Macroscopic organization of the cerebellum of the African giant pouched rat (*Cricetomys gambianus* - Waterhouse, 1840)

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ABSTRACT

The degree of folding or foliation and its functional implication is one of the major difference in the cerebellar cortex of rodents. The enlargement / reduction of individual lobules is thought to account for their specific behavioural differences. The macroscopic anatomy of the cerebellum in ten mature African Giant pouched rats (AGPR) is detailed here for the first time. The results showed that the division of the cerebellum in this species followed the same general pattern of having three lobes (anterior, posterior and flocculonodular) lobes. Also on the ventral aspect, three cerebellar peduncles that connected the cerebellum to the brain stem were observed. The lobule VI and its principal lateral continuation corresponds to the lobulus simplex. The lateral extension of lobule VII corresponds to the well developed lobulus ansiformis, consisting of Crus I (crus rostrale), Crus II (crus caudale) and the anterior part of the lobulus paramedianus. The largest lobule in the anterior lobe is lobule V and it is subfoliated into Va, Vb, Vc and Vd by small fissures, while the smallest lobule is lobule I, which is not sublobulated. As for the posterior lobe, lobules VI and IX are the broadest and are sublobulated into five and three sublobules, respectively. Lobule X is subfoliated into two lobules, Xa and Xb, and it was observed to be the smallest of the posterior lobes. The primary fissure was the deepest and most prominent fissure, followed by the precuminate fissure, while the precentral fissure was the smallest. In conclusion, the well-developed ansiform lobe of Crus I and Crus II in AGPRs may help in the excellent climbing strategies and the manipulative use of the forelimbs in grasping objects.

Key words: African giant rat, cerebellum, gross anatomy, lobes and lobules

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Introduction

The African giant pouched rat (*Cricetomys gambianus*) (AGPR) is one of Africa's largest rodents that live in savannas and around the edges of forests and human settlements. In the wild, AGPRs are nocturnal animals, although they have been seen foraging during the day, but with characteristic behaviour of sitting on their haunches and sniffing in all directions (ANONYMOUS, 1991). In captivity, they often sit up and ram large amounts of food into their cheek pouches, using their free forelimb (AJAYI, 1974). Apart from its large size, the AGPR is noted for its long body and strong long tail, with dusty grey as the overall body colour. Although these animals are terrestrials, they usually climb trees in search of fruit and other food, and are also excellent swimmers (ANONYMOUS, 1991).

The general conception that the cerebellum is concerned with the co-ordination of somatic motor activity, the regulation of muscle tone and mechanism that influence and maintain equilibrium and posture (FLETCHER, 2006), in emotional behaviour (STRATA et al., 2011) cognition and language (STOODLEY and SCHMAHMANN, 2009), is not new. Early in the morphological study of the cerebellum it was shown that the cerebellar form and size in difference species of animals are related to the peculiarities of their body build, their motor habits and skills. This further provides clues to the special role of the cerebellum in motor control.

Considering the role of the cerebellum in motor activity (FLETCHER, 2006; STRATA et al., 2011), the cerebellum can be seen to play a significant part in the behaviour of AGRP in the wild and in captivity. In rodents such as the white rat, the cerebellum has shown a relatively broad vermian region and extended cerebellar hemispheres, with large paraflocculus, extending beyond the lateral border of the hemispheres (LARSELL, 1952). The cerebellar hemispheres have been observed to be largest in man (SULTAN and BRAITENBERG, 1993), hence, man is considered to have the largest number of complex motor programs, due to the longer folia in this region for independent motion of the limbs. WELKER (1990) had earlier shown that differences in relative sizes of cerebella are related to behavioural differences. Along the same lines, DEMAEREL (2002), in agreement with early researchers, reported that expansion of individual folia is correlated with behavioural differences among species.

The literature contains only a very few studies on the African giant rat, especially its biology and physiology (AJAYI, 1974; KELANI and DUROTOYE, 2002; BYANET et al., 2008, 2009). The objective of the present study was to examine the gross structural regions of the cerebellum and relate these regions to function in live animals, which characterized the behaviour of AGPR in the wild and captivity.

