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Cerebellar gross anatomy of the African grasscutter (*Thryonomys swinderianus* - Temminck, 1827) during foetal and postnatal development

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ABSTRACT

In Nigeria, the African grasscutter (*Thryonomys swinderianus*) is bred as a mini-livestock, and research model. This study provides some information on the ontogeny of its cerebellum through gross observations of external cerebellar features from foetuses on foetal days 60 and 90, neonates on postnatal day 3, juveniles on postnatal day 72 and adults on postnatal day 450. On foetal day 60, the cerebellum was a smooth, semi-circular mass, devoid of folia or sulci; cerebellar lobes and vermal lobules were not present. On foetal day 90, the vermis was distinct, but vermal lobules were indistinct. On postnatal day 3, the cerebellar cortex was convoluted with the folia and fissures of grossly distinct lobes. The cerebellar vermis was divided into all the lobules typical of mammalian vermis; while the lingula, central lobule, culmen and declive were on the cerebellar dorsum, the folium, tuber, pyramis, uvula and nodulus were caudally located. The culmen was undivided and the crus rostralis was unpaired. On postnatal day 72, the pre-central fissure was deeper than that observed on postnatal day 3; the culmen was divided into the pars rostralis and pars caudalis; the crus rostralis was bifoliated by a fissural line. On postnatal day 450, the cerebellar fissures were deeper than before; the vermal and hemispheric lobules were better delineated. The bifoliation of the crus rostralis was more evident. The intra-crural fissure was very distinct and referred to as the great horizontal fissure. The results of the present study will add to the data base of rodent neuroanatomy, necessary for teaching and research.

Key words: African grasscutter; cerebellum; gross anatomy; vermis; flocullus; paraflocullus

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Introduction

Rodents are the widest order of placental mammals as they comprise more than half of the known mammals (AYDIN et al., 2008). The African grasscutter is a member of the sub-order *Hystricomorpha* and family *Thryonomyidae*. It is found in virtually all African countries, including Nigeria (VAN DER MERWE, 2007). They reside in grassland or in wooded savannah, along riverbanks (ASIBEY and ADDO, 2000). An adult grasscutter is a large rodent, the second largest rodent in Africa, after the North African crested porcupine (SKINNER and CHIMIMBA, 2005). An increasing amount of interest is currently being expressed in the biology of the African grasscutter. This may not be surprising as this wild rodent has become a staple source of meat for the vast majority of people in Africa, thus it is bred. It is the rodent species most hunted by local villagers in southern Nigeria, due to the quality of its meat and the income that can be derived (ASSOGBADJO et al., 2005). As an integral part of the mini-livestock industry, it contributes to both local and export revenues in most West African countries (OPARA, 2010). It has also been established as a laboratory model (ASIBEY and ADDO, 2000).

The vertebrate cerebellum is involved in the co-ordination of somatic motor activity, the regulation of muscle tone and the maintenance of equilibrium and posture (FLETCHER and WEBER, 2003). For example, the central lobule is involved in the limb musculature, a degree of coordination in walking and swimming (IWANIUK et al., 2006) while the culmen is involved in the movements of the lower extremities of the forelimb, lips and tongue (GRODD et al., 2001; SCHMAHMANN, 2004). Furthermore, the declive has been regarded as the oculomotor vermis as it receives proprioceptive, vestibular and auditory inputs, and plays a vital role in the guidance and modification of eye movements (VOOGD and BARMACK, 2006). Recent evidence also suggests that the mammalian cerebellum participates in higher order functions, including cognition, language processing and emotion (TAVANO et al., 2007; STRATA et al., 2011).

The study of the cerebellum of the African grasscutter is of value in understanding the behaviour of the rodent, knowledge of which will enhance its maintenance in captivity. Secondly, understanding how the cerebellum of the African grasscutter develops will serve as a lead to understanding any gross pathological conditions of the cerebellum in the rodent. Thirdly, the present study will add to the data base of rodent neuroanatomy, necessary for teaching and research.

Unfortunately, the only information on the gross morphology of the cerebellum of the African grasscutter in the available literature is on the structure of the adult cerebellum by NZALAK et al. (2008) and BYANET et al. (2012). Also, the mature cerebellum of some rodents such as white rats (LARSELL, 1952), mice (INOUYE and ODA, 1980), chinchillas and squirrels (SULTAN and BRAITENBERG, 1993) and the African giant pouched rat (BYANET et al., 2013; IBE et al., 2014) have been extensively studied.

Conversely, no detailed anatomical study of the cerebellar development in the African grasscutter, as the rodent advances from foetal to adult stages has been undertaken, hence this study. Accordingly, the study was aimed at describing the gross morphological changes that occur in the cerebellum of the African grasscutter on foetal days 60 (F60) and 90 (F90), and postnatal days 3 (P3), 72 (P72) and 450 (P450).

Materials and methods

Experimental animals and management. Four nulliparous African grasscutter does, not more than 5 months old, and 1 mature buck, were used for the prenatal brain developmental study. A total of 11 foetuses were explanted on foetal day 60 (F60) and 9 foetuses were explanted on foetal day 90 (F90) from the does. Furthermore, 27 animals, 9 each of 3 day (P3) old neonates, 72 day (P72) old Juveniles and 450 day (P450) old adults were used for the postnatal brain developmental study. The nulliparous does were mated on the farm, and the pregnant females were transported by road, in wooden cages, to the Veterinary Histology Laboratory of the Michael Okpara University of Agriculture Umudike, Nigeria, for foetal explantation. The explanted foetuses, and the postnatal brain samples, were preserved in 10% buffered formalin for this study.

The animals were physically examined under careful restraint. Apparently healthy ones were utilized for the study. They were fed twice daily, at 8.00 am and 6.00 pm. They were fed with fresh guinea grass (*Panicum maximum*), fresh cane grass (*Eragrostis infecunda*) and commercial rodent pelleted concentrates. Drinking water was provided *ad libitum*. The feeding troughs and drinkers were sterilized daily using Milton®.

Mating and pregnancy diagnosis. The nulliparous does were housed singly until they attained sexual maturity at 7 months. Hand-mating was conducted by transferring the nulliparous does to the buck in the colony paddocks. Prior to the transfer, the body weight of each female, vaginal status (open, sealed, closed), and the date and time of the transfer were recorded, after which the females were left with the male until they mated.

During the females’ stay with the male, they were examined at 6 hour intervals for post-pairing perineal changes which are indicative of successful mating. These include perforation of the vaginal membrane, vulva congestion and the presence of a copulatory plug in the vagina or on the floor of the cage, as reported by ADDO (2002). On observing any of the signs, the females were immediately and permanently separated from the male, weighed, and the date and time of the appearance of the mating-signs were recorded.

