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Hermann Dexler's "Beiträge zur Kenntnis des feineren Baues des Zentralnervensystems der Ungulaten." [1] An Annotated English Translation of the Original German Article

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Part IV: Telencephalon –
Literature Survey, Foetal Stages, Two Embryos
(with Dexler's Figures 19-24, 33)

Abstract

In this part of the translated text, Dexler offers a comprehensive analysis of the problem of elaborating a schematisation of the equine brain's surface architecture. He strongly refuses to simply adopt the scheme of the carnivore brain to the brain of the horse because, e.g., the convolutions of the equine brain are no arched convolutions (from a formal point of view), but rather track-like convolutions of an angular shape. Dexler recognises the homologies valid for all mammals, i.e., the Fissura longitudinalis cerebri, chorioidea, hippocampi, and rhinalis. In contrast, he shows that the positions and schematisations of other sulci are very heterogeneous, e.g., of the Fissura Sylvii, cruciata, and suprasylvia.

Dexler's descriptions of foetal stages highlight primary sulci that serve as landmarks for the orientation and schematisation, i.e., on the medial surface, the Sulcus corporis callosi and the Fissura callosomarginalis; he uses them to discuss (among others) the Sulcus cruciatus and the Sulcus transversus. As for the dorsal surface, he emphasises the significance of the Fissura suprasylvia that encircles the entire hemisphere and takes a very characteristic course referred to as its *Kantennähe* (Proximity to the Border). On the lateral surface of the foetal hemispheres, the Fissura Sylvii, praesylvia, coronalis, diagonalis, and ectosylvia are highlighted. Dexler states that a classification in all detail of the hemispheres at hand is not possible due to significant asymmetries. He realises that the abundance of side branches and secondary grooves makes the orientation more difficult in adult brains. This applies for the gyri as well, but Dexler addresses this topic also in order to display the major tools for orientation.

Keywords: Brain, Horse, Sulcus, Gyrus, Schematisation, Principles

Introduction

Part I of the English translation comprised the first pages (i.e., pages 288-290) of Dexler's article, presenting his general remarks on the problems and challenges of neuroanatomical descriptions of the brain. Part II (i.e., pages 290-322) dealt with the Rhombencephalon and Part III (i.e., pages 322-333) focussed on the Mes-encephalon and the Diencephalon.

Technical Notes: This English translation does not aim to transfer the characteristic rhetorical style of early 20th century German language into idiomatic English. Rather, it attempts to present Dexler's anatomical descriptions, interpretations and discussion in plain modern English. Dexler's personal rhetorical style has been maintained whenever necessary in order not to omit relevant information. Whenever any German wording or term could not be appropriately translated into adequate contemporary English, the text or a footnote presents the *German words in italics* together with equivalent English synonyms and/or relevant explanations, or the term is replaced by the current version according to the Nomina Anatomica Veterinaria [N.A.V.] (2017). Dexler's Latin nomenclature has been maintained in the text, even though it does not always conform to the current version of the N.A.V..

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Dexler's original article contained only a small number of keywords that indicated a thematic division of the text; there were no true chapter headings. The following short list of topics has been compiled in order to give the readers of this translation at least a brief overview beforehand for better orientation (not all of them are headings that can be found in the text):

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Contributions to the Knowledge of the Fine Structure of the Central Nervous System of Ungulates

By Prof. Hermann Dexler

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in Prague)

Part IV now continues with pages 333-347 of the original article.

TELENCEPHALON

When we look at the surface of the cerebral cortex of an adult horse we are presented with such a confusing abundance of serpentine-like and angular grooves and convolutions that it is actually difficult for us to find our way. It certainly requires some effort to understand and to apply the various schemes. And yet, after some searching, a rough identification of the outlines of the main grooves is relatively easy. Beyond this, there is such a considerable quantity of secondary and parallel grooves, junctional convolutions and variations that it can be very difficult to deduce the basic plan of the architectonics. Regarding the details, most relevant studies refer either to the brain pattern of carnivores without making a real effort to actually transfer it, or they pay no attention to the details, supposing they are of secondary or even of no relevance.

As proof of the difficulties involved in making a consistent schematisation I would only like to mention the fact that until today one has not even been able to reach a uniform opinion concerning the position of the Fissura cruciata (SCHELLENBERG), Fissura Sylvii (HOLL), or Fissura suprasylvia (BRADLEY). Transferring the pattern of grooves of the equine brain to that of carnivores even only in its main features always has some kind of forced style[3] about it and is ultimately in many cases not at all possible. The gap between both objects is quite considerable; it has been, however, bridged and this could not be achieved without major schematisation. Already the much greater length of the (equine) Cerebrum compared to the much shorter canine brain contributes a lot to this. From a purely objective point of view, the convolutions of the equine brain are no arched convolutions[4], but track-like[5] convolutions of an angular shape[6] that are split many

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[2] *k.k.:* imperial and royal (Austrian and Hungarian)

[3] *etwas Gewaltsames:* an action of forcing an object into a given framework that does not accurately fit

[4] *Bogenwindungen:* arched convolutions, i.e., arched gyri (here and throughout the text)

[5] *Windungszüge:* track-like convolutions; cord-like/strand-like gyri (referring to the course and shape of the convolutions)

[6] *winkelig gebrochen*: angular, bent like an angle

times. They can be regarded as arched convolutions only in the genetic but not in the formal sense. They do not proceed in an arched course around a Sᴜʟᴠɪᴀɴ fissure, but are more or less longitudinally oriented, in particular, those lying more dorsally. The argument of HOLL that the vertex part of the folds is strongly bent, as is generally the case in ungulates, can change little about this.

