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VERSITA

F. K. STUDNIČKA (1894): FISHES AND AMPHIBIANS ALSO HAVE THE CEREBRAL CORTEX

Miloš Judaš*

University of Zagreb School of Medicine, Croatian Institute for Brain Research, Salata 12, 10000 Zagreb, Croatia

Abstract

The aim of this paper is to provide translation of probably the first report (Studnička 1894) demonstrating that the telencephalon of all vertebrate taxa (including fishes and amphibians) is characterized by the presence of the cerebral cortex (pallium). This report was one of those initiating a century-long and still not fully resolved discussion concerning homologies of various pallial subdivisions in different vertebrate taxa and probably the first to draw attention to the importance of careful study of the pallium in representatives of agnathans (Cyclostomes) such as lampreys (Petromyzonts) and hagfishes (Myxinoids). This article also briefly reviews the current status of comparative research on vertebrate telencephalon, and provides historical notes which position Studnička's report in its historical context.

Keywords

• Comparative neuroanatomy • Cyclostoma • Evolutionary neuroscience • Hagfish • Lamprey • Myxine • Pallium • Petromyzon

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1. Introduction

The past decades have witnessed major advances and significant changes in our interpretation of the evolution of the brain of vertebrates and their cerebral cortex [for comprehensive reviews, see 1-3]. A brief overview of current and generally accepted concepts would seem appropriate to set the context for the report translated here and its historical relevance. However, the general reader will probably also benefit if we first define some basic terms. *Chordates* are Deuterostome animals with a notochord. Extant chordates comprise three major groups: urochordates (tunicates, or sea squirts), cephalochordates (e.g., Branchiostoma/Amphioxus), and vertebrates (or craniates) [1]. While *Acrania* are chordates with no obvious head (such as the lancelet, Branchiostoma, previously known as Amphioxus), *Craniate* is a chordate with fully developed head, but with or without jaws. Thus, while *Cyclostomes* or *Agnatha* are jawless lampreys (Petromyzontids) and hagfishes (Myxinoids) with a circular mouth, the *Gnathostomes* are vertebrates with true jaws. Recent molecular analysis has convincingly demonstrated that *Agnatha* are monophyletic and bona fide members of the vertebrate clade [4,5]. Thus, lampreys and hagfishes are currently treated as members of the cyclostome radiation and the latter as one of the four major vertebrate radiations [1]. Therefore, the four major vertebrate radiations are the agnathans/cyclostomes and three radiations of gnathostomes which comprise: *chondrichthyans* (ratfishes, sharks, skates, and rays), *actinopterygians* (ray-finned fishes), and *sarcopterygians* (fleshy-finned fishes and their four-limbed derivatives, the tetrapods) [1]. The *tetrapods* are vertebrates with four feet, generally including amphibians, reptiles, birds, and mammals. Furthermore, most of the vertebrate taxa are *anamniotes* (their embryos lack an amniotic membrane). In contrast, *amniotes* have an amniotic membrane that encases the embryo in amniotic fluid during development; thus, amniote vertebrates do not need to lay their eggs in water for development [1]. While fishes and amphibians are anamniotes, the amniotes are the nonamphibian tetrapod land vertebrate descendants of ancestral sarcopterygians, i.e. reptiles, birds and mammals [1]. Finally, the *telencephalon* is the rostral expansion of the brain including pallium and subpallium. *Pallium* is the dorsal part of the telencephalon that arises from the rostral, dorsal neural folds, including hippocampus, cortex, and part of the amygdala [6].

A century ago, at the time of Studnička's report, it was a usual practice to designate fishes and amphibians (*Anamniota*) as „lower" vertebrates, while the *Amniota* – or even mammals only – were considered as „higher" vertebrates [7]. Thus, previously influential theory of the rhinencephalon (smell-brain) suggested that the telencephalon of fishes is largely dominated by secondary olfactory input, and ascending sensory systems reaching the telencephalon were believed to exclusively characterize amniotes, or even mammals only [for review, see 7]. This theory is clearly echoed in the discussion between Studnička and Burckhardt at the end of the report translated here.

In the modern comparative research, that old-fashioned *Scala naturae* metaphor of the vertebrate brain climbing slowly up the ladder of progres from fish to human has been replaced by the common theme of a

* *E-mail: mjudas@hiim.hr*

largely conservative Bauplan of vertebrate brain organization, upon which innumerable variations are independently generated along various major phylogenetic lines [7, 8].

While a dorsal part of the pallium lying between the medial and lateral pallia has been identified in all *Gnathostoma*, the question of whether any or all of the dorsal pallium in various anamniotes is homologous to the nonlimbic pallial areas in amniotes is one of the most important unresolved questions in comparative neurobiology [1]. Note that this question currently is not focused on the existence of the cerebral cortex in general, but rather on the existence of possible anamniote homologues for six-layered neocortex of amniotes (and especially mammals). In attempting to fully resolve these questions, comparative neuroanatomists have focused on several defining features of the nonlimbic pallium in amniotes (which in mammals consists of the neocortex), including the receipt of ascending sensory projections from the diencephalon and the absence of afferent projections from the olfactory bulb [1].