Materials and methods

Source of animals and study location. A total of ten (10) adults AGPRs, without sex variations were used in this study. The AGPRs were live - trapped in the wild, in Zaria, and reared under laboratory conditions in the Department of Veterinary Physiology and Pharmacology, Ahmadu Bello University, Zaria. They were transferred in laboratory cages to the Veterinary Anatomy Research Laboratory, Ahmadu Bello University, Zaria, where the research was conducted.

The protocol for the research project was approved by the Ethical Committee of Ahmadu Bello University, Zaria, Nigeria. The environment, housing and management of the animals were similar to that stipulated in the Guide for the Care and Use of Laboratory Animals, 8th Edition, National Research Council, USA, downloaded from the National Academic Press, Washington D.C. site www.nap.edu.

Brain extraction and fixation. Each animal was weighed alive using a Mettler Balance, (Model P 1210, AG, Switzerland, with sensitivity of 0.01 g) and sacrificed after anaesthesia with chloroform (within 2-5 minutes) in a closed container. The head of each was decapitated at the atlanto-axial joint using a small sharp knife and forceps, and skinned. Brain extraction from the skull was done according to the method described by FLETCHER (2006), but with modifications due to peculiarity of these rodents. The cerebellum of each rodent was separated from the brain stem by cutting through the cerebellar peduncles using forceps and a surgical blade, and fixed in Bouin's solution.

Gross morphological observations. Different systems of nomenclature have been reported in the literature for lobes, lobules and fissures. In this study, the BOLK (1906) nomenclature of the cerebellar hemisphere base from his comparative anatomical studies of mammalian cerebellum and method of arrangement of vermial lobules (indicated with roman numerous) in white rats (LARSELL, 1952) and the general divisional arrangement cerebellum in animals (FLETCHER, 2006) were used.

In this nomenclature, the surface landmarks on the dorsal aspect of cerebellum were designated as: i) the vermis, ii) paravermis and iii) cerebellar hemispheres. On the ventral surface, the three cerebellar peduncles, which connect the cerebellum to the brainstem were named with colour circles such as: red color for rostral, black colour for middle and green colour for caudal peduncles. A mid-sagittal section of the vermis was made to identify the lobes, lobules and fissures. The primary lobules were numbered with roman numerals (I, II, III,…) and sublobules were also alphanumerically numbered (a, b,…).

To capture images, a digital microscopic eyepiece (Scope Photo, Version 3.0 of 2003-2007) was attached to the computer, and macro-photographic pictures of the dorsal, ventral and mid-sagittal views of each cerebellum were taken (size 640 x 480 jpg pixels). The images were processed using software (Motic Images Plus, 2.0 ML, Multi

Language Version http://www.motic.com. Motic China Group Co., Ltd) of 2001-2007 and documented in Microsoft Office Word 2007. The lobes, lobules, subfolia and fissures were determined. For terminology, the Nomina Anatomica Veterinaria (2005), 5th Edition was used.

Results

The cerebellum structure in this study was observed to be the second largest part of the brain, after the telencephalon. It had three divisions; the vermis, paravermis and bilateral hemispheres (hemisphaerium cerebelli) and three lobes: the anterior (lobus rostralis), posterior (lobus caudalis) and flocculonodular (lobus flocculonodularis) (Fig. 1). Ventrally, the cerebellum was connected to the brain stem by three cerebellar peduncles: the rostral cerebellar peduncle (pedunculus cerebellaris rostralis), the middle cerebellar peduncle (pedunculus cerebellaris medialis) and the caudal cerebellar peduncle (pedunculus cerebellaris caudalis) (Fig. 2).
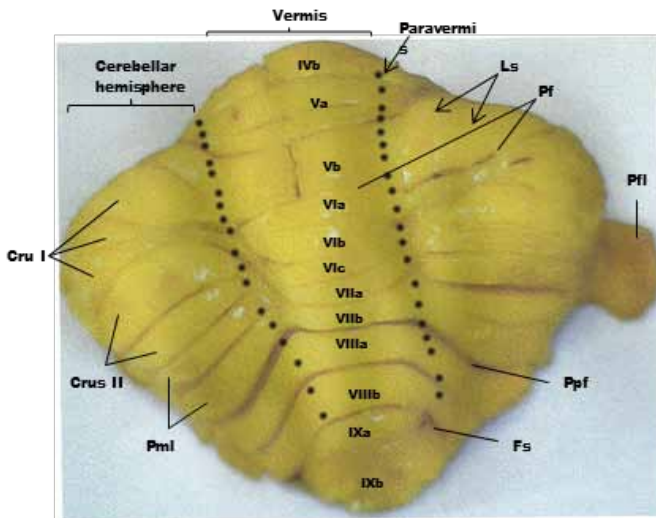