The horse is an exception; its fourth arched convolution does not have a vertex as it ends earlier and, according to HOLL, the first one has lost the character of an arched convolution. Finally, the four homologised arched convolutions are found in some locations, i.e., latero-caudal and medio-caudal, spread over such a large area that within the same area one has to assume additional[7], independent grooves, which despite all efforts cannot be homologised.

Many of the viable schemes do not sufficiently support our attempts to find our way around the labyrinth. They are either too simple (a criticism of which the scheme of ELLENBERGER perhaps cannot be spared) or they are too forced[8]. The object is pressed into the desired shape for the sake of the theory. SCHELLENBERG finds that the subdivision of the frontal ends of the poles of the hemispheres of the goat resembles that of the human. In a rigorously performed homologation, he also transfers it to the respective cortex pattern of the horse. Even if he may be permitted to make his desired transfer from human to goat, this cannot be done in the case of the horse. A morphological comparison of the human frontal brain with that of the horse completely lacks any justification. Despite all due tolerance, the scheme does not conform to the objective findings. Another less fundamental objection is that some schemes (particularly those of the lateral surface) are drawn in such a crude manner that they show almost no similarity to the equine brain.

Even when, after careful dissection of many brains, one has become aware of the main features of the pattern of grooves, one cannot get beyond the plentiful items in question that are subject to a personal opinion; only then do we realise the difficulties standing in the way of a clear recognition. We do recognise the homologies that are valid for all mammals also for horses, i.e., the Fissura longitudinalis cerebri, the Fissura chorioidea, the Fissura hippocampi and the Fissura rhinalis; we further realise that homologising with the carnivore brain is the most advantageous approach, even more so as MARTIN has shown at least on the brain of cattle that such a procedure is reasonable from an ontogenetical point of view. Besides this, however, quite a number of questions remains open, despite the avid attention that has been paid to the subject (KÜKENTHAL, ZIEHEN, TURNER, CLARKE, SMITH, MARTIN, HOLL, SCHELLENBERG, etc.), so that our schematisations have to be regarded as imperfect or insufficient. Even the attempted, rough classification as lobes has caused a lot of objections.

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[7] *neue:* new; however, not strictly in a chronological sense (rather in terms of being additional)

[8] *gewaltsam:* oppressive, forced; meaning to put a thing into a framework which does not fit properly

Already the question regarding those items that can facilitate a distinction of certain areas of the cerebral cortex includes a great many of the afore-mentioned objections. If, for instance, SCHELLLENBERG is in favour of a broader interpretation of ELLENBERGER's term *Occipitalhirn*[9] (by attributing to it not only the part which is delineated by the Sulcus occipitotemporalis and collateralis, but including also the part marked by a transverse line that caudally touches the Splenium corporis callosi), one can surely agree with this view. ELLENBERGER, however, referred to this earlier by distinguishing between a small occipital lobe in the anatomical sense and a large occipital lobe in functional terms (page 757 of the latest edition of his *Handbuch der Anatomie* [10]). We have to argue the case for a larger occipital (brain) area if we consider the radial influx areas[11] of GRATIOLET's fascicle. Unfortunately, this still does not bring the matter to a conclusion because the anatomical delineation of the visual cortex area is not yet known.

The physiological principle of classification (which is in many ways superior to the mere morphological one) reveals its limitations soon enough at this point. SCHELLENBERG wants to deduce homologous cortex areas from studies on the fine structure of the *Sigmoidalrinde*[12] of carnivores and ungulates. The results of these endeavours are not yet available. In the older editions of FRANK's *Anatomie der Haustiere*[13], the motor cortex areas revealed by MARCACCI by means of electrical stimulation are displayed as sharply outlined circles in the schematic representation of the sheep's brain where they are located far rostral in the frontal part of the brain on both sides of the Fissura coronalis. Similar data were presented on the horse brain by ARLOING in 1878. He found that a certain form of electrical stimulation[14] of cortical areas surrounding the Fissura cruciata did not cause motor activity. According to what I have seen in horses together with KREIDL, and later on in goats and sheep, alone and together with MARGULIES, the precise localising of the motor cortical centres of certain groups of muscles urgently requires verification. ZIEHEN, who had the chance to perform an electrical cortical stimulation on the brain of a Virginian opossum, emphasises the partial overlap of the discovered centres.

If I wanted to delineate, on the basis of data available to me, a motor area in the horse's brain, I would have to include almost the entire frontal and parietal parts of the brain as far as the visual cortex for the time being. However, such a statement would go too far as long as it remained without being supported by exact investigations. A certain congruence of these functionally homologous cortex areas cannot be denied if we attribute a predominantly sensomotor cortex area to the rostral half of the hemisphere, and a predominantly sensory cortex area to the

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[9] *Occipitalhirn*: occipital part of the brain; occipital brain (here and throughout the text)

[10] *Handbuch der Anatomie:* "Handbook of Anatomy"

[11] *Einstrahlungsgebiete*: areas which receive radially arranged nerve fibers

[12] *Sigmoidalrinde*: cortex of Gyrus sigmoideus

[13] *Anatomie der Haustiere*: "Anatomy of Domestic Animals"