2. Evolution and homologies of cerebral cortex in amniotes (reptiles, birds and mammals)

The reptilian telenc ephalon contains two major divisions, the pallium (telencephalic roof) and the subpallium. The pallium includes the medial, dorsal, and lateral cortices, the pallial thickening, dorsal ventricular ridge (DVR), and several amygdaloid nuclei [6]. The lateral cortex is the primary target of the main olfactory bulb, and reciprocates this connection; the medial cortex is generally regarded to be a hippocampal region; the dorsal cortex appears to be a general (nonhippocampal, nonolfactory cortex) cortical area [for review, see 6].

There is general agreement about the homologues between the reptialian and avian cortical regions [for review, see 6], and the lateral, dorsal, and medial cortices are generally compared to the piriform, general (nonolfactory, nonhippocampal), and hippocampal cortices of mammals [6,9]. The available connectivity and neurochemical data together indicate that [6]: (a) the best comparison of the mammalian general cortex (including isocortex) is with the avian hyperpallium and dorsolateral cortex and with reptilian dorsal cortex; (b) the changes during the transition from the reptilian to avian forebrain were not dramatic, since recognition of homologous regions is fairly straightforward; and (c) the reptile to mammal transition is marked by a massive hypertrophy of the dorsal (general) cortex. Finally, assuming that the forebrain of the common tetrapod ancestor was similar to that of extant amphibians, the amphibian-reptile transition was marked by segregation of pallial fields: the medial pallium gave rise to the medial and dorsal cortices of reptiles, the dorsal and lateral pallia gave rise to the pallial thickening and most of the lateral cortex, and the ventral part of the lateral pallium gave rise to the DVR and overlying lateral and amygdalar cortices [6].

3. Evolution and homologies of cerebral cortex in anamniotes (fishes and amphibians)

Fishes. The telencephalon of all fishes includes a pallium and a subpallium, and pallium also receives non-olfactory inputs [7,10]. For the purpose of this article, it is sufficient to focus on pallium of agnathans. All hagfishes are marine scavengers, which feed by entering the body cavities of dead or dying fishes; lampreys are true parasites, which attach to the body surface of other fishes, and (while some lampreys are marine) all spawn in freshwater rivers. Lampreys undergo a larval (ammocoete) stage followed by a metamorphosis to the adult form [1]. The brain of hagfishes is strikingly complex, in contrast to that of lampreys, although hagfishes do not have complex behavioral repertoires, and their visual system is markedly reduced [1]. Recent studies on the forebrain of petromyzontids and myxinoids have been well summarized in several reviews [7,11-13]. The myxinoid pallium apparently does not show three pallial divisions typical of gnathostomes, but is rather homogeneously organized as a cortex with five distinct neuronal layers throughout [14]. Olfactory bulb input is extensive in the hagfish pallium, but remains restricted to two pallial layers [7]. While secondary olfactory projections are also extensive in the lamprey pallium [15], all hagfish pallial layers receive additional dorsal thalamic input [14,16]. In addition, there are reciprocal connections both with the olfactory bulb and the dorsal thalamus [7]. The lamprey pallium also receives dorsal thalamic input [15]. The fact that diencephalic sensory input reaches the pallium in both lampreys and myxinoids demonstrates that the telencephalon (and pallium) is not exclusively of olfactory nature as the old smell-brain theory would predict [7].

Amphibians. Modern amphibians (*Lissamphibia*) form the three orders: *Anura* (frogs and toads; 29 families, about 4086 species), *Urodela* (newts and salamanders; 10 families, about 545 species), and *Gymnophiona* (caecilians; 6 families, 170 species) [17]. It is also assumed that the lungfishes (*Dipnoi* – 6 species) are the living sister group to tetrapods and the closest nontetrapod relatives of modern amphibians [17,18]. In zoology and evolutionary biology, amphibians have always played a problematic role, and the evolutionary status of the brains of amphibians has always created difficulties [17]. The brains of frogs, and especially of caecilians [19] and salamanders [20], appear to be simpler than those of chondrichthyans and osteichthyans, and even of cyclostomes in some respects. However, today it is widely accepted that lissamphibians have undergone secondary simplification which arises from „paedomorphosis" and is related to enlarged genome and cell size [17, for review, see 21 and 22] . On the other hand, the degree to which the morphology of the amphibian telencephalon is primitive or secondarily simplified remains undecided [17].

The amphibian pallium was traditionally divided into a medial, dorsal, and lateral pallial fields [23], but recent gene expression data led to a subdivision of the lateral pallium into a lateral and ventral pallium as different types [8]. In addition, the rostral portion of the pallium appears to be a pallial region of its own [17]. Finally, recent connectivity data lead to conclusion that both the dorsal and lateral pallia are comparable to those of the reptilian lateral cortex, wheres the medial pallium is comparable to both the reptilian medial and

dorsal cortices [9, review in 6]. Briefly, one can distinguish six areas of the pallium of frogs and salamanders, but the homologies and functions of these pallial regions are largely unclear [17]. Most authors agree that the medial pallium is homologous to at least parts of the mammalian hippocampus (Ammon's horn and subiculum) and that a dentate gyrus is lacking [17, 24]. The lateral pallium in the traditional sense is generally considered an olfactory pallium and homologous to the mammalian piriform cortex, while the function of the dorsal pallium is unclear. It receives essentially the same sensory and associative afferents as the medial pallium, but lacks extra-telencephalic and extra-pallial efferents; unimodal sensory areas are lacking and the dorsal pallium appears to have integrative-associative and limbic but no primary sensory functions [17].