Early pregnancy was ascertained by the use of a lvaginal mucosal swab, as is the routine in most commercial grasscutter farms. Yellow colouraton of the swab is indicative of early pregnancy. Late gestational pregnancy was evident by changes in body weight, the gravid nature of pelvic region and enlarged teats.

Caesarean section. The foetuses were explanted via caesarean section. Each pregnant doe was anaesthetized using 40 mg/kg of sodium pentobarbital, intraperitoneally. The caesarean section was based on Bowers's procedure (BOWERS et al., 2001). In summary, a 3.0 cm caudal midline laparotomy incision was made. The mesentery and colon were displaced to expose the uterine horns. A 2.0 cm longitudinal incision was made along the antimesenteric border in the mid-portion of each uterine horn. The foetuses and placentas were gently extruded through the hysterotomy. Afterwards, the uterine incisions were closed with a continuous non-locking 5-0 polyglycolic acid suture, and the deep abdominal fascia as well as peritoneum was closed with 4-0 polyglycolic acid sutures. The skin was closed separately using the same material.

Brain extraction and study. Once a foetus was explanted and decapitated, the fibrous skull tissue was excised with scalpel blade and thumb forceps to expose the brain. The head was then post-fixed in Bouin's solution for 24 hours to enable easy brain extraction. After 24 hours, the samples were transferred to 10% neutral buffered formalin. The post-fixed tissues were exposed by making a longitudinal cut along the mid-cranial line with a scalpel blade. The cut fibrous tissue was removed by gentle traction. This exposed the dura mater, which was cut with a scalpel blade along the same line. The falxcerebri and tentorium cerebelli were pulled from the longitudinal and transverse fissures of the brain, respectively, by gentle traction. This facilitated easy extraction of the brain.

For the postnatal brain samples, the animals were sedated by intraperitoneal injection of 20 mg/kg Thiopental Sodium (Rotexmedica, Trittau, Germany) and immediately weighed using a digital electronic balance (Citizen Scales (1) PVT Ltd., sensitivity: 0.01 g). Thereafter, they were euthanized with a lethal dose of the same drug. Each skull containing the brain was obtained after skinning and stripping off all the facial muscles. Shortly thereafter, craniotomy preceded brain extraction. Specifically, brain extraction was performed in a caudo-rostral and dorso-ventral direction, using scalpel blades, thumb forceps and a pair of scissors. The meninges and underlying blood vessels were gently removed to expose the intact brain. In order to separate the cerebellum from the brainstem, the floculli of the cerebellum were manually raised to expose the cerebellar peduncles. These peduncles were then severed on both sides, starting with the laterally located brachium restiformis, followed by the middle brachium pontis and then the brachium conjuctivum.

The structural characteristics of the cerebellum were examined in all the foetal and postnatal brain samples using the naked eye and with the aid of a hand lens. These included the shape, size and surfaces of the cerebellum. Also, the presence or absence of cerebellar lobes and lobules, folia or sulci, as well as the changes in these structures in different developmental ages, were evaluated. Photographs of dorsal and caudal views of the cerebellum were taken with a digital camera (Eastman Kodak® Model 14650, Rochester, New York, U. S. A.: 12.5 megapixels). NOMINA ANATOMICA VETERINARIA (2017) was used for nomenclature.

Measurements of the weight, volume and dimensions of the whole brain and cerebellum from all the foetal and postnatal brain samples constituted the macro-morphometric study. Weight measurements were obtained using a Mettler balance P 1261 (Mettler instrument AG. Greifensee, Switzerland) with a sensitivity of 0.01 g. The dimensions of the whole brain and cerebellum were obtained using a Vernier caliper MG6001DC (General Tools and Instruments Co., New York) with sensitivity of 0.01 cm, and converted to millimetres. The landmark for the absolute length of the cerebellum was the rostral-caudal extent of the vermal lobule, while the landmark for the absolute width of the cerebellum was the extent from the onset of the paraflocullus on one cerebellar hemisphere to the end of the paraflocullus on the second cerebellar hemisphere. Volume measurement was obtained by the water displacement method. Each specimen was totally submerged into a known volume of bi-distilled water (Lifespan Pharmaceutical Ltd., Zaria, Nigeria) at 20 0C in a graduated cylinder. The volume difference in the cylinder was immediately recorded. This was equal to the volume of the specimen in millilitres. The relative length of the cerebellum was calculated by dividing the absolute cerebellar length by the absolute brain length, expressed as a percentage. The relative weight of the cerebellum was calculated by dividing the absolute weight of the cerebellum by the absolute brain weight, expressed as a percentage.

Statistical analysis of the data. Data obtained were expressed as mean ± SEM (standard error of the mean) and presented in tables and graphs. Differences between the mean values were subjected to one-way analysis of variance (ANOVA), followed by Turkey's post hoc test. The association between the values of brain weight and length with the weight and dimensions of the cerebellum were determined using Pearson's coefficient of correlation at a 95% confidence interval. Values of $P<0.05$ were considered significant. GraphPad Prism version 4 (GraphPad Software Inc., San Diego, California) for Windows 8, was used for the statistical analysis.

Results

Description of the Cerebellum on F60 (foetal period). At this foetal stage, the cerebellum was not visible on the dorsal view of the intact brain (Fig. 1). It was slightly displaced to a caudo-ventral position by the fast developing corpora quadrigemini. It was a smooth, semi-circular mass, devoid of any folium or sulcus. The cerebellar lobes and vermal lobules were not yet evident.

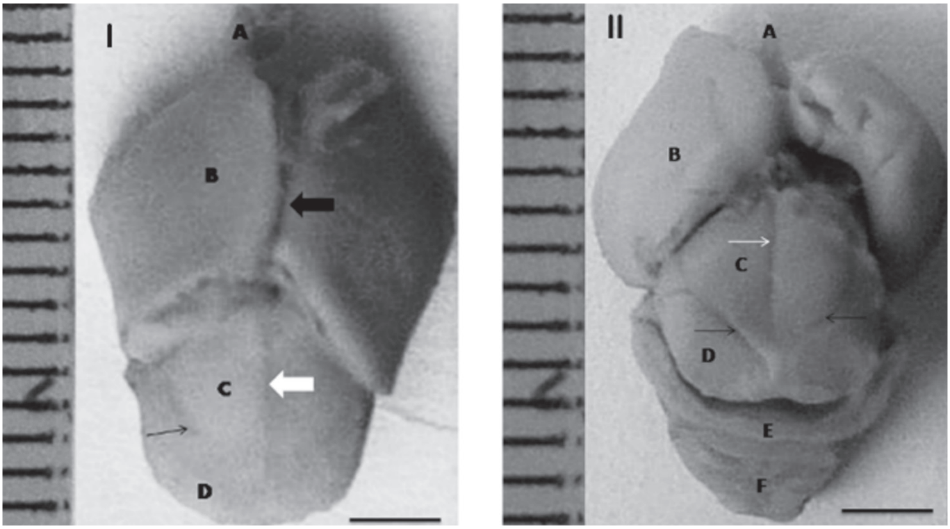

Fig. 1. Dorsal view of the intact foetal brain of the African grasscutter at F60 (I) and F90 (II)
A: olfactory bulb; B: Cerebral cortex; C: Rostral colliculus; D: Caudal colliculus. E: Cerebellum; F: Medulla oblongata. White block arrow (Fig. 1 I): pre-fissural line of rostral colliculi; White line arrow (Fig. 1II): longitudinal fissure of rostral colliculi; Black line arrow (Fig. 1 I): incomplete demarcation of the inter-collicular transverse fissure. Black line arrow (Fig. 1 II): Inter-collicular transverse fissure. Black block arrow (Fig. 1 I): Longitudinal fissure. Scale bar = 3.5 cm.