[14] *Faradisation*: electrical stimulation; the procedure is not described

hemisphere's posterior parts. We can go even further in saying that everyone aiming at evoking muscle contractions originating from the cerebral cortex would begin (in any mammalian) with exposing and touching the area of the rostral part of the hemisphere's dorsolateral surface. One would rightly expect a certain topographical sequence of the three main motor centres, i.e., hind leg, front leg and facial area[15], of which the type of topographical arrangement (according to ZIEHEN's statement) is transversal in primates, shows a transition to the longitudinal type in carnivores, and is longitudinal in ontogenetically lower species of mammals. And yet, the arrangement of the motor centres can vary markedly, like in rodents where the front limb's centre is located rostral to the hind limb's centre. According to ARLOING's scheme, an even greater displacement would be supposed in horses. In any case, the horse (like the sheep) is probably subordinate to the dog in terms of numbers of motor centres. It would certainly be wrong to imagine these centres to be as astonishingly finely differentiated as they are in the brains of humans, of more highly developed monkeys, or even of dogs. However, even once our knowledge about the localisations of these centres in the brains of ungulates has become more advanced than it is at present, using this for the exact delineation of functionally homologous areas will still not be possible. This is due to the proven overlap of some centres that must be imagined as being defined by mixed zones rather than by a line; this is due to their different significance for ipsilateral and contralateral movements in different animals; this is due to the intensive intermingling with sensory areas; and, finally, this is due to the fact that the function of the pyramidal tract has not been fully determined up until today.

We are not much better off when looking at the site of termination of the olfactory tract. BROCA's proposal to include the entire Gyrus fornicatus in the olfactory centre was not adopted because it could not explain the incongruity between the development of this convolution and the rudimentary development of the other parts of the central olfactory apparatus. The same is true for LÈSBRE's and FORGEOT's re-application of BROCA's scheme.

In his lectures, EDINGER voices his doubts about the affiliation of the Gyrus fornicatus to the olfactory brain, and ZIEHEN is the authoritative spokesman supporting the opinion that both the physiological characterisation and the precise anatomical definition of the olfactory brain are not possible at the present time; the term *Riechhirn*[16] only serves for a superficial orientation. For this purpose, the term Rhinencephalon has been attributed only to those basal parts of the hemisphere that are located in front of the Chiasma opticum, namely: The Pars anterior rhinencephali with the Bulbus, the Tractus olfactorius with the Trigonum olfactorium, and the Pars posterior with the Substantia perforata anterior and the Gyrus subcallosus.

Finally, one should emphasise the main point, initially raised by ZIEHEN, that certain functional centres are not always distributed uniformly around certain

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[15] *Fazialisgebiet*: area supplied by the facial nerve (Nervus facialis)
[16] *Riechhirn*: olfactory brain

lobes and grooves. The physiological orientation[17] in the regions of the rostral part of the hemisphere remains totally obscure. One merely has to read ANTON's tentative version about the functional significance of the frontal part of the brain in humans, and one will refrain from the desire to delineate it accordingly in the brain of mammals both in functional and subsequently in topographical terms. These few examples may demonstrate that a physiological principle of classification of the cerebral cortex cannot be sufficient, least of all in horses, where (apart from few experimentally acquired physiological data) we are totally dependent on conclusions by analogy.

The same is partly true when applying the Cerebrum's interior anatomical subdivision to its correlations with the cortex. If, for instance, we stayed with the common supposition that the *Inselgebiet*[18] should be regarded as the cortical area adjacent to the Claustrum, we would indeed have a fixed orientation landmark for the extent of this area. Yet, the features of homology concerning the third and fourth arched convolutions are not further elucidated by this, and, in addition, the nomenclature of the first and second arched convolutions will be shifted and thereby disassociated with the terms from the literature. In conclusion, we have to emphasise that a uniform principle for classifying convolutions, grooves, and lobes is lacking in the horse, more so than in any other gyrencephalic animal. The desired homologies are deduced from comparing the localisations, the depths, and the continued existence of the examined objects; the resulting findings should be subject to assessments by means of ontogenetical and physiological methods. In consideration of all these factors, a schematic pattern has been elaborated from the fundamental statement of ELLENBERGER on this subject; despite substantial objections from peer authors, we would like to regard this scheme as the MOST COMMON one.

These results, together with some necessary additions, shall serve as the basis for our examination.

Fig. 19. Map of the sulci of a Cerebrum of an equine foetus of 56 cm in length; medial view, original size.

Bw *Balkenwindung*, Gyrus callosus; **c** Sectional area where the Diencephalon was cut in order to remove the brain stem; **ca** Commissura anterior; **cmc** Caudal end of Fissura callosomarginalis; **cmo** Rostral end of Fissura callosomarginalis; **d** Gyrus dentatus; **ecl** Fissura ectolateralis; **enl** Fissura entolateralis; **f** Fimbria; **h** Fissura hippocampi; **l** Fissura lateralis; **sla** Fissura sublimbica anterior; **slp** Fissura sublimbica posterior; **ss** Caudal end of Fissura suprasylvia; **sp** Caudal end of Fissura postrhinalis; **3, 2, 1** Radial branches of Fissura callosomarginalis.

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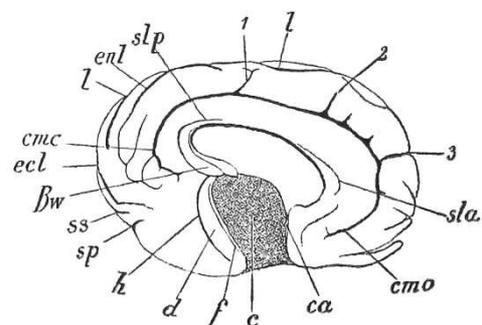
[17] *Physiologische Orientierung*: the assignment of certain functions to certain areas
[18] *Inselgebiet*: the cortical area called Insula

Blueprint sketches[19] from photographs in which the outlines of the scheme become subordinate to the natural form will support my written descriptions.