Fig. 1. Dorsal view of the cerebellum of the African Giant rat showing its longitudinal zones: the centrally placed vermis and its lobules (IV - IX), the paravermis (dotted lines) and the cerebellar hemispheres. The hemispheric parts of the vermis are the lobulus simplex (Ls), the ansoparamedian lobule consisting of the crus I and crus II; the paramedian lobule (Pml) and the paraflocculus (Pf). Primary fissure (Pf), separate the rostral lobe from caudal lobe, prepyramidal fissure (Ppf), separated lobule VIII from lobule VII, while fissura secunda (Fs) separated lobule IX from VIII. Fixative: Bouin's solution.
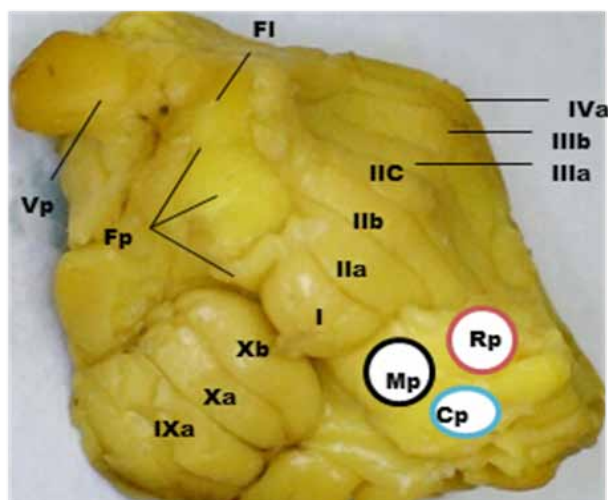
Fig. 2. The ventral view of the cerebellum of the African Giant rat showing the vermal lobules of the rostral (I - IV) and caudal (IX-X) lobes. The flocculonodular lobe is compose of the flocculus (fl) and the nodulus or lobule X. The floccus is conneted with the nodulus by a long and slender stalk, the floccular peduncles (Fp). The cerebellar peduncles consisting of the rostral (Rp), middle (Mp) and caudal (Cp) peduncles. Also present on the ventral aspect is the ventral paraflocculus (Vpf). Fixative: Bouin's solution.

The anterior lobe. The anterior lobe of the corpus cerebelli showed the relationship between the vermian and hemispheral lobules. Most of the hemispheral lobules were observed to be the direct lateral extensions of the vermian segments, and were delimited by fissures that first appeared in the vermis and spread latero-ventrally pari passu with the lobules they delimit. Five lobules (I - V) were recognized in this anterior lobe with their sublobules (Figs. 3, 4 and 5).