Thus, the amphibian dorsal pallium possesses no unimodal, topographically organized areas as found in the mammalian isocortex and the avian hyper-, meso-, and nidopallium [25], and is most probably homologous to the limbic-associative cortex of mammals [17]. Finally, pallial premotor and motor areas are likewise missing in amphibians as well as in lizards and turtles [17].

In summary, the differences between amphibians on the one hand and mammals and birds on the other concern mostly the connection between thalamus and pallium/cortex, the intra-telencephalic connections of the pallium/cortex, predominantly to the striatopallidum, and the further differentiation, enlargement, and specialization of pallial/cortical structures. This further differentiation of the thalamocortical system apparently has occurred independently in mammals and birds originating from different reptilian ancestors [17].

4. Conclusion and introduction to translation of Studnička's report

Preceeding remarks demonstrate that at present there is a general agreement that all vertebrates posses a cerebral cortex (pallium) and unresolved questions concern the exact homologies of various pallial components in different taxa. However, at the end of XIX. century, most leading authorities questioned the very existence of any type of cerebral cortex in the so-called „lower vertebrates" (fishes and amphibians – especially Petromyzonta and Myxine, as representatives of supposedly most primitive, agnathan, fishes) was questioned. The report of Studnička, translated here, represents probably the first attempt to reverse that theoretical attitude and to demonstrate that all vertebrates indeed have at least some kind of the cerebral cortex. Not surprisingly, that report initated a long and heated polemics, and echoes of century-old arguments can be detected even in certain present day discussions. It is also interesting to note that the realization that even the „lower vertebrates" have a cerebral cortex came surprisingly late – in the closing years of the XIX. century – that is, well after the introduction of major classical neurohistological methods (Nissl, Weigert, and Golgi staining) and after the firm establishment of the neuron theory through the seminal studies and monographs of Wilhelm His, Auguste Forel, Camillo Golgi, Santiago Ramón y Cajal, Gustav Retzius and Arthur Van Gehuchten (for an extensive review, see [26, for an extensive review see 27].

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TRANSLATION OF : F. K. Studnička (1894)

Towards the history of the „Cortex cerebri".

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The present report, originally entitled *Zur Geschichte des „Cortex cerebri",* was delivered by F. K. Studnička in 1894, as a lecture on the 8. Meeting of the German Anatomical Society held in Strassburg i. E., from 13. to 16. May 1894 (during the Fifth Session of the meeting). It was subsequently published in Transactions (*Verhandlungen*) of that meeting, in a supplement volume to the official journal of the society, the *Anatomischer Anzeiger*.

Gentlemen! Let me be permitted to report on the first appearance of the so-called gray „cortex" in the prosencephalic hemispheres of the series of vertebrates. The cerebral cortex of mammals was alredy known to old anatomists. However, its presence in the brain of birds received its first detailed description by Bumm (Bumm 1883). That it is also present in the brain of reptiles, we have learned from Stieda's work on the brain of turtles (Stieda 1875a,b). The cortex of reptiles, which are the lowest among *Amniota*, is quite interesting; it has been recently studied by several authors, such as Schulgin, Köppen (Köpen 1888, 1892), Adolf Meyer (Meyer 1892) and especially by Edinger (Edinger 1888). It has been realized that one can homologize a large part of it (i.e., the part located in the posteromedial part of hemispheres, along the fornix) with the well-known Ammonic cortex of mammals, which is known as an olfactory centre. In addition, it was demonstrated that this formation is directly connected with the olfactory bulb. Until recently, it was generally thought that cortical formation does not exist in the prosencephalic hemispheres of Amphibians, until the studies of Nakagawa (Nakagawa 1891) demonstrated that in a certain Urodele (*Spelerpes ruber*) there are small groups of neurons in the medial part of the pallium which are separated from the central (periventricular) grisea and may represent a primitive cerebral cortex. In his studies, Burckhardt (Burckhardt 1892) also observed that in the *Triton* a small part of the hemispheric pallium represents a probable homolog to the Ammonic cortex of higher animals. Finally, Oyarzun found scattered neurons in outer layers of the amphibian pallium (Oyarzun 1890).

It is quite peculiar that the cerebral cortex is present in the hemispheric pallium of lungfishes (*Dipnoi* – esp. the *Protopterus*), as their brain is generally simpler than that of Amphibians. That cortex was first depicted in figures published by Fulliquet (Fulliquet 1886), and then described in detail by Burckhardt (Burckhardt 1892, 1894a,b,c). He showed that – just like in reptiles – the Ammonic cortex is here also separated from the remaining cortex. As one can conclude from Burckhardt's illustrations, the Ammonic cortex is here better developed and contains more cells than the remaining portion of the hemispheric cortex, which is formed only by separate groups of neurons.