Description of the Cerebellum on F90 (foetal period). At this foetal stage, the cerebellum was visible on the dorsal view of the intact brain (Fig. 1(II): E). The cerebellum was still smooth, semi-circular, and devoid of any folium or sulcus. The vermis was distinct from the floculli, but the vermal lobules were not distinct. The paraflocullus was also indistinct. The cerebellum was separated from the cerebral cortex by the large corpora quadrigemini. It was dorsal to the medulla oblongata.

Description of the Cerebellum on P3 (neonatal period). On a dorsal view of the intact brain, the cerebellum was caudal to the cerebrum from which it was separated by the transverse fissure and the corpora quadrigemini. It assumed a dorso-caudal position. The cerebellum was the largest structure after the cerebrum, thus, it was larger than the corpora quadrigemini, unlike in the foetal brain. The cerebellum completely occluded the rhomboid fossa, forming the roof of the fossa. The cerebellar cortex was no longer smooth, but coiled with folia and fissures. The lobes were grossly distinct. They consisted of an unpaired vermis and the cerebellar hemispheres, consisting of the paired flocculus and the paraflocculus. The cerebellar vermis was divided into all the lobules typical of mammalian vermis. These included the lingula, central lobule, culmen, declive, folium, tuber, pyramis, uvula and nodulus. While the rostral lobules, which included the lingula, central lobule and culmen as well as the declive, were very visible on the dorsal view of the cerebellum, the folium, tuber, pyramis, uvula and nodulus were visible from a caudal view. Furthermore, while the culmen formed the dorsal summit in which the cerebellum reached its highest elevation, the declive formed the onset of the caudal slope.

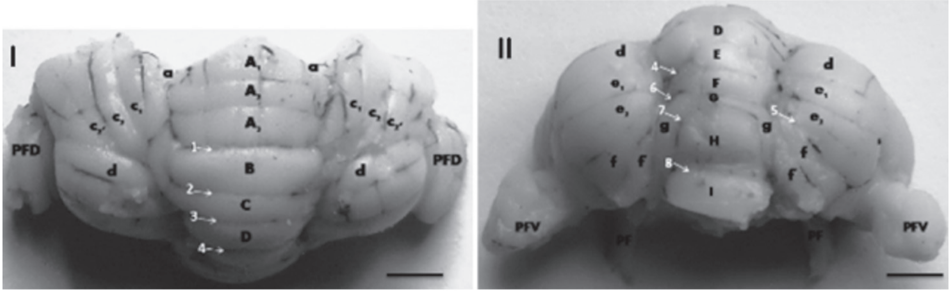

Fig. 2. Dorsal (I) and caudal (II) views of the cerebellum of the African grasscutter at P3
A1: Lingula (pars rostralis); A2: Lingula (pars medialis); A3: Lingula (pars caudalis); B: Central lobule; C: Culmen; D: Declive; E: Folium; F: Tuber; G: Pyramis; H: Uvula; I: Nodulus; PFD: paraflocullus dorsalis; PFV: Paraflocculus ventralis; a: Vinculum lingula; c1: Lobulus quadrangularis (pars rostralis); c2 and c2/: Lobulus quadrangularis pars caudalis; d: lobules simplex; e: Lobulus ansiformis (crus rostralis); f: Lobulus ansiformis (crus caudalis); f': Lobulus paramedianus; g: n-shaped ventral projection of pyramis into the cerebellar hemisphere; 1: Pre-central fissure; 2: Post-central fissure; 3: Rostral superior fissure (primary fissure); 4: caudal superior fissure (post-clival fissure); 5: Inter-crural fissure (great horizontal fissure); 6: Pre-pyramidal fissure; 7: Post-pyramidal fissure (secondary fissure); 8: pre-nodular fissure; 9: Post-nodular fissure. Note that the great horizontal fissure (inter-crural fissure) has not been fully delineated. Also note that the crus rostralis of the lobulus ansiformis has not bifoliated. Scale bar = 1.4 cm.

On the dorsal view of the cerebellum, the lingula was the largest vermal lobule, pentagonal in shape, and delineated into the pars rostralis, pars medialis and pars caudalis by intra-lobular fissures (Fig. 2(I): A1; A2; A3). The small lateral extension of the lingula, the vinculum lingula, was also evident. Caudal to the lingula was the central lobule, separated from the former by a conspicuous pre-central fissure. The culmen was an undivided vermal lobule separated from the central lobule by the post-central fissure. The culmen extended into the cerebellar hemispheres as the lobulus quadrangularis. In each of the paired floculli, the lobules quadrangularis further divided into a pars rostralis and a bifoliated pars caudalis (Fig. 2(I): c; c1; c2; c2/). Caudal to the culmen, and separated from it by the primary fissure, was the declive. This vermal lobule also extended into the cerebellar hemisphere as the lobulus simplex. On this view, the dorsal surfaces of the paired parafloculli were grossly visible. They were coiled, presenting folia and fissures. The parafloculli were located on either side of the floculli and were the smallest of the three cerebellar lobes.