Lobule I in our study was relatively small, rounded, short and not subfoliated. It slanted in an antero-ventral direction and lay so far behind the lower margin of lobule II that it was not visible when viewed dorsally and had no lateral representation. A short precentral fissure separated lobule I from lobule II, and tapered towards its deep end. Lobule II was relatively slender and long and clearly subflobulated into IIa IIb and IIc by intracentral fissures 1 and 2. An intra-central fissure separated lobule II from lobule III (Figs. 3 and 4).
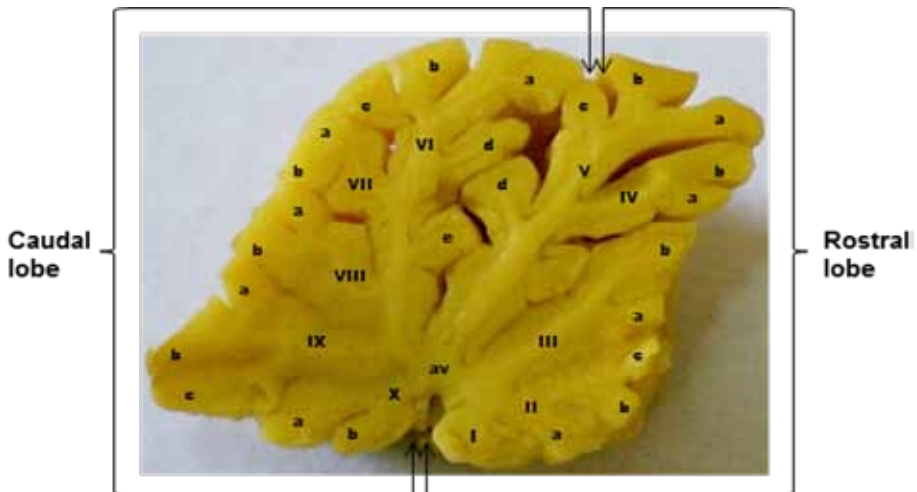
Fig. 3. Midsagittal section of the cerebellum of African giant rat showing the vermal lobules of the cranial lobe (I - V) and the caudal lobe (VI - X) from with their subfolia (a, b…) using primary fissure and cerebellar ventricle as the landmarks. The arbor (av) size is small and narrow, its brancles also are relatively narrow. Fixative: Bouin's solution.
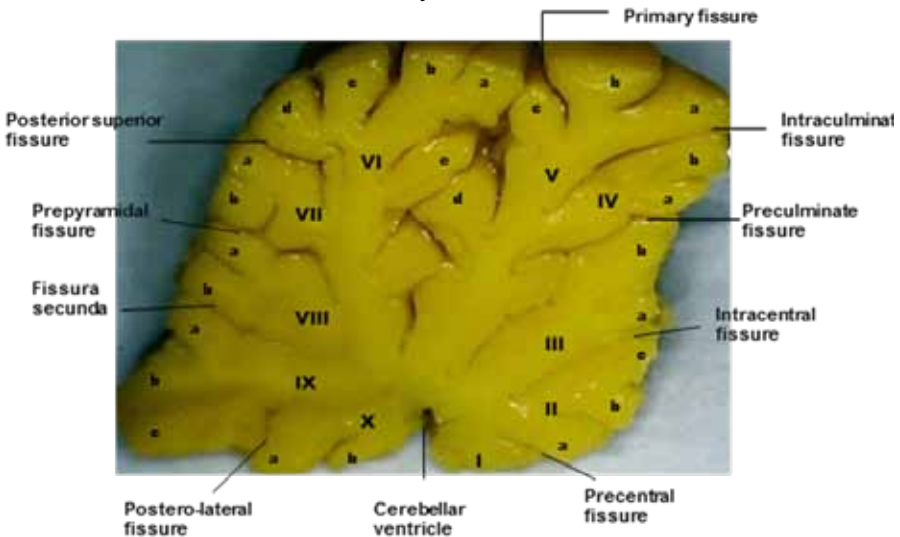