Thus, according to previous findings, lungfishes and amphibians were the lowest vertebrates possessing the cerebral cortex in their telencephalic hemispheres. However, the studies I have performed demonstrate that more or less distinct cerebral cortex is also present in the hemispheres of Cyclostome brains.

But, before we can discuss that cortex, it is necessary to clarify what exactly can be regarded as telencephalic hemispheres in the brain of Cyclostomes – especially of Petromyzontids, which display a more ancestral pattern of organization. As you know, if we put aside older views (e.g. of Johannes Müller), there are two views on the brain of Petromyzontids in the current literature.

According to the older view, presented in the publications of Burt Green Wilder (Wilder 1875, 1876, 1877, 1887), and especially of Ahlborn (Ahlborn 1883) and subsequently of S. P. Gage (Gage 1893) and my own (Studnička 1894), the walls of the hemispheres (which contain the pallium) are in all their parts of the same thickness, and the rostral part of the so-called third ventricle is in the interhemispheric space covered by the *Tela chorioidea* and partly (i.e., rostrally) by the upper part of the *Lamina terminalis* (which partly corresponds to the *Lamina supraneuroporica* of Burckhardt).

According to the second view, first exposed by Edinger (see, e.g., Edinger 1888) and accepted in the textbook of Wiedersheim (Wiedersheim 1883 and subsequent editions), what was designated as „hemispheres" by earlier authors is in fact homologous to basal ganglia (*Corpora striata*) of Amniota, and just the *Tela* represents the pallium proper of the quite reduced and un-paired prosencephalon. These authors interpret the brain of Petromyzon in the same way as Rabl-Rückhard has interpreted the brain of Teleosts (Rabl-Rückhard 1883).

The appearance of the grey hemispheric cerebral cortex is mainly restricted to the hemispheric pallium. According to authors who accept the second view, that pallium is developed just as an epithelial membrane; therefore, one naturally cannot think of it as the cerebral cortex. According to authors who accept the first view, in contrast, the pallium is conceived as the massive wall and thus it is possible that cerebral cortex can develop within it.

According to my investigations, *Petromyzon* really possesses in that part of the brain small groups of neurons, quite similar to those observed in the pallium of *Protopterus* or *Spelerpes*. Now, I regard these cell groups as real, although quite primitive cerebral cortex (these cell groups are not equally distinct in all analyzed specimens, and sometimes the cells were scattered through the hemispheric wall).

To that one can put forward an objection, that it is quite possible for cerebral cortex to develop below the surface of the *Corpus striatum*, and not just within the pallium, and that that could be (if one accepts the second view) even quite possible because the *Corpus striatum* has to perform the function of the rudimentary pallium in addition to its own function. Well, of course, that can be decided only by further study of the development and comparative anatomy of the so-called „*Corpus striatum*".

I will here only try to focus your attention to those brain parts which are situated between the hemisphere and the *Tela*, or (according to the first view) between the *Corpus striatum* and the pallium (see Figure 1). You may observe that there is no cortex developed in that part, which (according to the second view) must belong to the pallium and represent a massive component of it. If we accept the first view, we have to regard that part as the inner margin of the hemisphere; it is located at the same place in which in other animals (e.g., already in reptiles) the fornix is situated.

I believe that it will be ascertained beyond any doubt that these cell groups in the brain of *Petromyzon* represent a real cerebral cortex, if we compare it with a closely related brain of *Myxine*.

The investigations of Retzius (Retzius 1893) have demonstrated that in *Myxine* all forebrain ventricles are almost completely obliterated. Now, I have observed that in that massive forebrain, the well developed cerebral cortex composed of two layers of neurons (even three layers in the medial part of the hemisphere) is present exactly in the same location in which the above mentioned cell groups are observed in the *Petromyzon*.

It is known that in any vertebrate in which the hemispheric cerebral cortex is present (perhaps with the exception of Amphibians), the Ammonic cortex is separated from the remaining cortex and that this Ammonic cortex becomes relatively larger as we descend along the series of vertebrates towards the lower forms.

As I tried to demonstrate in an earlier publication (Studnička 1894), a certain kind of the cerebral cortex is present in hemispheres of Cyclostomes which are homolog only to the most caudal part of hemispheres of higher vertebrates. Let me put forward the hypothesis that this entire cortex should be compared only with the Ammonic cortex of other vertebrates, and that it also represents an olfactory centre. Thus, Cyclostomes still do not possess other types of cortical formations, which could serve other functions. It is probable that here the