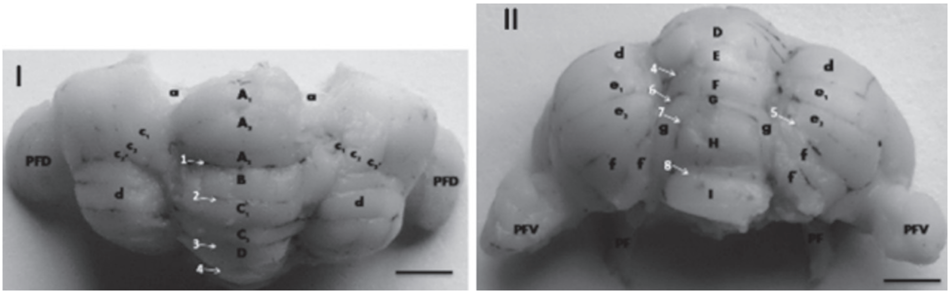

Fig. 3. Dorsal (I) and caudal (II) views of the cerebellum of the African grasscutter at P72
A1: Lingula (pars rostralis); A2: Lingula (pars medialis); A3: Lingula (pars caudalis); B: Central lobule; C1: Culmen (pars rostralis); C2: Culmen (pars caudalis); D: Declive; E: Folium; F: Tuber; G: Pyramis; H: Uvula; I: Nodulus; PFD: Paraflocullus dorsalis; PFV: Paraflocculus ventralis; a: Vinculum lingula; c1: Lobulus quadrangularis (pars rostralis); c2 and c2/: Lobulus quadrangularis pars caudalis; d: lobules simplex; e: Lobulus ansiformis (crus rostralis); f: Lobulus ansiformis (crus caudalis); f/: Lobulus paramedianus; g: n-shaped ventral projection of pyramis into the cerebellar hemisphere; 1: Pre-central fissure; 2: Post-central fissure; 3: Rostral superior fissure (primary fissure); 4: Caudal superior fissure (post-clival fissure); 5: Great horizontal fissure (inter-crural fissure); 6: Pre-pyramidal fissure; 7: Post-pyramidal fissure (secondary fissure); 8: pre-nodular fissure; PF: Pedunculus flocculi. Scale bar = 1.4 cm.

On the caudal view of the cerebellum, the vermal and hemispheric lobules were arranged in a dorso-ventral fashion (Fig. 2(II)). A post-clival fissure separated the declive from the folium. The folium extended into the cerebellar hemisphere as the crus rostralis of the lobules anseriformis. The crus rostralis was presented as an unpaired part of the lobules anseriformis (Fig. 2(II)). Caudal to the folium is the bean-shaped tuber which also extended into the flocullus as the crus caudalis of the lobules anseriformis and as the lobules paramedianus. The crus rostralis and crus caudalis were separated by the intra-crural fissure (Fig. 2(II): 5). At this age, this fissure was not so well developed to be referred to as the great horizontal fissure. The pyramis, presented as the smallest vermal lobule at this age, was separated from the folium by the pre-pyramidal fissure and from the uvular by the post-pyramidal fissure. The pyramis slightly extended ventrally in an n-shaped fashion (Fig. 2(II): g). The uvula was the second largest vermal lobule. It was separated from the pyramis by a post-pyramidal fissure and from the last lobule, the nodulus, by a pre-nodular fissure. The ventral surface of the paraflocullus was visible from this view of the cerebellum.

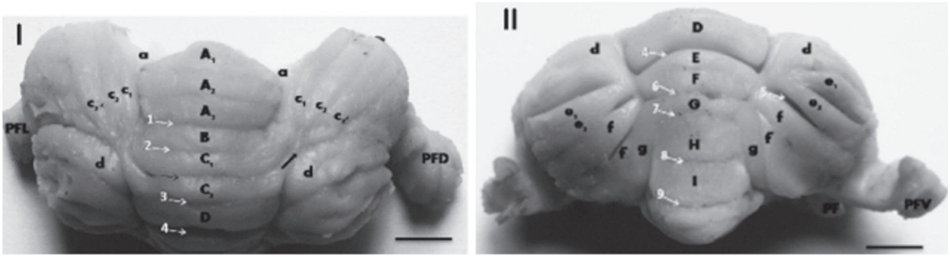

Fig. 4. Dorsal (I) and caudal (II) views of the cerebellum of the African grasscutter at P450
A1: Lingula (pars rostralis); A2: Lingula (pars medialis); A3: Lingula (pars caudalis); B: Central lobule; C1: Culmen (pars rostralis); C2: Culmen (pars caudalis); Black line arrow: Intra-lobular fissure of culmen. Black block arrow: Extension of culmen into the cerebellar hemisphere; D: Declive; E: Folium; F: Tuber; G: Pyramis; H: Uvula; I: Nodulus; PFD: Paraflocullus dorsalis; PFV: Paraflocculus ventralis; a: Vinculum lingula; c1: Lobulus quadrangularis (pars rostralis); c2 and c2/: Lobulus quadrangularis pars caudalis; d: Lobules simplex; e: Lobulus ansiformis (crus rostralis); f: Lobulus ansiformis (crus caudalis); f': Lobulus paramedianus; g: n-shaped ventral projection of pyramis into the cerebellar hemisphere; 1: Pre-central fissure; 2: Post-central fissure; 3: Rostral superior fissure (primary fissure); 4: Post-clival fissure (caudal superior fissure); 5: Great horizontal fissure (inter-crural fissure); 6: Pre-pyramidal fissure; 7: Post-pyramidal fissure (secondary fissure); 8: Pre-nodular fissure; 9: Post-nodular fissure; PF: Pedunculus flocculi. Scale bar = 1.4 cm.

Description of the Cerebellum on P72 (juvenile stage): On the dorsal view of the cerebellum, the lingula was the largest vermal lobule and delineated into the pars rostralis, pars medialis and pars caudalis by intra-lobular fissures (Fig. 3(I): A1; A2; A3). However, there was a slight division from the pentagonal shape of the neonatal lingula, as the angle of the vinculum lingula was increased by the large caudal colliculus. Also, the pre-central fissure was observed to be deeper than that observed in the neonates. Furthermore, the culmen was divided into a pars rostralis and a pars caudalis, probably due to increased size of the lobule at the juvenile stage (Fig. 3(I): C1; C2). While the pars rostralis of the culmen extended into the hemisphere to form the pars rostralis of the lobules quadrangularis, the pars caudalis of the culmen formed the bifoliated pars caudalis of the lobules quadrangularis in the cerebellar hemisphere (Fig. 3(I):c; c1; c2; c2/). The lobulus simplex was visibly larger than was observed in the neonatal sample. The paraflocullus was the same as in the neonates.

On the caudal view of the juvenile cerebellum, the dorso-ventral arrangement of the vermal and hemispheric lobules was maintained (Fig. 3(II)). A post-clival fissure separated the declive from the folium. The folium extended into the cerebellar hemisphere as the crus rostralis of the lobules anseriformis. However, unlike what was observed in the neonatal cerebellum, the crus rostralis was bifoliated, although the fissure was not well developed to distinctly separate the two folia of the crus rostralis (Fig. 3(II): e1; e2). The tuber maintained the bean-shape and extended into the flocullus as the crus caudalis of the lobules anseriformis and as the lobules paramedianus. Also, the intra-crural fissure was still not distinct enough to be referred to as the great horizontal fissure. The pyramis was still the smallest vermal lobule and extended ventrally in an n-shape. However, unlike what was observed in the neonatal cerebellum, the ventral extension of the two sides of the pyramis had advanced into the ventral aspect of the cerebellum (Fig. 3(II): g). The morphology of the uvula and nodulus was the same as in the neonates. Also, the ventral surface of the paraflocullus (Fig. 3(II): PFV) and the cerebellar peduncles (Fig. 3(II): PF) were visible from this view of the cerebellum.