Fig. 4. Midsagittal section of the cerebellum of African giant rat showing the vermal lobules (I - X) with their subfolia (a, b…) and the major fissures that separate the lobules. Fixative: Bouin's solution.
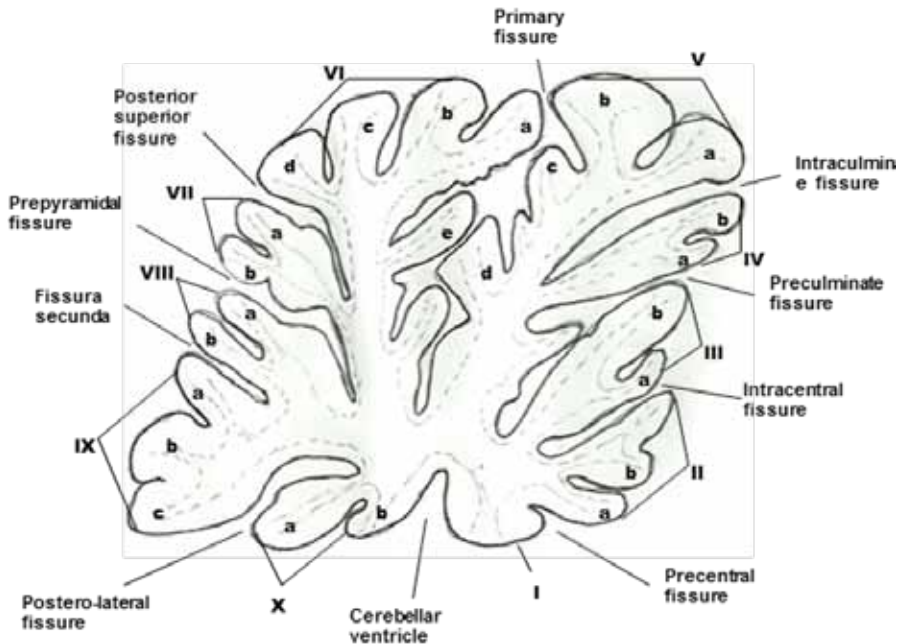
Fig. 5. Line drawings of mid-sagittal sections through the cerebellum of the cerebellum of African giant rat showing the vermal lobules (I - X) with their subfolia (a, b…) and the major fissures that separate the lobules.

The lobule III was broader than lobule II and had two sublobules (IIIa and IIIb), which were separated by a short sulcus. The subfolium IIIa was slanted in an antero-ventral direction and was also shorter than IIIb, while, IIIb slanted antero-dorsally with its dorsal-most part forming a slight upper lip. A deep preculminate fissure separated lobule III from lobule IV, and was the longest fissure in the anterior lobe (Figs. 3 and 4). Lobule IV extended anteriorly and posteriorly to the general anterior surface of the cerebellum, with an expanded exposed surface, and sublobulated into IVa and IVb. An intraculminate fissure delimited lobule IV from lobule V (Fig. 4).

The largest and longest lobule in the anterior lobe was lobule V. It fanned out rostrally and slanted anteriorly and dorsally. It had four sublobules (Va, Vb, Vc and Vd) separated by small fissures. The primary fissure (fissura prima), the longest fissure of the cerebellum in this study, slanted ventrally and separated lobule V from lobule VI, that is, it separated the rostral lobe from the caudal lobe.

The posterior lobe. The first lobule of the posterior lobe, lobule VI, was sublobulated into VIa, VIb, VIc, VId and VIe. Its lateral extension lay between the primary fissure and the superior posterior fissure, together forming the lobulus simplex. The surface of the lateral part of the lobule simplex was formed by only two broad subfolia (Fig. 1). Subfolia VIa and VIb were separated by long declival sulcus 2, while subfolia VIb and VIc were separated by a longer fissure, the declival sulcus 1. The posterior superior fissure was noted to be relatively short and narrow, and it separated lobule VI from lobule VII (Figs. 4 and 5).

The shortest lobule of the posterior lobe was lobule VII, with two sublobules, VIIa and VIIb, separated by the ansoparamedian fissure. A short pre-pyramidal fissure separated it from lobule VIII (Fig. 4). The lateral extension of lobule VII was an ansoparamedian lobule (lobulus ansiformis) which was subdivided into Crus I (crus rostrale), Crus II (crus caudale) and the anterior part of the paramedian lobule (lobulus paramedianus) (Fig. 1). Crus I was divided into two folia and Crus II consisted of three broad folia that tapered toward the vermis (Fig. 1).

The pyramis [vermis] or lobule VIII was observed to be subfoliated into VIIIa and VIIIb by a shallow groove, the intra-pyramidal sulcus 1 (Figs. 4 and 5). This lobule was broader than lobule VII and curved slightly posteriorly and dorsally. The deepest fissure in the posterior lobe, the fissura secunda, separated lobule VIII from lobule IX. One of the broadest lobules in the posterior lobe was lobule IX. It was sublobulated into IXa, IXb and IXc, by uvular sulci 2 and 1, respectively. A curved fissure, the postero-lateral fissure, separated lobule IX from lobule X (nodulus) (Figs. 3, 4 and 5).