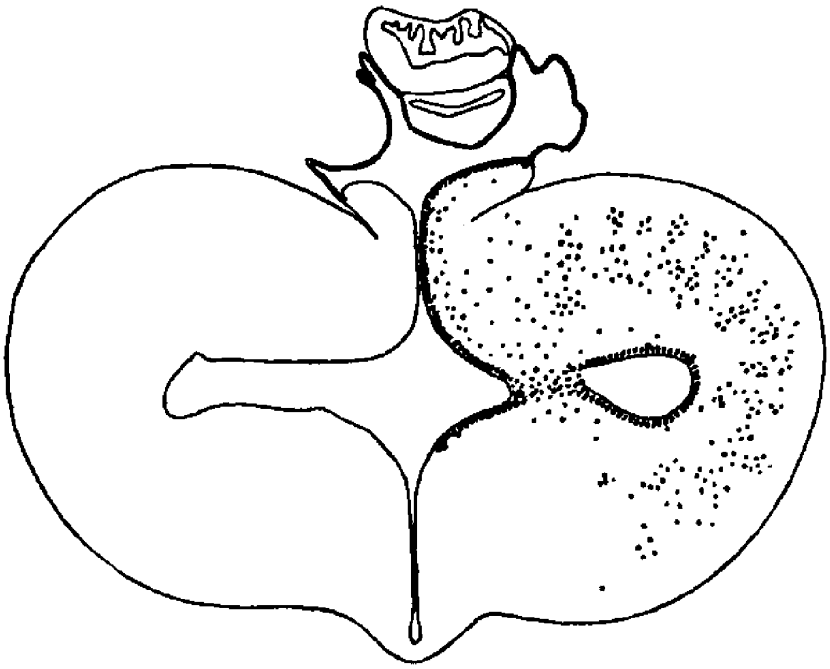

Figure 1. Coronal section through the hemisphere of *Petromyzon Planeri*.

entire hemisphere represents just a higher olfactory centre.

In favor of this interpretation of the cerebral cortex of cyclostomes as an olfactory centre speaks the following observation: this cortex is much better developed in the blind *Myxine* (which also has a more developed olfactory apparatus) than in the *Petromyzon* which is endowed with the sense of vision.

To conculde this short report, let me note that the cortex of *Petromyzon* was alrready illustrated in the publication of Mss. Susanne Phelps Gage (Gage 1894 – Plate VIII, Figs 105 and 106), and the cortex of *Myxine* was already (although quite schematically) illustrated in two figures in the publication of Retzius (Retzius 1893). However, although these authors included it in their illustrations, they did not conceive depicted structure as the cerebral cortex.

Discussion

BURCKHARDT agrees that the forebrain of lower fishes has exclusively olfactory functions. However, that is exactly the reason not to accept the homology of cortex in prosencephalon of lower fishes with the cortex of amphicoele brains in which the cerebral cortex represents a substrate for quite different functions.

STUDNIČKA: I have really observed numerous radially coursing nerve fibres in some cortical layers of the Myxine brain – thus, they may belong to the olfactory radiation. The same fibers were not so easily observed in the brain of Petromyzon; however, on sections stained with the Golgi method, I was able to observe nerve fibers which originate from neurons of the „Cortex" and stretch to the medial brain regions.

Translator's References:

Note on references: In translating Studnička's report, I have tried to retain his style as far as possible, only turning the phrases and sometimes breaking the sentences when it was necessary to produce readable English. Studnička also used several, rather inconsistent, methods for giving bibliographic references (for transcription of the original report, see Supplement 1). Some of them appear as footnotes, and others in parentheses in the text. Studnička often gives just an author's family name without a bibliographic reference. He also misspelled the names of certain authors – e.g., Nakagava instead of Nakagawa). I have traced relevant references in all such cases, except for „Schulgin" (mentioned in the text without any additional data). Thus, I have added a complete new reference list including citations given in full (and adding first names of authors as well as full titles of old German scientific journals, to enhance their proper tracking and recognition), and corrected as was often necessary. Accordingly, I inserted the proper references in brackets in the present translation. To see how Studnička in fact quoted them, see the transcription of the original report in the Supplement 1.

Note on authors: František K. Studnička (1870 – 1955) was a renowned histologists, the founder and first head of the Histological-Embryological Institute at the School of Medicine of the University J. E. Purkinje in Brno, and later at the Charles University in Prague. Researchers cited by Studnička were: Friedrich Ahlborn (1858 – 1937), zoologist from Göttingen; Anton Bumm (1849 – 1903), a student of Bernhard von Gudden, professor of psychiatry in Munich and director of psychiatric institutions in Deggendorf and Erlangen; Rudolf Burckhardt (1866 – 1908), eminent zoologist, naturalist and palaeontologist of the University of Basel (where his father was a Rector), who died as the director of the Zoological Station Rovigno (Rovinj, Istria – part of Croatia); Adolf Meyer (1866 – 1950), a swiss-american neurologist and psychiatrist who studied psychiatry at the University of Zurich under Auguste Forel and neuropathology under Constantin von Monakow, and in 1892 moved to United States; a German neuroanatomist and histologist Hermann Rabl-Rückhard (1839 – 1905); Ludwig Stieda (1837 – 1918), an eminent professor of anatomy at the University of Dorpat (University of Tartu – Estonia) and University of Königsberg; Susanna Phelps Gage (1857 – 1915) was embryologist and comparative anatomist at the Department of Histology and Embryology of the Cornell University, married to Simon Gage, professor of anatomy and physiology at Cornell University, and student of the famous Cornell professor Burt Green Wilder. The names of Ludwig Edinger and Gustav Retzius are probably well enough known to any student of neuroscience. I was not able to uncover full biographical data on Georges Fulliquet, Max Köppen, Isaac Nakagawa, A. Oyarzun and Robert Wiedersheim, However, Robert Wiedersheim was author of widely used and esteemed German Textbook of Comparative Anatomy; A. Oyarzun arrived from Santiago de Chile and performed the qouted study under the guidance of Ludwig Edinger at the Senckenberg's Institute in Frankfurt am Main; Isaac Nakagawa performed his research under the supervision of Professor Henry Fairfield Osborn in the Class of 1877 at the biological Laboratory of Princeton College and the list of Princeton alumni states that he was subsequently a B.Sc. at the Bacteriological Institute in Tokyo and subsequently a professor in the Government Medical College at Sendai.