For easier orientation, I shall begin with the brain of an equine foetus of 56 cm in length (nose to tip of the tail). The distance between the frontal pole of the hemisphere and the end of the sacral part of the spinal cord was 38 cm. The latter lay 3 cm caudal to the position of the medial iliac angle[20], i.e., still in the region of the tail's root.

The orientation on the young, already grooved Cerebrum (of which the pattern of grooves is represented in the following figures without any omissions) was easy, because the formation of the secondary grooves[21] had barely begun. The hemisphere was 5 cm in length.

MEDIAL SURFACE

The SULCUS CORPORIS CALLOSI is still very shallow (it is deepest in the part associated with the Genu corporis callosi); here, as well as next to the Splenium corporis callosi, it is accompanied by a very shallow secondary groove; the rostral part of the latter is equivalent to the FISSURA SUBLIMBICA ANTERIOR, while the caudal part is equivalent to the FISSURA SUBLIMBICA POSTERIOR; a connection between the two is already vaguely indicated.

More peripherally, the FISSURA CALLOSOMARGINALIS encircles the Corpus callosum at a distance of 4 mm. It begins with a bifurcation quite close to the brain's base, then, with its caudal end, turns towards the hemisphere's area facing the Lamina quadrigemina[22]; here, it either ramifies into two short branches or connects with the FISSURA ENTOLATERALIS. At the convexity of this arched line[23] (of which the rostral part is identified by FLATAU and JACOBSEN as the Fissura genualis), several short radial grooves[24] originate from the border of the Pallium[25]; only one of these, i.e., the most rostral one, actually cuts into it[26]. This one could be regarded as the SULCUS CRUCIATUS. From the middle part of the Fissura callosomarginalis, another relatively deep branch ascends and runs as far as the

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[19] *Pausen*: blueprint sketches, i.e., drawings on tracing paper placed on a photograph

[20] *Innerer Darmbeinwinkel*: medial iliac angle, i.e., where the dorsomedial border and the craniodorsal border of Os ilium meet; this site is enlarged to represent the Tuber sacrale (ZIETZSCHMANN et al. 1943)

[21] *Nebenfurchen*: secondary grooves

[22] *Vierhügelfläche der Hemisphäre*: the hemisphere's area in the vicinity of the Lamina quadrigemina

[23] the arched line is the Fissura callosomarginalis

[24] *Radialstrahlen*: radially arranged grooves

[25] *von der Mantelkante*: from the border of the Pallium; ambiguous description because these radial grooves truly originate from the Fissura callosomarginalis (see Fig. 19, *cmc* and *cmo*), while the term *Mantelkante* (border of the Pallium) refers to the adjacent convolution of which the dorsal border represents the dorsal border of the hemisphere, i.e., Margo dorsalis

[26] meaning that it carves/cuts into the convolution of which the dorsal border is referred to as the *Mantelkante* (see Fig. 19, 1)

Pallium's border. Only with some probability can it be homologised with SCHELLENBERG's FISSURA TRANSVERSA because it does not yet have any other connections. The ends of the Fissura entolateralis, lateralis, ectolateralis, and postrhinalis (coming from the caudo-lateral surface) all reach the caudal end of the medial surface; they end at the Gyrus hippocampi. The Fissura ectolateralis extends the furthest, while the Fissura lateralis already ends at the caudal border[27] of the hemisphere. A Fissura hippocampi is clearly formed at the medial surface of the Gyrus hippocampi, next to the Gyrus dentatus; it begins at the caudal end of the Truncus corporis callosi and ends at the medial surface of the Lobus pyriformis, i.e., before it reaches the base of the brain.

DORSAL SURFACE

The small Fissura entolateralis runs far medial on the caudal pole of the hemisphere, parallel to the Fissura longitudinalis cerebri. At the site of its previously mentioned unification of the Fissura entolateralis with the Fissura callosomarginalis, a thin branch of a groove ascends in a dorso-rostral direction; it may be regarded as the *Anlage* (Primordium) of a FISSURA POSTSPLENIALIS. Lateral to the Fissura entolateralis, the grooves succeed in the following order: FISSURA LATERALIS, ECTOLATERALIS, SUPRASYLVIA and ECTOSYLVIA.

Fig. 20. Map of the sulci of a cerebral hemisphere of an equine foetus of 56 cm in length (from nose to tip of tail); dorsal view, original size.
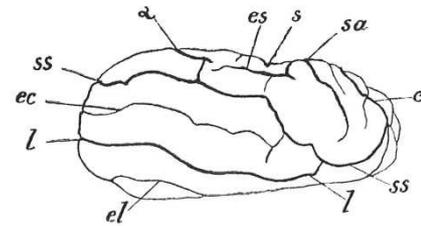
a Sulcus H of FLATAU-JACOBSON; **c** Fissura coronalis; **ec** Fissura ectolateralis; **el** Fissura entolateralis; **es** Fissura ectosylvia; **l** Fissura lateralis; **s** Fissura sylvia; **sa** Fissura sylvia anterior; **ss** Fissura suprasylvia.

