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HISTOGENESIS OF THE CEREBELLAR CORTEX IN THE CAMEL

(With One Table and 16 Figures)

By

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النمو الهستولوجي لقشرة المخيخ في الجمل

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أجرى هذا البحث علي مخيخات ثمانية عش من أجنة الجمال التي تراوحت أطوالها بين ١١ره١٢ سم، كما اشتملت مواد هذا البحث على مخيخات أربعة من الجمال البالغة. جهزت العينات للفحص الميكروسكوب لدراسة التطور النسيجي لقشرة المخيخ في الجمال خلال فترة الحياه الجنينية وفي الجمال البالغة. ولقد وجد بصفة عامة أن تتابع هذه التغيرات في الجمل لايختلف اختلافا جوهريا عنها في الفقاريات الأخرى ولكنه لوحظ أن قشرة المخيخ في الجمل تكون مكتملة النمو نسبيا عند نهاية فترة الحياه الجنينيه الأمر الذى يمكن أن يلقى الضوء لتعليل اعتماد هذه الحيوانات على نفسها في الوقوف والحركة بعد الولادة بفترة وجيزة.

SUMMARY

The present investigation was carried on the cerebellum of 18 camel fetuses ranging from 11-125 cm CVR length. The cerebellum of 4 adult camels (6-10 year old) was also studied. The specimens were processed for different histological stains including Einarson's gallocyanine, Holm's silver and rapid Golgi Cox methods.

The external granular layer reached its maximum thickness at 51 cm CVR length, then it decreased to about 1-2 cells in thickness at 125 cm CVR length. The molecular and internal granular layers increased in thickness on the expence of the external grnular layer. The Purkinje cell layer was formed of 3-4 cells in thickness up to 100cm CVR length where it was disposed into a single row of cells. At 125 cm CVR length the Purkinje cells increased in size but did not attain their mature form.

INTRODUCTION

The role of the cerebellum is very important in requlation of the reflex tone of skeletal musculature, in control of voluntary activity and in maintenance of equilibrium. The histogenesis of the cerebellar cortex revealed variegrated rates of development

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during both the pre- and postnatal life in various mammalian species and man (NOOR EL-DIN, 1966 in mice, HANAWAY, 1967 in chickens, ZECEVIC & RAKIC, 1976 in man, ALTMAN & WINFREE, 1977 and GABR, MOHAMED & HASSANEIN, 1985 in rats and GABR, 1978 in rabbits). The lack of available literature dealing with the histogenesis of the cerebellar cortex of camels promotes the carrying out of the present investigation.

MATERIAL and METHODS

18 fetuses of one-humped camel (Camellus dromedarius) were used in the present study representing the whole prenatal life (Table 1). Another 4 specimens at ages of about 6 and 10 years (two for each age) were also employed.

The fetuses were collected from Cairo slaughter house shortly after evisceration. The cerebelli were processed for histological technique. Sagittal sections were done at 10 U thickness and stained with Einarson's gallocyanine, Holm's silver and some cerebelli were processed for rapid Golgi Cox method (DRURY andWALLINGTON, 1980).

Table (1): Distribution of the material.

Age (CVR/cm)	11	21	32	40.5	51	62	71.5	83	90	100	111	119	125
Number	2	1	1	1	2		1	1	1	1	2	1	2

RESULTS

11-40.5 cm CVR length :

The primordium of the cerebellum is formed of neuroepithelial cells (Fig. 1/a), the mantle layer (Fig 1/b), the elements of the internal granular layer together with the Purkinje cell layer (Fig. 1/c), the molecular layer (Fig. 1/d) and the external granular layer (Fig. 1/e). The cerebellar surface shows the beginning of folding (Fig. 1/f). The external granular layer consists of neuroblast cells (Fig. 2/a). The molecular layer is very thin (Fig. 2/b). The Purkinje cell layer is formed of 3-4 cells in thickness, each cell shows a flask-shaped nucleus (Fig. 2/c). The internal granular layer can not be distinguished.