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SUPPLEMENT 1: TRANSCRIPTION OF THE ORIGINAL 1894 REPORT OF F. K. STUDNIČKA

The present report, originally entitled *Zur Geschichte des „Cortex cerebri"*, was delivered by F. K. Studnička in 1894, as a lecture on the 8. Meeting of the German Anatomical Society held in Strassburg i. E., from 13. to 16. May 1894 (during the Fifth Session of the meeting). It was subsequently published in Transactions (*Verhandlungen*) of that meeting, in a supplement volume to the official journal of the society, the *Anatomischer Anzeiger*.

Herr F. K. STUDNIČKA: Zur Geschichte des „Cortex cerebri".

Anatomischer Anzeiger, Ergänzungsheft zum IX. Band (1894.): Verhandlungen der Anatomischen Gesellschaft auf der achten Versammlung in Strassburg i. E., vom 13.-16. Mai 1894., pp. 193-197.

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M. H.! Ich erlaube mir hier einige Worte über das erste Auftreten der sogenannten grauen Rinde oder des „Cortex" der Vorderhirn-Hemisphären in der Reihe der Wirbeltiere mitzuteilen:

Die graue Rinde des Säugetiergehirns war schon den ältern Anatomen bekannt, diejenige der Vögel wurde dagegen erst von BUMM (1883) eingehender beschrieben. Dass sich eine solche auch in dem Reptiliengehirn befindet, darauf machte uns in seiner Arbeit über das

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Cheloniergehirn erst STIEDA (1875) aufmerksam. Der Cortex der Reptilien, der niedersten Amnioten, ist ziemlich interessant; er wurde in der letzten Zeit von mehreren Autoren eingehender studirt, so von SCHULGIN, KÖPPEN, AD. MAYER und besonders von EDINGER. Es wurde erkannt, dass man einen grösseren Teil desselben an der medianen hinteren Partie der Hemisphären, gleich an dem Fornix, mit dem bekannten Ammonscortex der Säugetiere, bekanntlich einem Riechcentrum, homologisiren darf; man hat unter anderem die directe Verbindung dieser Formation mit dem Bulbus olfactorius bewiesen.

Man war bis unlängst allgemein der Meinung, dass die Vorderhirnhemisphären der Amphibien einer Cortexformation ganz entbehren, bis die Untersuchungen von NAKAGAVA (Journ. of Morph., 1891) uns gezeigt haben, dass bei einem Urodelen – bei Spelerpes ruber nämlich – in der medianen Partie des Hirnmantels kleine, von dem centralen Hirngrau getrennte Gruppen von Ganglienzellen sich befinden, die uns eine primitive Hirnrinde darstellen sollen. Auch BURCKHARDT macht in einer seiner Arbeiten (Ueber Protopterusgeh., 1892) die Bemerkung, dass sich bei Triton an einer kleinen Stelle des Palliums der Hemisphäre eine vielleicht dem Ammonscortex der höheren Tiere homologe Hirnrinde befindet. Einzelne Zellen in den äusseren Schichten des Amphibienpalliums bewies endlich noch OYARZUN (A. f. m. A., 1890).

Es ist sehr sonderbar, dass die Dipnoer, speciell der Protopterus, dessen Gehirn im Ganzen einfacher als das der Amphibien gebaut ist, eine Hirnrinde in dem Pallium der Hemisphären besitzen. Es war FULLIQUET (Recueil zool. suisse, 1886), der sie zuerst auf seinen Abbildungen gezeichnet hatte; detaillirter beschrieb sie in der letzten Zeit BURCKHARDT; er hat gezeigt, dass – ganz ähnlich wie bei den Reptilien – auch hier der Ammonscortex von dem übrigen Cortex der Hemisphären gesondert ist. Der Ammonscortex ist hier, wie man nach den Abbildungen BURCKHARDT's schliessen kann, besser entwickelt und zellenreicher als der übrige Cortex der Hemisphären, der nur durch einzelne Gruppen von Ganglienzellen gebildet wird.