Description of the Cerebellum on P450 (adult period): On the dorsal view of the cerebellum, the lingula was the largest vermal lobule and delineated into the pars rostralis, pars medialis and pars caudalis by intra-lobular fissures (Fig. 4(I): A1; A2; A3). It maintained the pentagonal shape of the neonatal lingula. The central lobule remained undivided, while the pars rostralis and pars caudalis of the culmen were better delineated due to the deeper intra-lobular fissure (Fig. 4(I): black line arrow). The extension of the pars caudalis of the culmen into the cerebellar hemispheres, to give rise to the pars caudalis of the lobules quadrangularis, was very evident (Fig. 4(I): black block arrow). The pars caudalis of the lobules quadrangularis was bifoliated (Fig. 4(I): C2; C2/). The declive and lobulus simplex were more developed and the post clival fissure completely separated the declive from the folium. The paraflocullus had increased in size, although it retained the gross morphology described in the neonates.

On the caudal view, the dorso-ventral arrangement of the vermal and hemispheric lobules was retained (Fig.4(II)). The vermal and hemispheric lobules were more delineated due to the more conspicuous inter-lobular fissures. Also, the bifoliated crus rostralis of the lobules anseriformis was more evident, as the fissure completely separated the two parts (Fig. 4(II): e1; e2). The tuber maintained its bean-shape and extended into the flocullus as the crus caudalis of the lobules anseriformis and as the lobules paramedianus. Also, the intra-crural fissure, which separated the crus rostralis from the crus caudalis in the lobules anseriformis, was now very distinct and could be referred to as the great horizontal fissure. The n-shape of the pyramis was more evident (Fig. 4(II): G; g) as the two sides of the pyramis extended ventrally and contributed to the formation of the ventral surface of the paraflocullus (Fig. 4(II): PFL). The morphology of the uvula and nodulus was the same as in the neonates and juveniles. Also, the cerebellar peduncles (Fig. 4(II): PF) were visible from this view of the cerebellum.

Morphometric features of the developing cerebellum at different postnatal stages. The morphometric parameters of the whole brain and cerebellum of the African grasscutter on P3, P72 and P450 are presented in Tables 1, 2 and 3, respectively.

Table 1. Morphometric parameters of the body and brain of the African grasscutter on post natal day 3 (n = 9)

Parameter	Minimum	Maximum	Mean ± SEM
Live weight (g)	100.76	117.12	109.76 ± 3.12
Nose-rump length (mm)	150.00	176.00	160.00 ± 2.99
Tail length (mm)	65.00	75.00	70.67 ± 0.96
Brain weight (g)	3.70	4.33	4.19 ± 0.08
Brain length (mm)	37.00	41.00	39.12 ± 0.46
Brain volume (mL)	4.02	4.94	4.38 ± 0.10
Cerebellum absolute weight (g)	0.50	0.59	0.54 ± 0.01
Cerebellum absolute length (mm)	10.50	11.00	10.74 ± 0.05
Cerebellum width (mm)	16.10	17.15	16.66 ± 0.15

Table 2. Morphometric parameters of the body and brain of the African grasscutter on post natal day 72 (n = 9)

Parameter	Minimum	Maximum	Mean ± SEM
Live weight (g)	249.50	300.50	273.39 ± 6.70
Nose-rump length (mm)	200.00	245.00	216.89 ± 5.18
Tail length (mm)	79.00	92.00	84.78 ± 1.58
Brain weight (g)	6.65	7.00	6.77 ± 0.04
Brain length (mm)	50.90	55.00	53.18 ± 0.52
Brain volume (mL)	8.91	9.92	9.41 ± 0.11
Cerebellum absolute weight (g)	0.96	1.00	0.98 ± 0.02
Cerebellum absolute length (mm)	16.90	17.60	17.37 ± 0.07
Cerebellum width (mm)	21.00	22.00	21.58 ± 0.13

Table 3. Morphometric parameters of the body and brain of the African grasscutter on post natal day 450 (n = 9)

Parameter	Minimum	Maximum	Mean ± SEM
Live weight (g)	2200.00	3500.00	2925.56 ± 141.96
Nose-rump length (mm)	430.00	499.00	470.33 ± 8.47
Tail length (mm)	132.00	194.00	173.32 ± 7.92
Brain weight (g)	11.35	13.00	12.22 ± 0.23
Brain length (mm)	60.10	70.00	63.74 ± 1.47
Brain volume (mL)	10.05	11.81	10.42 ± 0.8
Cerebellum absolute weight (g)	1.33	1.72	1.49 ± 0.04
Cerebellum absolute length (mm)	19.89	21.90	20.39 ± 0.20
Cerebellum width (mm)	24.00	25.56	24.76 ± 0.16

There was a very significant positive correlation ($P<0.01$) between nose-rump length and the length of the cerebellum on P450 ($r = 0.83$). This implies that the cerebellar length had increased at approximately the same rate as the nose-rump length in the adult African grasscutter. This was subjected to regression analysis, and a regression formula was deduced on a graph (Fig. 5) as follows:

$y = 0.013x + 14.07$

where y = cerebellar length; x = known nose-rump length

Thus, for an adult African grasscutter whose nose-rump length has been obtained (x), the approximate length of the cerebellum (y) can be deduced from the above formula.

There was a significant increase ($P<0.05$) in the relative weight of the cerebellum from 10.56 ± 0.48% on P3 to 14.47 ± 0.12% on P72. On P450, the value was 12.17 ± 0.37%. This decrease was not statistically significant ($P>0.05$).

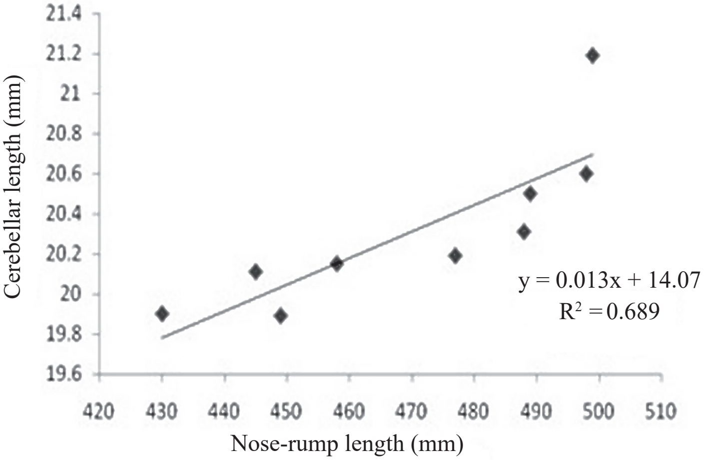

Fig. 5. The positive linear relationship between nose-rump length and cerebellar length in the African grasscutter on P450

There was a significant increase ($P<0.05$) in the relative length of the cerebellum from 27.48 ± 0.40% on P3 to 32.66 ± 0.34% on P72 (Fig. 6). Thereafter, the relative length of the cerebellum was 32.13 ± 0.82% on P450, a value that was almost the same as that of the juveniles (P72). The difference in the value of the relative length of the cerebellum between the juveniles and adults was not significant ($P>0.05$).