51-90 cm CVR length :

The external granular layer increases in width, where it ranges between 5-7 cells in thickness (Fig. 3/a). The cells of this layer are rounded with darkly stained nuclei which undergo several mitotic activities. The component cells of this layer are more densely-packed towards the juxtapial region. The molecular layer is thin, demonstrating relatively few cellular elements (Fig. 3/b). Some of these cells are fusiform in shape with their longtudinal axis prependicular to the pial surface. Other cells are rounded with large darkly stained nuclei. The Purkinje cells are closley-packed and forms 3-4 cells thick layer (Fig. 3/c). These cells are larger than those of theexternal and internal granular layers. The internal granular layer is studffed with several cells presenting rounded and oval nuclei (Fig. 3/d). This layer is more or less paler than

those of the external granular layer and relatively thicker at the top of the folia than at the bottom and sides of the fissures. Their is no definite line of demarcation between theinternal granular layer and the white matter core as the latter is occupied by numerous fusiform cells (Fig. 4).

100-111 cm CVR length :

The external granular layer is about 2-5 cells in thickness (Fig. 5/a). The molecular layer contains relatively few, small-sized cells with rounded, vesicular or darkly-stained nuclei (Fig. 5/b). It contains also fusiform cells arranged mostly in a plane prependicular to that of the surface of the folia. The molecular layer presents, in addition vertical and horizontal fibers which are the axons of the internal granular cells (Fig. 6). The Purkinje cells become larger than those of the before mentioned stage and arrange themselves in one row parallel to the surface (Fig. 5/c). The internal granular layer, presents small, rounded cells arranged in clusters or glomeruli (Fig. 5/d). Their nuclei contain fine granular chromatin. some large cells, of various shapes (Golgi cells of the granular layer) are found dispersed among the granular cells. There is a sharp line of demarcation between the internal granular layer and white matter (Fig. 7).

119 cm CVR :

The external granular layer decreases obviously in thickness to reach 1-3 rows of cells (Fig. 8/a). Most of its component cells are well differentiated with occasional mitotic activity. The molecular layer increases in thickness retaining the same histological picture as in the previouus stage (Fig. 8/b). The Purkinje cells layer simulates that of the before mentioned stage, however the intervals between the Purkinje cells increases (Fig. 8/c). The internal granular layer is histologically similar to the before described stage (Fig. 8/d). The white matter is obviously demarcated from the internal granular layer. It is formed mainly of horizontal fibers which run parallel to the pail surface (Fig. 9).

125 cm CVR length :

The changes at this stage is more quantitative than qualitative. The external granular layer becomes 1-2 row in thickness (Fig. 10/a). The molecular and internal granular layers increased in thickness (Fig. 10/b&d). The Purkinje cells increased in size, but it still do not attain the full mature features (Fig. 10/c).

6 & 10 years old :

The cerebellar cortex consists, from within outward, of granular layer, Purkinje cell layer and molecular layer (Fig. 11).

The neurons of the granular layer bear long axons (Fig. 12) which ascend into the molecular layer and bifurcate in a T-shape manner to form the vertical and horizontal fibers which engage the dendritic tree of Purkinje cells. Some Golgi cells are also demonstrated within the granular layer. The dendrites of these cells also course into the molecular layer and are engaged mainly by parallel fibers. The basket cells

are found mainly in the deep part of the molecular layer (Fig. 13). Their axons engage the cell bodies and proximal segment of Purkinje cells.

The Purkinje cells have flask-shaped bodies with broad base towards the granular layer. They have a single or two long and thick primary dendrite (Fig. 14) arising from the narrow end of the soma and directed towards the pial surface. These primary dendrites have smooth surface. They divide into several secondary dendrites which have dendritic spines. The secondary dendrite redivides into a dichetomnous manner giving smaller dendrites which are highly stuffed with dendretic spines. The axons of Purkinje cells arise from the broad base of the cell soma and run towards the granular layer (Fig. 15). Some astrocytes could also be demonstrated (Fig. 16).