Die Dipnoer und die Amphibien wären also nach den bisherigen Kenntnissen die niedersten Wirbeltiere, bei denen die Hirnrinde in den Hemisphären sich befindet. Meinen Untersuchungen zufolge besitzt aber auch das Cyclostomengehirn eine mehr oder weniger deutlich ausgeprägte Hirnrinde in den Hemisphären.

Bevor wir von diesem Cortex reden können, ist es nötig, zu fragen, was wir eigentlich bei den Cyclostomen, speciell den Petromyzonten, bei welchen ursprünglichere Verhältnisse zu finden sind, als Hemisphären betrachten sollen. Wie bekannt, existiren in der Litteratur

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zwei Deutungen des Petromyzontengehirns, wenn man nicht von den älteren, z. B., der von JOH. MÜLLER reden will.

Nach der älteren, die z. B. von B. G. WILDER, besonders von AHLBORN und jetzt wieder von S. P. GAGE und mir (Anat. Anz. Bd. 9, No. 10) vertreten wird, sind die Wände der Hemisphären, das Pallium inbegriffen, überall gleich dick, und der vordere Teil des sog. Ventriculus III ist oben zwischen den Hemisphären durch die Tela chorioidea und teils, vorn nämlich, durch den oberen Teil der Lamina terminalis (Lam. supraneuroporica BURCKHARDT's z. Th.) gedeckt.

Nach der zweiten Ansicht, die zuerst EDINGER in seinen „Untersuchungen über das Vorderhirn" ausgesprochen, und der sich auch WIEDERSHEIM in seinem „Lehrbuche" angeschlossen hat, sind die „Hemisphären" nach der Bezeichnung der früheren Autoren nur den Basalganglien (Corpora striata) der Amnioten homolog, die Tela stellt uns dagegen das eigentliche Pallium eines ganz reducirten unpaaren Grosshirns dar. Das Petromyzontengehirn soll man nach diesen letzteren Autoren auf dieselbe Art auslegen, wie bekanntlich RABL-RÜCKHARD das Teleostiergehirn ausgelegt hat.

Das Auftreten der grauen Hirnrinde der Hemisphären ist hauptsächlich auf das Pallium derselben beschränkt. Nach den Autoren,

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die die zweite Auslegung vertreten, ist das Pallium nur epithelial entwickelt, infolgedessen kann hier von einer Hirnrinde natürlich keine Rede sein, nach den ersteren dagegen ist das Pallium massiv, und es wäre ganz möglich, dass es auch in ihm zur Bildung eines Cortex kommen konnte.

Nach meinen Untersuchungen besitzen wirklich die Petromyzonten in diesem Teile des Gehirns kleine Gruppen von Ganglienzellen, ganz denen ähnlich, wie sie zum Beispiel in dem Pallium von Protopterus oder Spelerpes sich finden. Ich halte nun diese Zellengruppen für eine wirkliche, ganz primitive Hirnrinde. (Diese Zellengruppen sind nicht in allen untersuchten Exemplaren gleich deutlich ausgeprägt, manchmal liegen die Zellen nur zerstreut in der Hemisphärenwand).

Man könnte einwenden, dass es ganz möglich ist, dass auch unter der Oberfläche eines Corpus striatum eine Hirnrinde sich entwickeln könnte und nicht nur in dem Pallium, und dies wäre, so könnte man, die zweite Ansicht anerkennend, meinen, um so eher möglich, da doch das Corpus striatum auch die Function des rudimentären Palliums übernehmen musste. Da natürlich kann nur das Studium der Entwickelung und vergleichenden Anatomie des sog. „Corpus striatum" entscheiden.

Ich erlaube mir nur noch an dieser Stelle auf denjenigen Teil des Gehirns, der zwischen der Hemisphäre und der Tela, nach der anderen Deutung zwischen dem Corpus striatum und dem Pallium liegt, hinzuweisen (vergl. Figure 1). In diesem Teile, der doch schon zu dem Pallium gehören müsste, einen massiven Teil desselben darstellend – wenn die zweite Ansicht angenommen wäre – ist nämlich kein Cortex entwickelt. Wenn wir die erste Deutung anerkennen, müssen wir diesen Teil als den inneren Rand der Hemisphäre betrachten; er befindet sich hier auf derselben Stelle, wo anderswo (z. B. schon bei Reptilien) der Fornix zu finden ist.

Ich glaube, dass dann jeder Zweifel, ob jene Zellgruppen im Petromyzontengehirne einen wirklichen Cortex darstellen, wegfällt, wenn wir dasselbe mit dem nahe verwandten Myxinehirn vergleichen.

Die Untersuchungen von RETZIUS (Biol. Unters. V) haben uns gezeigt, dass bei Myxine alle Ventrikel des Vorderhirns bis auf kleine Spuren obliterirt sind. Ich habe nun beobachtet, dass in diesem massiven Vorderhirne, genau an jenen Stellen, wo bei Petromyzon die bekannten Zellgruppen sich befanden, eine schön entwickelte Gehirnrinde

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die aus zwei, in der medianen Partie der Hemisphäre aus drei Schichten von Ganglienzellen gebildet ist, sich findet.