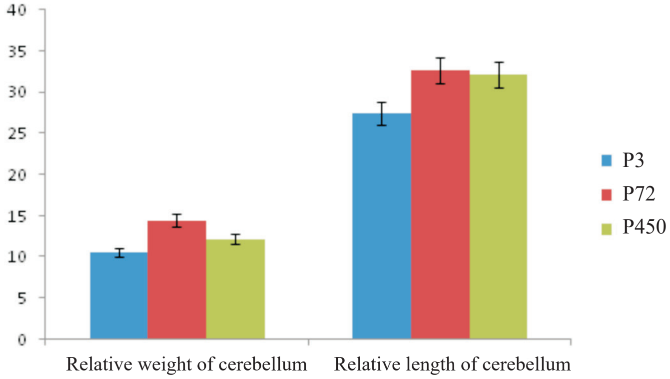

Fig. 6. Graph of the relative weight and length of the developing cerebellum of the African grasscutter at different postnatal stages

Discussion

LARSELL (1952) used Roman numerals to delineate the nomenclature of vermal lobules, while the Nomina Anatomica Veterinaria (2017) used the specific names of the lobules. In their atlas, NAIDICH et al. (2009) married Larsell's nomenclature with that of the 2005 edition of Nomina Anatomica Veterinaria, and reported lobule I as the lingula, lobules II and III as central lobule, lobules IV and V as the culmen, lobule VI as the declive, lobule VII as the folium and tuber, lobule VIII as the pyramis, lobule IX as the uvula and lobule X as the nodulus. Due to this discrepancy in the nomenclature of the vermal lobules, authors who use Larsell's nomenclature state that the vermis has 10 lobules, while those who adopt the Nomina Anatomica Veterinaria's classification state 9 lobules in the cerebellar vermis.

The complex modification of the vermal and hemispheric cerebellar lobules in different species has been attributed to the complexity of the specific function of the different lobules. The lingula was found to be the largest vermal lobule in all postnatal periods, pentagonal in shape, subfoliated into 3 parts and presenting a lateral extension, the vinculum lingula. This is different from the African giant pouched rat, as BYANET et al. (2013) observed that this first vermal lobule was relatively small, rounded, not subfoliated, and had no lateral representation in the animal. The present result in the African grasscutter is also different from that of the naked mole rat, as MARZBAN et al. (2011) reported that lobules I (equivalent to lingula), II and III (equivalent to central lobule) were fused in the naked mole rat. According to the work of MANNI and PETROSINI (2004), tail musculature activity is represented in the lingula. Based on this, the well-developed lingula in the African grasscutter is debatable, as the tail of the adult

African grasscutter from the present study is relatively shorter than that of other rodents, such as the African giant pouched rat as reported by IBE et al. (2011).

The central lobule was small and not subfoliated in all the postnatal periods in the present study. This is different from the African giant pouched rat as BYANET et al. (2013) reported that this second vermal lobule was long and subfoliated into 3 parts by intra-central fissures. The central lobule has been implicated in the activation of the voluntary movement of the hind limb (RIJNTJES et al., 1999). Study of the hindlimb structure of the African grasscutter is lacking in the available literature. There is a need to study the musculature of the hind limb of the African grasscutter to correlate it with the functional significance of the central lobule.

Developmental analysis of the culmen in the present study showed that at foetal days 60 and 90, the culmen, as well as all other vermal lobules, were indistinct; by postnatal day 3, the lobules quadrangularis had advanced in development, whereby it had further divided into a pars rostralis and a bifoliated pars caudalis, while the culmen remained undivided. It was not until around postnatal day 72 that the culmen was divided into a pars rostralis and a pars caudalis, a feature that was maintained in the adult. This developmental pattern implies that the cerebellar hemisphere developed earlier than the cerebellar vermis. The subsequent division of the culmen into sub-lobules was probably due to the increase in cell size and the number of new cells, so that there was a need for more surface area to be occupied by the lobule. This increase in neuronal growth points to more synaptogenesis and extends the known function of the culmen. The culmen is involved in the co-ordinate movement of the forelimb (GRODD et al., 2001; SCHLERF et al., 2010). It is well developed in the adult African grasscutter, as observed in the present study, similar to the adult African giant pouched rat (BYANET et al., 2014). These rodents are known to make good use of their forelimbs in grasping food, which they direct to their mouth. This action may be linked to the well-developed culmen. Conversely, the culmen, equivalent to Lobules IV and V, is not well developed in the mole rat, as the lobules quadrangularis were not observed in the adult rodent (MARZBAN et al., 2011).

There were no marked morphological changes in the declive as the African grasscutter advanced in age, except for the increase in size of the declive and its hemispheric extension, the lobulus simplex. It maintained its dorso-ventral orientation, a slanting position that earned it the name declive. Similarly, MARZBAN et al. (2011) observed that the declive (Lobule VI) was prominent in the adult naked mole rat and not fused with any other vermal lobule. The lobulus simplex was also evident in the adult mole rat (MARZBAN et al., 2011). Electrical stimulation of the declive and lobulus simplex by MOTTOLESE et al. (2013) resulted in localized motor response in the neck and facial muscles, respectively. The anatomy of these body parts have not been studied in the African grasscutter, so thus cannot be related to the developed declive and lobulus simplex.

Postnatal development of the hemispheric extensions of the folium advanced from the undivided crus rostralis of the lobules anseriformis on postnatal day 3 to a partially bifoliated crus rostralis (presented with fissural line) in juveniles and finally, a completely bifoliated crus rostralis in the adult. However, the vermal folium remained undivided in all postnatal periods. This observation, similar to that observed in the culmen, buttresses the hypothesis made in the present study, that the cerebellar hemisphere developed earlier than the vermis. The hemispheric extension of the tuber presented 2 divisions, the crus caudalis of the lobules anseriformis and the lobules paramedianus. This division of the tuber is unlike that of the African giant pouched rat, as reported by BYANET et al. (2013). SULTAN and BRAITENBERG (1993) also reported a developed hemispheric extension of the tuber in the squirrel. The folium and tuber are involved in co-ordinating fore- and hind limb movement (SCHLERF et al., 2010), necessary for activities such as climbing. While the squirrel and African giant pouched rats are good climbers, the African grasscutter is not known to be a good climber, probably due to the poorly developed folium and tuber.