The first groove (i.e., the Fissura lateralis) runs relatively straight, almost parallel to the Pallium's border, and joins the Fissura suprasylvia superficially (at the rostral third of the hemisphere) by means of a very shallow groove. The second groove (i.e., Fissura ectolateralis) is also straight in its caudal part, but in its rostral part it is bent at an angle; it ends at the site where the two aforementioned grooves are joined. On the left hemisphere, it reaches over to the Fissura suprasylvia by means of a secondary branch. The third groove (i.e., Fissura suprasylvia) takes an even more pronounced zigzag course and is the longest of all. It begins ventro-medially at the Gyrus hippocampi on the Facies cerebellaris cerebri[28], runs around the caudal border of the hemisphere, ascends in an oblique meandering course towards the dorso-rostral surface to approach the Fissura longitudinalis cerebri in the anterior third of the hemisphere and (at the frontal part of the Cerebrum) turns back in a

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[27] *Umbeugekante*: curved rim where the hemisphere's lateral side bends to continue as the medial side

[28] *Kleinhirnfläche der Hemisphäre*: Facies cerebellaris cerebri; medial surface of the hemisphere that faces the Cerebellum; this (inofficial) term is used here and throughout the rest of the translation

rostro-lateral direction; finally, it runs ventro-laterally towards the Fissura Sylvii[29]. In this way, it encircles the entire hemisphere. Beginning at its *Kantennähe*[30], its descending branch is accompanied (already in this early stage of development) by a series of secondary grooves; therefore, it is not appropriate to claim that the descending branch is equivalent to the Fissura praesylvia. A confusion with a Processus anterior fissurae Sylvii would be possible; however, a confusion with the Fissura diagonalis is out of the question.

The Fissura ectosylvia is incompletely visible in the dorsal view of the hemisphere.

LATERAL SURFACE

It is noticeable on the lateral surface that the part of the hemisphere demarcated as the olfactory brain by the well-developed Fissura rhinalis reaches a lot further dorsally than it is usually the case in adult animals. The formation of grooves is already much more complicated here and, because of this, more difficult to classify. On taking a closer look at the caudal branch of the Fissura rhinalis we realise that the entire border of the part of the hemisphere that lies dorsal to it overlaps the fissure like a bulgy rim; by lifting the rim up one can proceed into a deep fissure which, according to FLATAU and JACOBSEN, is the same as the Processus posterior fissurae Sylvii. The medial wall of the fissure, i.e., the Insula, has not yet developed folds such as in adult animals, but is totally even[31].

Fig. 21. Map of the sulci of a cerebral hemisphere of an equine foetus of 56 cm in length (from nose to tip of tail); lateral view, original size.

a Sulcus H of FLATAU-JACOBSON; **el** Fissura ecto-lateralis; **es** Fissura ectosylvia; **d** Fissura diago-nalis; **l** Fissura lateralis; **llp** Longitudinal sulcus of the Lobus pyriformis; **ps** Fissura praesylvia; **rha** Fissura rhinalis anterior; **s** Fissura sylvia; **sa** Ramus anterior fissurae sylviae; **sp** Fissura sylvia posterior; **ss** Fissura suprasylvia; **ssp** Fissura suprasylvia posterior.
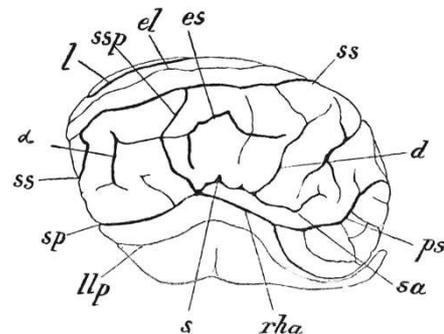
Approximately in its middle part, the Fissura rhinalis has a ventrally oriented bend; just in this location, a convolution descending from the frontal part of the brain enters underneath the ventral border of the cerebral Pallium. At the site of submergence of this convolution, the Pallium's border contains several notches; these, or one of these, can be identified as the Fissura Sylvii. The continuation

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[29] in the original text (here and in other parts of it) it is called Fissura Sylvii, while in the figure legends it is referred to as Fissura sylvia

[30] *Kantennähe*: Proximity to the Border; here (and later in the text) Dexler uses this term to refer to the distinct part of the groove that takes a bent course close to the dorsal border (see figure 20 on page 9)

[31] i.e., without grooves or folds

extending caudally is the Processus posterior fissurae Sylvii[32], while the dorso-rostral extension is the Processus anterior[33] of this groove. In Figure 21 it is interrupted by a convolution. In front of this convolution, another deep groove forms a ventral demarcation line of the Insula and runs to the Pallium's border in a rostro-dorsal direction; this groove may represent the FISSURA PRAESYLVIA and the FISSURA CORONALIS. Behind the above mentioned convolution, yet another deep groove extends transversally across the Pallium; it connects (dorsally) with the Fissura suprasylvia and probably can be referred to as the FISSURA DIAGONALIS. Finally, one encounters another groove in the region dorsal to the Fissura Sylvii; it passes by the Fissura Sylvii in a zigzag manner and might be identified as the FISSURA ECTOSYLVIA. This assumption could not yet be made with complete certainty because this deep groove leads towards a fissure that is perhaps identical with the "*Secondary Groove a*" of FLATAU and JACOBSON. It is crossed by a vertical branch of the Fissura suprasylvia, namely FISSURA SUPRASYLVIA POSTERIOR according to these authors. A further classification of the hemispheres at hand, and particularly of the frontal pole, is not possible due to significant asymmetries; they are so pronounced that, for instance, on one hemisphere (which is not shown in the figures) the assumed equivalents of the Fissura ectosylvia and of the Fissura "*a*" (FLATAU-JACOBSON) extended like a straight, uniform groove arranged completely parallel to the caudal two-thirds of the Fissura suprasylvia; due to this, the striking impression arose that the caudal areas of the cerebral cortex were divided by five parallel grooves into six straight, longitudinally arranged bulges. In the frontal parts of the brain, however, these bulges terminated as irregular, mainly obliquely arranged, s-shaped convolutions.