Es ist bekannt, dass überall in der Reihe der Wirbeltiere, wo in den Hemisphären eine graue Hirnrinde sich befindet, vielleicht mit einziger Ausnahme der Amphibien, der Ammonscortex von dem übrigen getrennt ist, und dass er, je niedriger in der Reihe der Wirbeltiere wir herabsteigen, desto grösser im Verhältnisse zu dem übrigen Cortex ist.

Bei den Cyclostomen finden wir an den Hemisphären, die, wie ich anderswo (im Anat. Anz. Bd. 9, No. 10) zu beweisen versuchte, nur der hintersten Partie der Hemisphären höherer Wirbeltiere homolog sind, nur eine Art von Cortex. Ich erlaube mir nun die Hypothese auszusprechen, dass dieser ganze Cortex nur mit dem Ammonscortex anderer Tiere zu vergleichen ist, und wie dieser ein Riechcentrum ist. Zu einem Auftreten der übrigen Rindenformation, an die sich vielleicht andere Functionen binden, wäre es hier also noch nicht gekommen. Es ist wahrscheinlich, dass hier die ganze Hemisphäre nur ein höheres Riechcentrum darstellt.

Für die Anschauung der Gehirnrinde der Cyclostomen als eines Riechcentrums spricht auch der Umstand, dass bei den sehenden Petromyzonten die Hemisphärenrinde weniger gut, bei der blinden Myxine, die einen stärker entwickelten Riechapparat besitzt, auch die Hirnrinde stärker entwickelt ist.

Zum Schluss dieser kurzen Mitteilung erlaube ich mir noch zu bemerken, dass der Cortex der Petromyzonten bereits auf den Abbildungen in einem Werke von Mss. SUSANNE PHELPS GAGE [1]), und der von Myxine (aber nur ganz schematisch) auf zwei Abbildungen im 5. Bd. der „Biolog. Untersuchungen" von RETZIUS gezeichnet ist, natürlich aber ohne als solcher gedeutet zu werden.

1) The Brain of Diemyctylus viridescens. The WILDER Quart. Cent. Book, Ithaca NY. 1893 (Pl. VIII, Fig. 105, 106.),

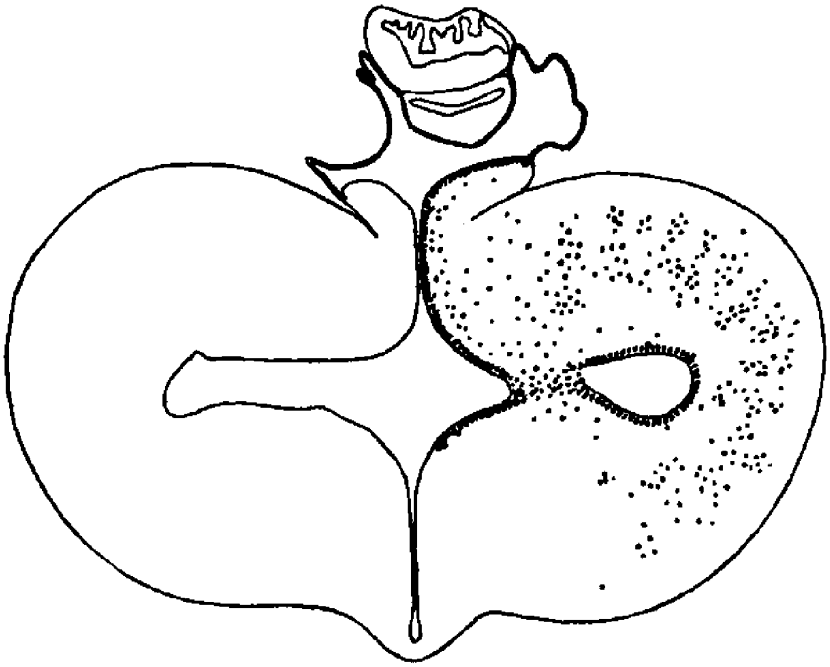

Figure 1. Ein Querschnitt durch die Hemisphären von *Petromyzon Planeri.*

Discussion

Herr BURCKHARDT ist derselben Ansicht, dass die Vorderhirne niederer Fische fast ausschliesslich olfactorischer Function dienen, sieht aber gerade darin das Hindernis, von einer Homologie der Rinde im Vorderhirn der niederen Fische mit derjenigen im amphicölen Hirn, bei welchen die Hirnrinde ganz anderer Function dient, zu sprechen.

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Herr STUDNIČKA: Ich habe wirklich an dem Gehirn von **Myxine** zahlreiche Nervenfasern in den einzelnen Cortexschichten gesehen, die radiär verlaufen, - also vielleicht eine Riechstrahlung. An dem Gehirn von Petromyzon kann man solche Fasern nicht so leicht sehen, aber an Präparaten, die mit der GOLGI'schen Methode angefertigt wurden, konnte ich von den Zellen des „Cortex" einzelne gegen die mediane Gegend des Gehirns auslaufende Nervenfasern sehen.