Data from the morphometric results of the present study revealed that the increase in the relative cerebellar weight and length from P3 to P72 was statistically significant. The difference in value of the same parameter from P72 (juvenile) to P450 (adult) was not statistically significant, despite the wide age gap between the juveniles and the adults. This points to the fact that cerebellar neurogenesis and the increase in neuron size is very rapid in neonatal African grasscutters compared to juveniles and adults. Also, the decrease in the relative weight of the cerebellum from juvenile to adult indicates that the cerebellum increases in size at a slower rate than the body size as the animal advances from juvenile to adulthood. Furthermore, the regression formula deduced from the regression analysis of nose-rump *vs*. cerebellar lengths in the adult African grasscutter offers the advantage of obtaining the approximate length of the cerebellum in a live adult African grasscutter whose nose-rump length is known. In a sexual dimorphic study of the cerebellum of adult grasscutters by BYANET et al. (2012), the length and width of the adult cerebellum did not differ between the two sexes, but the cerebellar circumference of the adult male grasscutter was more than that of the female, and this was attributed to the large, round head of the male grasscutter. BYANET et al. (2012) also stated that the length of the cerebellum in the mature female grasscutter was positively correlated to the length of the brain, head, body and tail.

From the available literature, it was discovered that there is marked variability in the functional significance of the different vermal and hemispheric lobules of the mammalian cerebellum. While some authors report that a particular body part is represented by different lobules, others report that a lobule represents more than one body part. However, the consistent report from various neuroimaging and electrophysiological studies is that the lingula, central lobule, culmen, declive and lobulus simplex co-ordinate the motor activities of the tail, hind limbs, forelimbs, neck and facial muscles, respectively (RIJNTJES et al., 1999; MANNI and PETROSINI, 2004; KAPRELI et al., 2007; SCHLERF et al., 2010; MOTTOLESE et al., 2013). Studies have also linked the posterior vermal lobules (tuber, pyramis, uvula and nodulus) to the coordination of the voluntary movement of the fore and hind limbs. The anatomy and functional development of these skeletal muscles have not been reported in the African grasscutter. Thus, the significance of the morphological findings of these cerebellar lobules cannot be discussed.

Conclusion

The present study has expounded the external features of the cerebellum of the African grasscutter in foetal and postnatal developmental periods. Attention was focussed on lobar and lobular differentiation. From the present study, it was hypothesized that the cerebellar hemisphere developed earlier than the cerebellar vermis. Also, while some vermal lobules became well developed in the adult, others did not attain full development. The results of the present study have added to the information available on rodent brain development.

References

ADDO, P. G. (2002): Detection of mating, pregnancy and imminent parturition in the grasscutter (*Thryonomys swinderianus*). Livestock Res. Rural Dev. 14, 8-13.

ASIBEY, E. O. A., P. G. ADDO (2000): The Grasscutter, a promising animal for meat production. In: African Perspectives, Practices and Policies Supporting Sustainable Development. (Turnham, D., Ed.), Weaver Press, Harare, Zimbabwe, p. 120.

ASSOGBADJO, A. E., J. T. C. CODJIA, B. SINSIN, M. R. EKUE, G. A. MENSAH (2005): Importance of rodents as a human food source in Benin. Belg. J. Zool. 135, 11-15.

AYDIN, A., S. YILMAZ, Z. E. OZKAN, R. ILGUN (2008): Morphological investigations on the circulus arteriosus cerebri in mole-rats (*Spalax leucodon*). Anat. Histol. Embryol. 37, 219-222.

DOI: 10.1111/j.1439-0264.2007.00834.x

BOWERS, D., D. McKENZIE, D. DUTTA, C. R. WHEELESS, W. R. COHEN (2001): Growth hormone treatment after cesarean delivery in rats increases the strength of the uterine scar. Am. J. Obstet. Gynecol. 185, 614-617.

DOI: 10.1067/mob.2001.117185

BYANET, O., B. I. ONYEANUSI, S. A. OJO (2012): Sex differences in the cerebellum and its correlates with same body traits in the African grasscutter (*Thryonomys swinderianus*-Temminck, 1827): morphometric study. BCN. 3, 15-21.

BYANET, O., O. A. SAMUEL, O. I. BARTH, N. A. JONATHAN (2013): Macroscopic organization of the cerebellum of the African giant pouched rat (*Cricetomys gambianus* - Waterhouse, 1840). Vet. arhiv 83, 695-707.

BYANET, O., T. DZENDA, M. H. SULAIMAN (2014): Dimensional sex differences in the cerebellum of the African giant pouched rat (*Cricetomys gambianus* - Waterhouse, 1840). Int. J. Biosci. 5, 1-10.

DOI: 10.12692/ijb/5.8.1-10

FLETCHER, T. F., A. F. WEBER (2003): Veterinary developmental anatomy. In: Veterinary Embryology Class Notes, pp. 54-61.

GRODD, W., E. HÜLSMANN, K. LOTSE, D. WILDGRUBER, M. ERB (2001): Sensorimotor mapping of the human cerebellum: fMRI evidence of somatotopic organisation. Hum. Brain Mapp. 13, 55-73.

DOI: 10.1002/hbm.1025

IBE, C. S., S. O. SALAMI, B. I. ONYEANUSI (2011): Macroscopic anatomy of the lower respiratory system in a nocturnal burrowing rodent: African Giant pouched rat (*Cricetomys gambianus*, Waterhouse 1840). Anat. Histol. Embryol. 40, 112-119.

DOI: 10.1111/j.1439-0264.2010.01048.x

IBE, C. S., B. I. ONYEANUSI, J. O. HAMBOLU (2014): Functional morphology of the brain of the African giant pouched rat (*Cricetomys gambianus*, Waterhouse, 1840). Onderstepoort Journal of Veterinary Research 81, e1-e7.

DOI: 10.4102/ojvr.v81i1.644

INOUYE, N., S. ODA (1980): Strain-specific variations in the folia pattern of the mouse cerebellum. J. Comp. Neurol. 190, 357-362.

DOI: 10.1002/cne.901900209

IWANIUK, A. N., P. L. HURD, D. R. WYLIE (2006): The comparative morphology of the cerebellum in caprimulgiform birds: evolutionary and functional implications. Brain Behv. Evol. 67, 53-68.

DOI: 10.1159/000089120

KAPRELI, E., S. ATHANASOPOULOS, M. PAPATHANASIOU, P. VAN HECKE, D. KELEKIS, R. PEETERS, N. STRIMPAKOS, S. SUNAERT (2007): Lower limb sensorimotor network: issues of somatotopy and overlap. Cortex 43, 219-232.

