron-microscopic findings (Horstmann 16, Fleischhauer 10) do not favour the view that the ependymal processes are supporting elements (Lenhossék 20 and others) but prove that the glial processes are always surrounded by a thin protoplasmic layer. It is hardly possible that any change in the metabolism of the ependymal cells should go without a corresponding one in the ganglion cells which they closely enfold with their processes.

Obviously there exists a close functional interrelationship between the ependymal processes and the ganglion cells which have entered into a morphologically distinct union. This reciprocal activity still awaits confirmation in detail by experiments in progress.

## Summary

The ependymal cells of the subcommissural organ in fish, amphibians, birds and mammals have been found to be arranged in several rows, each row consisting of a different type of cell. Gomori-positive secretion occurred in each, either apically or basally.

The fact that of all examined species the amphibians displayed the most intensive secretory activity may be explained by their particular oecological conditions. The appearance of the second and third cell rows is interpreted as a result of advanced differentiation.

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## ИССЛЕДОВАНИЕ ЭПЕНДИМАЛЬНОЙ НЕЙРОСЕКРЕЦИИ I. СРАВНИТЕЛЬНОЕ ИССЛЕДОВАНИЕ ПОЛОЖИТЕЛЬНОЙ СЕКРЕЦИИ ПО ГЁМЁРИ СУБКОММИСУРАЛЬНОГО ОРГАНА НА РАЗЛИЧНЫХ ПОЗВОНОЧНЫХ

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Исследовались субкомиссуральные органы рыб, земноводных, птиц и млекопитающих.

Эпендимальные клетки субкомиссурального органа располагаются в нескольких рядах, причем каждый ряд состоит из клеток иного типа. Положительная секреция по Гёмёри может иметь место во всех типах клеток в апикальной или базальной форме.

Принимая во внимание вышесказанное авторы описывают характера секреции различных видов позвоночных.

При сравнении отдельных видов самую интенсивную, распространяющуюся на все типы секреции, функцию авторы установили у земноводных. По их мнению это наблюдение находится в связи с экологическими условиями исследованных видов животных.

Появление второго и третьего клеточных рядов авторы приводили в связь с повышенной дифференцией.

## UNTERSUCHUNG DER EPENDYMALEN NEUROSEKRETION I. VERGLEICHENDE UNTERSUCHUNG DER GOMORI-POSITIVEN SEKRETION DES SUBCOMMISSURALEN ORGANS BEI VERSCHIEDENEN WIRBELTIEREN

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Die subcommissuralen Organe von Fischen, Amphibien, Vögeln und Säugetieren wurde untersucht.

Die Ependymzellen des subcommissuralen Organs bilden mehrere Reihen, wobei jede Reihe aus einem anderen Zellentyp aufgebaut ist. Die Gomori-positive Sekretion kann in jedem der Zellentypen in apikaler und basaler Form auftreten.

Es wurde der Sekretionscharakter der untersuchten verschiedenenTierarten beschrieben.

Vergleicht man die einzelnen Arten, so kann die intensivste, sich auf jeden Sekretionstyp erstreckende Funktion bei den Amphibien festgestellt werden, was mit den ökologischen Verhältnissen der betreffenden Arten zusammenhängen dürfte.

Das Auftreten einer zweiten und dritten Zellenreihe wird mit der höheren Differenzierung in Verbindung gebracht.

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