DISCUSSION

The external granular layer :

At the early stages of fetal development the marginal zone of the cerebellum is completly occupied by the external granular layer. This layer also expands over the surface and form the fissures of the grdually emerging folia. In the following stages the external granular layer spreads over the primitive molecular layer and Purkinje cells gathering beneath it. HAMELTON and MOSSMAN (1972); TABER and PIERCE (1973) supported the view that the external granular layer is formed from the migrated neuroblasts of the mantle layer.

HANAWAY (1967), in chickens, proposed that the cells of the external granular layer like Purkinje cells migrate radially. ALTMAN and BAYER (1978), in rats, concluded that the transient external granular layer arises by prolifertion of cells of lateral caudal cerebellar surface lining the 4th ventricle (germinal trigone). These cells migrate over the surface and continue to proliferate abundantly. The germinal trigone may be identical with rhombic lip (SIDMAN and RAKIC, 1973). Rhombic lip forms both the deep nuclear neurons and Purkinje cells. It is the source of cell population of the external granular layer (ALTMAN and BAYER, 1977).

In all vertebrates including the camel the external granular layer increases at first in thickness to reach a maximum of 6-8 cells. Proliferation of this layer is manifested by several mitotic figures which are scattered throughout the external granular layer.

The external granular layer persists for a period that varies according to the species. In camel it reduces in thickness to a single layer of cells and ultimately disappears at 125 cm CVR length. This occured also in precocial animals such as chickens or guinea pigs but it persists for some time after birth in altricial animals such as the mice, rats, rabbits and man. The cerebellum of the later is in a corresponding state of immaturity and its histogensis and morphogensis mainly occur after birth (NOOR EL-DIN, 1966; ALTMAN, 1969; GABR, 1978 and MARCUS, 1979). The external granular layer disappears after birth by 20-25, 60-90, 75 and 600 days in albino mice and rats, cats and rabbits, dogs and human respectively.

CEREBELLAR CORTEX IN THE CAMEL

The molecular layer :

The present work revealed that the molecular layer is very thin at 11 cm CVR length. It gradually increases in thickness to reach its maximum at the end of gestation. The increased thickness of the molecular layer could be attributed to the increase in cellular processes and neuropil by the advancement of age. This is in agreement with the results of RAFF and KERNOHAN (1944), NOOR EL-DIN (1966) and GABR (1978) and BERRY et al. (1981).

Purkinje cell layer :

The elements of Purkinje cells, in camel cerebellar cortex were arranged into 2-4 layers at early stages of fetal development. At 100 cm CVR length the became larger and arrange themselves into a single row parallel to the surface. With the advancement of development the Purkinje cells increase more in size, however, they do not attain their fully mature features even at the end of gestation.

In all vertebrates, the Purkinje cells are derived from the ventricular germinal zone and migrate out into superficial layers of the mantle layer of the cerebellar plate. They are initially small and arranged in an irregular rows up to 12 cell thick. They thined out to a single row during the subsequent growth of the cerebellum (MARCUS, 1979). Purkinje cells ornigate at 14-17 days prenatally in rat fetuses, at 11-14 days prenatally in mouse fetuses and at 3-6 days prehatching in chick embryoes. In all cases the production of Purkinje commences and ceases before that of any other type of cells in the cerebellar cortex. Purkinje cells remain quiescent for several days after their generation and migration. They grow very slowly until the prolifertion of the external granular cells occur. It begins to differentiate rapidly after the granule cells migrate past them from the external granular layer to the internal granular one. These events occur 4-20 days after birth in albino mice and rats, 3 month after birth in rabbits and from fetal month 4 to postnatal month 11 in human (ADDISON, 1911; GABR, 1978 and ALTMAN & WINFREE, 1977).

The differentiation of Purkinje cells in camels follow the same sequence as in other mammals, however the camel Purkinje cells follow a relatively rapid rate of differentiation and growth. This could explain the cerebellar maturity and dependancy of camel at birth.