At the brain's base, the BULBI OLFACTORII are very prominent. A prominence regarded as the TRIGONONUM OLFACTORIUM is equally well developed, but the formation of the olfactory roots[34] on it is not yet visible with a magnifying glass. Lateral to the Tuber cinereum (which protrudes from the diencephalon's base like a well-outlined half of a globe and is engirded with the Tractus optici), the olfactory brain continues into the very wide Lobi pyriformes; the latter are already grooved by a SULCUS LONGITUDINALIS gyri pyriformis on their lateral side.

Even though the asymmetry of the lateral pattern of grooves forces us to refrain from discussing the scheme of convolutions completely, I would still like to briefly address this topic because the relatively clear arrangement of the other grooves provides us with a valuable tool for orientation. Due to the abundance of side branches and secondary grooves of the brain in adult individuals, the situation (in the adult) is not as easily revealed as is the case here (in the foetus).

The only possible statement about the GYRUS SYLVIACUS and GYRUS ECTOSYLVIUS is this: In combination, both gyri form, even in this young brain, an agglomeration of

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[32] labelled as Fissura sylvia posterior in Figure 21
[33] labelled as Ramus anterior fissurae sylviae in Figure 21
[34] *Riechwurzel*: olfactory root, i.e., Tractus olfactorius (Stria olfactoria)

gyri which already are multiply divided; this demonstrates the striking deficits that are encountered when trying to classify the equine system of grooves according to the canine scheme.

The GYRUS SUPRASYLVIUS (between the Fissura lateralis and the Fissura suprasylvia or its rostral continuation, respectively) is at least visible in its medial and caudal parts as a doubled convolution approaching the Pallium's border in the rostral third where it is cut by a deep groove; it cannot be determined which part of the convolution can be regarded as its rostral continuation.

The GYRUS MARGINALIS (between the Fissura lateralis und the Fissura callosomarginalis) is the largest and the best developed. It runs next to the Pallium's border along the entire hemisphere. Its caudal beginning can be found in the dorso-medial region of the Gyrus hippocampi; from here it is split into two longitudinal halves by the Fissura entolateralis and ascends in a dorso-rostral direction; in the region of the medial, deep branch of the Fissura callosomarginalis, it becomes very narrow, but widens again further rostrally; at the frontal pole of the hemisphere, it is cut by the *Anlage* (Primordium) of the Fissura cruciata; then (no longer laterally demarcated by the Fissura lateralis, but by the Fissura suprasylvia), it enters an agglomeration of transversal gyri that cover the frontal pole of the hemisphere.

On the medial side of the hemispheres, towards the centre of the brain, the Gyrus fornicatus lies between the Fissura callosomarginalis and the Sulcus corporis callosi; caudo-laterally, the end sections of the Fissura ectolateralis and of the Processus posterior fissurae Sylvii also contribute to the demarcation of this Gyrus fornicatus. It is a continuous gyrus to which the usual tripartition can be applied already in this early stage, namely: A rostral third (located between the Pars anterior fissurae callosomarginalis and the Genu corporis callosi, i.e., the GYRUS GENUALIS; a middle third (between the middle part of the Fissura callosomarginalis and the Truncus corporis callosi, i.e., the GYRUS CINGULI; finally a caudal third (extending towards the brain's base), i.e., the GYRUS HIPPOCAMPI and LOBUS PYRIFORMIS. A narrowing, i.e., an ISTHMUS GYRI FORNICATI, is already indicated at the junction between the Gyrus cinguli and the Gyrus hippocampi. At the Splenium corporis callosi, one can see yet another small gyrus separated by the Fissura sublimbica; it extends ventrally to the Corpus callosum and represents the GYRUS CALLOSUS. A subdivision of the rostral areas of the Gyrus hippocampi is not yet possible.

The subdivision of the brain surface is so far developed in the demonstrated stage that inaccuracies arise in some points, e.g., in the caudo-lateral areas of the hemispheres. Consequently, we have examined earlier developmental stages in order to further improve our orientation. I, therefore, choose the brain of a FOETUS OF 30 CM NECK-RUMP LENGTH. The length of the cerebral hemisphere is 3 cm. The Cerebellum and the Lamina quadrigemina are still uncovered.

Fig. 22. Brain of an equine foetus of 30 cm in neck-rump length; five-sixths of the original size.

a Dorsal view.
cm Fissura callosomarginalis; **el** Fissura entolateralis; **l** Fissura lateralis; **ss** Fissura suprasylvia; **ssa** Rostral bending of the Fissura suprasylvia.