The flocculonodular lobe. On the ventral aspect, the nodulus (lobule X) and the two flocculi (pedunculus flocculi) with their connecting peduncles constituted the flocculonodular lobe. This lobe was not delimited from the corpus cerebelli, except on the lateral side, where the flocculus was entirely separated, except the stalk of attachment to the nodulus (Fig. 2).

Discussion

The cerebellum of each African giant rat in this study had a characteristic complex folial pattern, similar to rodents documented in the literature, such as, the white rat (LARSELL, 1952), the mouse (INOUYE and ODA, 1980) and the grasscutter (BYANET et al., 2012). Ten vermian lobules (I-X) of LARSELL (1967) that separate the mammalian cerebellum were conspicuously present in this study, which are said to be homologues of the ten folia (I-X) in the avian cerebellum (IWANIUK et al., 2006).

In the cerebella of the animals used in this study, the vermal region was relatively broad and slanted forward, with its width longer than its length, similar to those documented for mammals (BUTLER and HODOS, 2005). In comparative studies, RANSON

and CLARK (1991) reported that the vermis is well developed in those animals whose progressive movement and activities are largely dependent upon the trunk musculature or symmetric limb movement, as in birds and reptiles. MALCOLM and CARPENTER (1991), in agreement with this report, showed that lesions of the vermis were associated with disorders of the trunk in animals, and in particular, lesions of the anterior vermis result in abnormal co-ordination of the lower limbs.

In the present study, lobule I of the anterior lobe corresponded to the lingula lobule of the BOLK (1906) and LARSELL (1952) comparative anatomic nomenclature. It was small, short and not sublobulated as in rat and mouse cerebella (LARSELL, 1952; INOUYE and ODA, 1980), but three sublobules were reported in the grasscutter (BYANET et al., 2012). Functionally, lobule I is considered to play a vital role in the caudopelvic musculature; especially in supporting the viscera and in control of internal body pressure, as well as the activity of the tail (LARSELL, 1952; CHANG and RUCH, 1949). The results of this study do not support the hypothesis of these authors that lobule I is related to tail length, because AGPR has long tail, but a small lobule I.

The second lobule in the AGPR cerebellum was larger than lobule I and had three sublobules (IIa, IIb and IIc), with a precentral fissure separating the two lobules. In the rat, cat and monkey, lobule II has been reported to have two sublobules (LARSELL, 1953) and has been suggested to be related to the caudopelvic musculature and the activity of the tail. Therefore, this finding suggests that rather than lobule I, the well developed lobule II may be related to AGPR tail length and the caudopelvic musculature in the tail, in agreement with the report by LARSELL (1953).

The's lobulus centralis of NAIDICH et al. (2009) corresponds with lobule III in this work. Similar to the situation observed in the rat (LARSELL, 1970), lobule III in the AGPR was also sublobulated into two sublobules (IIIa and IIIb). In humans, BISPO et al. (2010) showed that lobule III is not subfoliated. In early research on cerebellar foliation pattern, LARSELL (1970) and SENGLAUB (1963) showed that absence of folium III and expansion of folia IV, V and VI in hummingbirds was due to their weak hind limbs and strong wings, respectively. Functionally, lobule III has been reported to be correlated with hind limb musculature or leg strength, and walking and swimming ability (LARSELL, 1967; IWANIUK et al., 2006). This may suggest a correlation between lobules III with the function of the hind limbs in motor activities, such as climbing and swimming (ANONYMOUS, 1991; MENSAH and OKEYO, 2005) in the AGPRs.

The largest lobule of the anterior lobe in this work was lobule V, the culmen (pars caudalis). It was also the second largest lobule of the entire cerebellum, after lobule VI. The functional topography of the human cerebellum was reviewed by STOODLEY and SCHMAHMANN (2009), who showed that tasks which employ finger movements are associated with the activity of lobule V. GRODD et al. (2001) also showed that a

relationship exists between movements of the lower extremities of the forelimb, lips and tongue with the vermis and hemisphere of lobules IV and V. The available literature indicates that African giant rats have the ability to stand upright or erect while feeding, using their forelimb to grasp pieces of grass (BYANET et al., 2009). A correlation may exist between the large size of lobule V and the use of forelimbs by the African giant rat, which represent hands in man (STOODLEY and SCHMAHMANNN, 2009), which may also function in that regard.