DOI: 10.1016/S0010-9452(08)70477-5

LARSELL, O. (1952): The morphogenesis and adult pattern of the lobules and fissures of the cerebellum of the white rat. J. Comp. Neurol. 97, 281-356.

DOI: 10.1002/cne.900970204.

MANNI, E., L. PETROSINI (2004): A century of cerebellar somatotopy: a debated representation. Nat. Rev. Neurosci. 5, 241-249.

DOI: 10.1038/nrn1347

MARZBAN, H., N. HOY, T. AAVANI, D. K. SARKO, K. C. CATANIA, R. HAWKES (2011): Compartmentation of the cerebellar cortex in the naked mole-rat (*Heterocephalus glaber*). Cerebellum 10, 435-448.

DOI: 10.1007/s12311-011-0251-8

MOTTOLESE, C., N. RICHARD, S. HARQUEL, A. SZATHMARI, A. SIRIGU, M. DESMURGE (2013): Mapping motor representations in the human cerebellum. Brain 136, 330-342.

DOI: 10.1093/brain/aws186

NAIDICH, T. P., H. M. DUVERNOY, B. N. DELMAN, A. G. SORENSEN, S. S. KOLLIAS, E. M. HAACK (2009): Duvernoy's Atlas of the Human Brain Stem and Cerebellum: High Field MRI, Surface Anatomy, Internal Structure, Vascularization and 3 D Sectional Anatomy. Springer Science and Business Media Publishing Company, pp. 95-135.

NOMINA ANATOMICA VETERINARIA (2017): International Committee on Veterinary Gross Anatomical Nomenclature. 6th ed. Hannover Columbia.

NZALAK, J. O., O. BYANET, S. O. SALAMI, A. D. UMOSEN, S. M. MAIDAWA, M. N. ALI, J. IMAM (2008): Comparative morphometric studies of the cerebellum and forebrain of the African giant rat (AGR) (*Crycetomys gambianus*-Waterhouse) and that of grasscutter (*Thryonomys swinderianus*). J. Anim. Vet. Adv. 7, 1090-1092.

DOI: javaa.2008.1090.1092

OPARA, M. N. (2010): Grasscutter I: a livestock of tomorrow. Res. J. For. 4, 119-135.

DOI: 10.3923/rjf.2010.119.135

RIJNTJES, M., C. BUECHEL, S. KIEBEL, C. WEILLER (1999): Multiple somatotopic representations in the human cerebellum. Neuroreport 10, 3653-3658.

SCHLERF, J. E., T. D. VERSTYNEN, R. B. IVRY, R. M. SPENCER (2010): Evidence of a novel somatopic map in the human neocerebellum during complex actions. J. Neurophysiol. 103, 3330-3336.

DOI: 10.1152/jn.01117.2009

SCHMAHMANN, J. D. (2004): Disorders of the cerebellum: ataxia, dysmetria of thought, and the cerebellar cognitive affective syndrome. J. Neuropsych. Clin. Neurosci. 16, 367-378.

DOI: 10.1176/appi.neuropsych.16.3.367

SKINNER, J., C. CHIMIMBA (2005): Lesser cane rat. In: The Mammals of the South African Subregion, 3rd ed. Cambridge, Cambridge University Press, pp. 96-97.

STRATA, P., B. SCELFO, B. SACCHETTI (2011): Involvement of cerebellum in emotional behaviour. Physiol. Res. 60 (Suppl. 1), 39-48.

SULTAN, F., V. BRAITENBERG (1993): Shapes and sizes of different mammalian cerebella. A study in quantitative comparative neuroanatomy. J. Hirnfor. 34, 79-92.

TAVANO, A., R. GRASSO, C. GAGLIARDI, F. TRIUZLI, N. BRESOLIN, F. FABBRO, R. BORGATTI (2007): Disorders of cognitive and affective development in cerebellar malformations. Brain 130, 2646-2660.

DOI: 10.1093/brain/awm201

VAN DER MERWE, M. (2007): Discriminating between *Thryonomys swinderianus* and *Thryonomys gregorianus.* Afr. Zool. 42, 165-171.

DOI: 10.3377/1562-7020(2007)42[165:DBTSAT]2.0

VOOGD, J., N. H. BARMACK (2006): Oculomotor cerebellum. Prog. Brain Res. 151, 231-268. DOI: 10.1016/S0079-6123(05)51008-2.

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IBE, C. S., S. A. OJO, S. O. SALAMI, J. O. AYO, E. IKPEGBU: Makroskopska građa malog mozga afričkoga divovskog trstičnog štakora (*Thryonomys swinderianus* - Temminck, 1827) tijekom fetalnog i postnatalnog razvoja. Vet. arhiv 89, 559-577, 2019.

SAŽETAK

U Nigeriji se afrički divovski trstični štakor (*Thryonomys swinderianus*) uzgaja kao mini stoka i model za istraživanje. U radu su prikazani podaci o razvoju njegova malog mozga, prikupljeni makroskopskim promatranjem vanjskih obilježja mozga kod fetusa u dobi 60 i 90 dana, novorođenčadi u dobi 3 dana, mladih životinja u dobi od 72 dana i odraslih životinja u dobi od 450 dana. Mali mozak fetusa u dobi od 60 dana bio je glatka, polukružna masa bez vijuga i brazda, na kojoj nisu bili prisutni moždani režnjevi ni vermisni režnjići. U dobi fetusa i u dobi od 90 dana bio je izražen vermis, ali vermisni su režnjići bili nejasni. Treći dan nakon porođaja kora maloga mozga je na vrlo izraženim režnjevima bila isprepletena s vijugama i usjeklinama. Vermis maloga mozga bio je podijeljen na sve režnjeve tipične za vermis sisavaca. Lingula, središnji režanj, kulmen i declive bili su na dorzumu maloga mozga, dok su folium, tuber, pyramis, uvula i nodulus smješteni kaudalno. Kulmen je bio nepodijeljen, a crus rostralis nesparen. 72 dana nakon porođaja predsredišnja usjeklina bila je dublja u odnosu na opažanja 3. dana nakon porođaja. Kulmen je bio podijeljen na pars rostralis i pars caudalis. Crus rostralis je linijom usjekline bio dvovijugav. Mali mozak životinja u dobi od 450 dana imao je dublje usjekline, a vermisni i hemisferični režnjevi bili su bolje razgraničeni. Dvovijugavost crus rostralis bila je još naglašenija. Intrakruralna usjeklina bila je vrlo izražena i prikazana kao velika vodoravna usjeklina. Rezultati ove studije nadopunit će bazu podataka o neuroanatomiji glodavaca koja je potrebna za poučavanja i istraživanja.

Ključne riječi: afrički divovski trstični štakor; mali mozak; makroanatomija; vermis; flocullus; paraflocullus