b Ventral view.
bo Bulbus olfactorius; **pa** Presumed *Anlage* (Primordium) of the Ramus anterior fissurae sylviae; **pp** Fissura postrhinalis; **rha** Fissura rhinalis anterior; **ssa** Rostral bending of the Fissura suprasylvia; **to** Trigonum olfactorium.
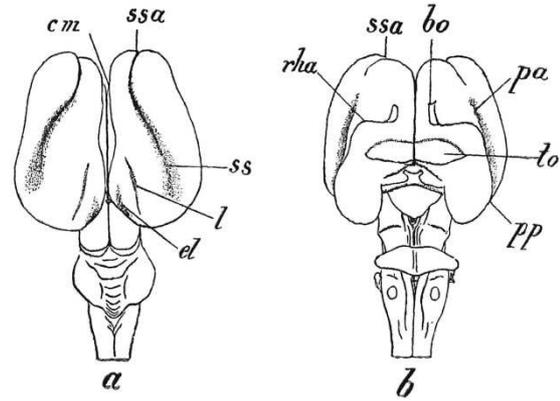
MEDIAL SURFACE

A Sulcus corporis callosi is already indicated; the FISSURA CALLOSOMARGINALIS is already deep, its rims are rounded and wide open. The FISSURA ENTOLATERALIS has already developed to a line-shaped depression; the GYRUS CALLOSUS is delineated by a groove that supposedly approaches from the Sulcus corporis callosi. The FISSURA HIPPOCAMPI is sharp and deep. The rostral end of the Fissura lateralis reaches so far across the most dorsal curvature of the Pallium's border that it becomes visible in the medial view; and in the rostral third of the medial surface we look at the embankment[35] of the Fissura suprasylvia. There is no FISSURA CRUCIATA.

Fig. 23. Hemisphere of an equine foetus of 30 cm in neck-rump length; five-sixths of the original size.

a Dorsal view.
cm Fissura callosomarginalis; **i** *Kantennähe* (Proximity to the Border) of Fissura suprasylvia; **l** Fissura lateralis; **ssa** Rostral bending of the Fissura suprasylvia; **ssp** Caudal end of the Fissura suprasylvia.

b Lateral view.
d₁ *Anlage* (Primordium) of a first indentation of the Gyrus secundus; **d₂** *Anlage* (Primordium) of a Fissura ectosylvia; **i** Area of the Insula; **rha** Fissura rhinalis anterior; **rhp** Fissura postrhinalis; **ssa** Rostral bending of the Fissura suprasylvia; **ssp** Caudal end of the Fissura suprasylvia.

c Medial view.
cc Fissura corporis callosi; **cm** Fissura callosomarginalis; **el** Fissura entolateralis; **h** Fissura hippocampi; **i** *Kantennähe* (Proximity to the Border) of Fissura suprasylvia; **l** Fissura lateralis; **slp** Fissura sublimbica posterior; **to** Trigonum olfactorium.

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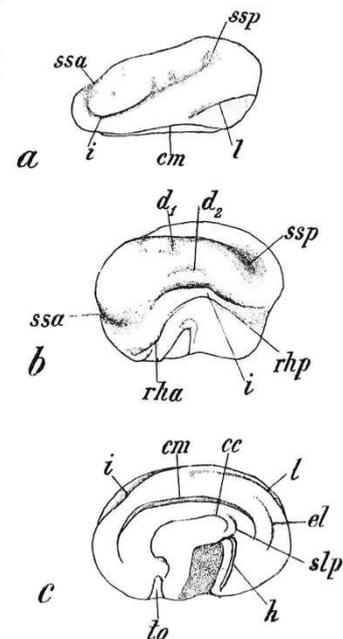
[35] *Böschung*: riverbank

DORSAL AND LATERAL SURFACES

At the caudal pole of the hemisphere, the Fissura lateralis extends close to the middle of the Pallium's border. In a position lateral to it, the Fissura suprasylvia is already delineated. We may assume that the barely visible, very shallow depression (located in the caudal area of the hemisphere) is its beginning; from here, a distinct groove ascends dorsally and medially, approaches very close to the Pallium's border – *Kantennähe*[36]–, then turns in a rostro-lateral, rostro-ventral, and ventro-caudal direction and finally (becoming shallower) disappears at the same height as the initial part. The connection of the dorsal branch with the ventral branch is so shallow and indistinct that the identification of this groove from here to its caudal end is not quite clear; its dorsal branch may surely be regarded as the *Anlage* (Primordium) of the Fissura suprasylvia and of the Fissura coronalis. The linking part that connects it[37] with the Fissura coronalis probably belongs to the future Fissura praesylvia, but certainly not to the Processus anterior fissurae sylviae because the latter develops later. Only in an equine foetus of 129 days of age did BRADLEY (see Fig. 33, Appendix 1, page 16) find such a branch to insert in-between the dorsal and the ventral branches of this large groove.

A small, longitudinal groove runs dorsally to the concavity of the ventral branch of the Fissura suprasylvia; if we want to regard it as the precursor of the FISSURA ECTOSYLVIA, we can conclude that the caudal part of the ventral branch belongs to the future PROCESSUS POSTERIOR FISSURAE SYLVII.

The FISSURA RHINALIS ANTERIOR begins at the base of the Bulbus olfactorius and, without interruption, continues into the Fissura rhinalis posterior; the latter is accompanied by a very delicate band and extends as far as the border of the Facies cerebellaris cerebri; here, it meets the Processus posterior fissurae Sylvii at a sharp angle.

CONVOLUTIONS

The Lobus falciformis[38] is already clearly delineated in all of its parts, and its subdivision is already well-developed; the FIMBRIA is wide; the GYRUS DENTATUS protrudes as a filiform ridge next to the sharply outlined Fissura hippocampi; the Trigonum olfactorium is well developed. The Processus mamillaris lobi pyriformis is still completely even.