Lobule VI of the posterior lobe in the present study was the most complex lobule in the entire cerebellum. Functionally in mammals, lobule VI has been regarded as the oculomotor vermis (VOOGD and BARMACK, 2006), because it receives proprioceptive, vestibular and auditory inputs and plays a vital role in the guidance and modification of eye movements (PAKAN et al., 2005). The well-developed lobule VI in the African giant rats may play an important role in their visual cues.

The AGPR cerebellum showed a mediolateral expansion of the ansiform lobe (Crus I and Crus II) and paraflocculus, similar to those observed in chinchillas and squirrels (SULTAN and BRAITENBERG, 1993). With respect to their behaviour, AGPRs live in burrowed holes among the rocks or underground. Also, they are nocturnal, with little stereovision, like chinchilla, and excellent climbing ability due to their better developed hind limbs and forelimbs for locomotion and grasping (ANONYMOUS, 1991). The AGPR's good climbing ability is similar to that seen in squirrels and primates, which have an enlarged ansiform lobe (SULTAN and BRAITENBERG, 1993). This suggests that there is a correlation between the specific enlargement of the ansiform lobe of the cerebellum in AGPR and motor activity such as climbing skills and the grasping ability of the forelimb.

Conclusion

Although the shape and cerebellar lobulated pattern in the AGPR is similar to other mammals, particularly rodent families, some differences in the relative size of individual lobules exist. The variations in the size of lobules may be suggestive of the motor function peculiarities of the AGPRs, which have shaped the behavior of the animals in the wild and captivity. We therefore suggest that the behavior of this animal in captivity, such as the ability to stand upright and use its forelimbs to grasp food and other materials, is correlated with its well-developed lobule V. Furthermore, the manipulative use of forelimbs, and hind limbs for climbing and swimming may be correlated with the large lobulus ansiformis (crus I and crus II). The well formed lobule II in this animal may aid the caudopelvic muscles that are attached to the strong, long tail. The exploration of other behaviours, that may also be correlated with lobule size in the AGPR and comparison with other rodents require further studies in this species.

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SAŽETAK

Stupanj vijuganja i njegova funkcionalna svrhovitost čine glavnu razliku u građi maloga mozga glodavaca. Pretpostavlja se da rast ili smanjenje pojedinačnih režnjeva pridonosi specifičnim razlikama u ponašanju. U radu je prviput iscrpnije opisana makroskopska anatomija malog mozga u 10 odraslih afričkih divovskih štakora kesičara. Rezultati su pokazali da podjela malog mozga kod te vrste slijedi uobičajeni oblik koji podrazumijeva postojanje 3 režnja (prednjeg, stražnjeg i flokulonodularnog). Također, u donjem dijelu opažene su tri moždana stabla (pedunkuli) koja povezuju mali mozak i veliki mozak. VI. režanj i njegov glavni postrani nastavak odgovaraju režnjiću lobulus simplex. Postrano proširenje VII. režnja odgovara dobro razvijenom lobulus ensiformis, koji se sastoji od crus I (crus rostrale), crus II (crus caudale) i prednjeg dijela lobulus paramedianus. Najveći dio prednjeg režnja čini režnjić V. koji je malom usjeklinom razgranat na Va, Vb, Vc i Vd. Najmanji je I. režnjić koji nije podijeljen na manje dijelove. U stražnjem režnju najprostraniji su režnjići: VI. podijeljen na 5 podrežnjića i IX. koji je podijejen na 3 podrežnjića. Režnjić X. je podijeljen u dva dijela, Xa i Xb, a najmanji je u stražnjem dijelu. Primarna usjeklina bila je najdublja i najizraženija, a nakon nje slijedi usjeklina, a zatim najmanja presredišnja. U zaključku, dobro razvijen ensiformni režanj crus I i crus II kod afričkoga divovskog štakora kesičara omogućuje izvrsne penjačke sposobnosti i vještu uporabu prednjih nogu pri hvatanju objekata.

Ključne riječi: afrički divovski štakor kesičar, mali mozak, makroanatomija, režnjevi, režnjići