The internal granular layer :

In camel fetuses of 51 cm CVR length there is no line of demarcation between the internal granular layer and white matter as the latter is highly stuffed with a great number of cells. At 100 cm CVR length the internal granular layer became distinct from the white matter which appears less cellular. Although the external granular layer decreases in thickness by the advancement of fetal age, both the molecular and internal granular layer increase in thickness. In adult camel cerebellum the granule cells are small in size and have many processes and the axon of each cell directes towards the molecular layer giving rise vertical and horizontal fibers at the molecular layer.

Golgi cells are larger and darker than the granule cells and have a profuse processes extending in all directions. Their axons form with dendrites of granule cells, mossy fibers. So the development of the granule cells in camel is as that of other animals such as mice, rats and rabbits as reported in mice by NOOR EL-DIN (1966), ALTMAN (1969) and GABR (1978) respectively.

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LEGENDS

Fig. (1): The cerebellum of 11 cm CVR length camel fetus, showing: **a,** neuroepithial cells; **b,** mantle layer; **c,** elements of internal granular layer and Purkinje cell layer; **d,** molecular layer; **e,** external granular layer; **f,** beginning of folding.

(Einarson's Gallocyanine, X 40).

Fig. (2): The cerebellar cortex of 11 cm CVR length camel fetus, showing: **a,** external granular layer; **b,** molecular layer; **c,** elements of internal granular layer.

(Einarson's Gallocyanine, X 400).

Fig. (3): The cerebellar cortex of 51 cm CVR length camel fetus, showing: **a,** external granular layer; **b,** molecular layer; **c,** Purkinje cell layer; **d,** internal granular layer.

(Einarson's Gallocynine, X 400).

Fig. (4): The cerebellar cortex of 51 cm CVR length camel fetus, showing no marked limits between the internal granular layer and the white matter.

(Einarson's Gallocyanine, X 40).

Fig. (5): The cerebellar cortex of 100 cm CVR length camel fetus, showing: **a,** external granular layer; **b,** molecular layer; **c,** Purkinje cell layer; **d,** internal granular layer.

(Einarson's Gallocynine, X 400).

Fig. (6): The cerebellar cortex of 100 cm CVR length camel fetus, showing the molecular layer demonstrating vertical and horizontal fibers.

(Holm's silver, 125).

Fig. (7): The cerebellar cortex of 100 cm CVR length camel fetus, showing a sharp line of demarkation between the internal granular layer and the white matter.

(Einarson's Gallocynine, X 400).

Fig. (8): The cerebellar cortex of 119 cm CVR length camel fetus, showing **a,** external granular layer; **b,** molecular layer; **c,** Purkinje cell layer; **d,** internal granular layer.

(Einarson's Gallocynine, X 250).

Fig. (9): The cerebellar cortex of 119 cm CVR length camel fetus, showing that the white matter (M) is formed mainly of horizontal fibers which run parallel to the pail surface.

(Holm's silver, X 250).

Fig. (10): The cerebellar cortex of 125 cm CVR length camel fetus, showing: **a,** external granular layer; **b,** molecular layer; **c,** Purkinje cell layer; **d,** internal granular layer.

(Einarson's Gallocynine, X 250).

Fig. (11): Cerebellar folium of 6 years old camel, showing **a,** moleculater; **b,** Purkinje layer, **c,** internal granular layer.

(Einarson's Gallocynine, X 40).

Fig. (12): Axon of adult granule cell ascending into the molecular layer.
(Rapid Golgi Cox, X 250).

Fig. (13): A basket cell within the deep part of the molecular layer.
(Rapid Golgi Cox, X 250).

Fig. (14): A Purkinje cell with profuse dendrites.
(Rapid Golgi Cox, X 250).

Fig. (15): A Purkinje cell with its axon directing towards the granular layer.
(Rapid Golgi Cox, X 250).