The longitudinal bulge (that is dorsally encircled by the Fissura suprasylvia and ventrally by the Fissura suprasylvia's seeming continuation) protrudes markedly over the hemisphere's curvature; in its middle part, it shows an indication of three spherical knobs. Its rostral end is strikingly prominent. Between this rostral end and the olfactory brain lies a tongue-shaped area of which the tip is oriented in the caudal direction; it emerges from the hemisphere's frontal pole

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[36] *Kantennähe*: Proximity to the Border (see figure 23 a and 23 c on page 13)
[37] i.e., the dorsal branch of the Fissura suprasylvia
[38] *Sichellappen*: Lobus falciformis

without any delineation; its caudal, totally flat area can be attributed to the region of the Insula.

Focussing on the general morphological pattern while having the aforementioned in mind, we encounter, from a strictly formal point of view, a strikingly obvious tripartition of the entire hemisphere: (1) A LOBUS FALCIFORMIS in a very advanced state of development; (2) a GYRUS PRIMUS lying on the Lobus falciformis and encircling the hemisphere caudally, dorsally, rostrally, and ventro-laterally; (3) a GYRUS SECUNDUS lying on the Gyrus primus in the longitudinal direction. Among the main convolutions, there is no Fissura cruciata, and no proper Fissura Sylvii, while the supposed Fissura ectosylvia is present just in its first stage of its *Anlage* (Primordium). The region of the Insula is completely uncovered. THE MOST DSTINCT CHARACTERISTICS OF THIS EARLY DEVELOPMENTAL STAGE ARE: LACK OF THE FISSURA CRUCIATA AND LACK OF A VERTICAL BRANCH OF THE FISSURA SYLVII AT A TIME WHEN ALL THE OTHER MAIN GROOVES HAVE ALREADY APPEARED; EXPOSITION OF THE COMPLETELY UNCOVERED REGION OF THE INSULA.

Younger embryos, in which the formation of grooves had already started at the Cerebrum's curvature, were not at my disposal. The youngest embryo was 4.8 cm long (NECK-RUMP LENGTH); its cranium (cut into continuous series of sections) contained (as expected) a brain with an EVEN surface. I observed the same in the cerebral Pallium of a young equine foetus of which the trunk had already straightened so far out of its ventro-concave bend that the dorsal contour of the head and back almost formed a straight line. The convexity of the forehead represented the rostral end of the body; THE DISTANCE FROM THE FOREHEAD'S POLE TO THE TUBER ISCHIADICUM was 14.2 cm; the head's length from nose to neck (between the ears) was 4 cm. The cerebral hemispheres were still small (as illustrated in Fig. 24); the Cerebellum was indicated merely by a transversal, penta-lobated[39] bulge.

Fig. 24. Brain of an equine foetus of 14 cm in length in medial, dorsal, and lateral views; original size.
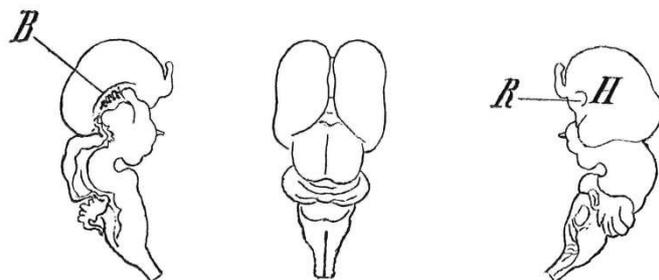
B Early indications of a sulcus dorsal to the Corpus callosum; **H** Hemisphere; **R** Lateral delineation of the Rhinencephalon.

IN THE PROXIMAL AREA, THE PALLIUM WAS DEMARCATED FROM THE OLFACTORY BRAIN BY A BAND BARELY VISIBLE WITH A MAGNIFYING GLASS; a *Bogenfurche*[40] was indicated also on

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[39] *fünflappig*: penta-lobated, i.e., consisting of five lobes; the author only wants to mention that the cerebellar bulge is not a uniform body at this stage of development; however, (as seen in Fig. 24) a separation into lobes is only vaguely indicated

[40] *Bogenfurche*: arched groove (here and throughout the text); the arched grooves delineate the arched convolutions *(Bogenwindungen)*

the medial surface by the overlap of the hemisphere's medial wall over the Diencephalon. The whole of the rest of the hemisphere was even. CONSEQUENTLY, WE MAY ASSIGN THE ONSET OF CORTICAL GROOVE FORMATION IN THE EQUINE BRAIN TO THIS STAGE OF DEVELOPMENT.


-------------------- End of Part IV --------------------

To be continued: Part V (pages 347-389 of the original article)

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APPENDIX 1

On page 345 of the original article (i.e., on page 14 of this translation), Dexler referred to his Fig. 33. This figure, however, appeared only later on page 353 of the original article (i.e., Part V of the translation). For added convenience, it is also presented here:

Fig. 33. Lateral surface of the cerebral hemisphere of a four-month-old equine foetus according to BRADLEY
(there were no explanations for the labels "l" and "s" in Dexler's figure caption; the labelling in BRADLEY`S paper was: **l** Lateral fissure, **s** Sylvian fissure).
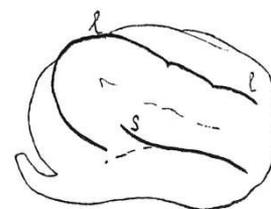
APPENDIX 2

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The following authors mentioned in this part of Dexler's original text are not referred to in his reference list:
ANTON, BROCA, CLARKE, FRANK, KÜKENTHAL, KREIDL, MARCACCI, MARGULIES, SMITH, TURNER

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