Fig. (16): Astrocytes demonstrated within the granular layer.
(Rapid Golgi Cox, X 250).

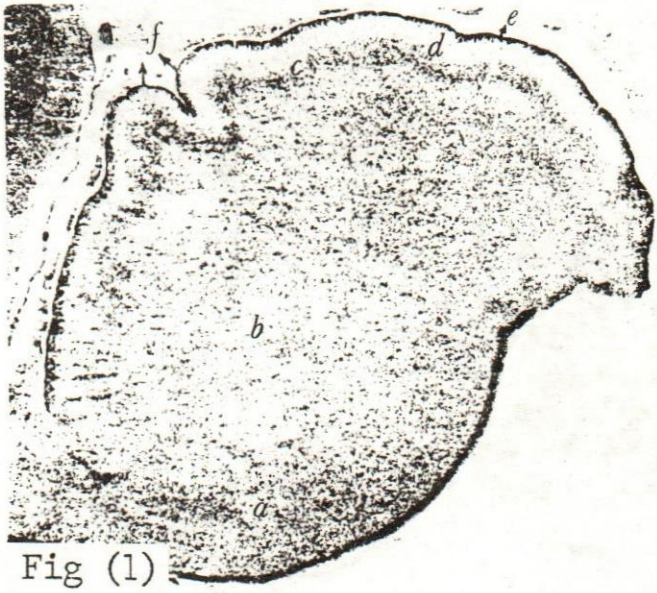
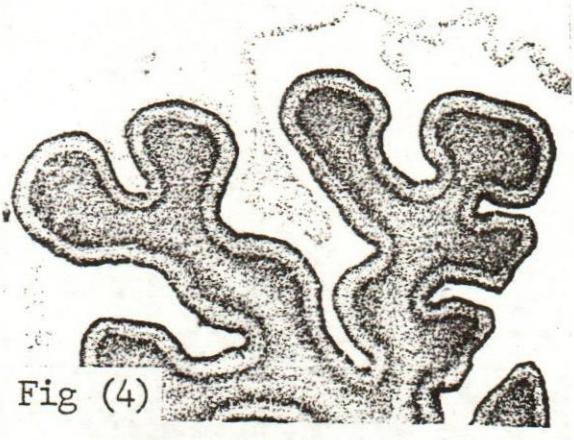


Fig (1)

Fig (2)

Fig (3)



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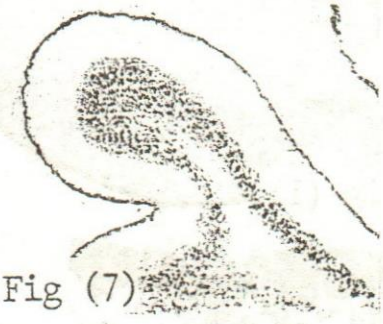

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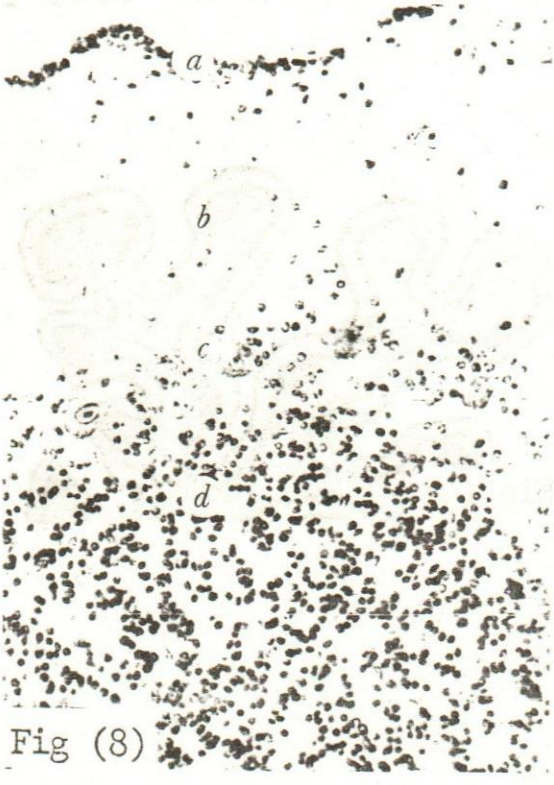

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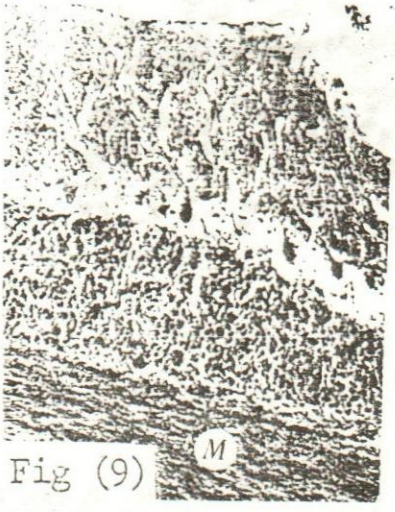

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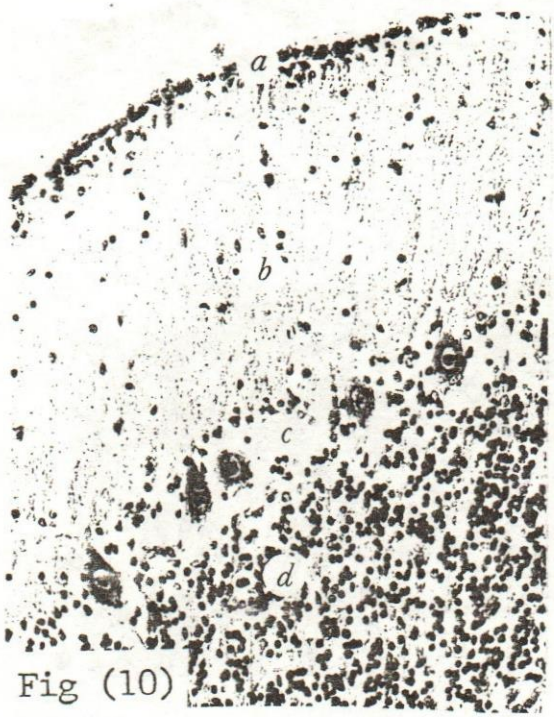

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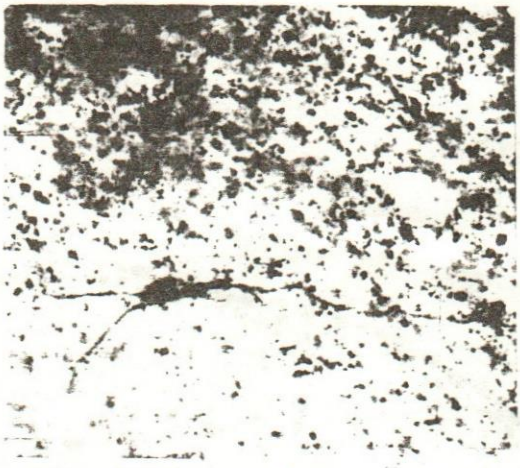

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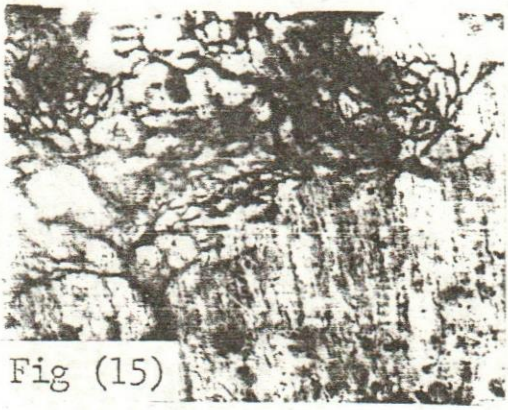

Fig (15)

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