

# A Golgi study of neurons in the camel cerebellum (*Camelus dromedarius*)

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## Abstract

Neurons in the cerebellar cortex of camels were studied using modified Golgi impregnation methods. Neurons were classified according to their position, morphology of their soma, density and distribution of dendrites, and the course of their axons. Accordingly, eight types of neurons were identified. Three types were found in the molecular layer: upper and lower stellate cells and basket cells, and four types were found in the granular layer: granule cells, Golgi Type II cells, Lugaro cells, and unipolar brush cells. Only the somata of Purkinje cells were found in the Purkinje cell layer. The molecular layer is characterized by the presence of more dendrites, dendritic spines, and transverse fibers. Golgi cells also show extensive dendritic branching and spines. The results illustrate the neuronal features of the camel cerebellum as a large mammal living in harsh environmental conditions. These findings should contribute to advancing our understanding of species-comparative anatomy in achieving better coordination of motor activity.

## KEYWORDS

camel, cerebellum, Golgi, neurons

## 1 | INTRODUCTION

The cerebellum plays an important role in controlling various sensory-motor functions. It is not involved in initiating movement but plays a key role in the coordination of voluntary muscle activity and in maintaining balance. It receives motor orders from the cerebral motor cortex and proprioceptive information from the muscles and joints through indirect pathways. It also receives afferent fibers from the somatosensory, vestibular, and visual systems. By comparing information from these sources, the cerebellum can detect errors in the motor activity of the body. As a result, it corrects these errors through

indirect pathways to the lower motor neurons in the brainstem and spinal cord (Hodos, 2009; Saab & Willis, 2003; Sokolov, Miall, & Ivry, 2017; Voogd & Glickstein, 1998). Thus, the cerebellum is essential for making fine adjustments to motor actions. Furthermore, it plays an important role in certain cognitive and language processes (Buckner, 2013; Hatten, 2020; Mariën & Borgatti, 2018; Schmähmann, 2019; Sokolov et al., 2017).

The anatomy of the cerebellum in different species varies widely, in most cases reflecting the adaptation of the organism to its environment (Johnson, Lahti, & Blumstein, 2012). In weakly electric fish such as *Mormyrid*, the cerebellum is exceptionally larger than the

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rest of the brain because of its involvement in the generation of electric discharges in this type of fish (Bullock, 1982; Meek, 1992). In Chondrichthyans, such as some species of sharks and Actinopterygii, such as teleosts, the cerebellum is relatively large with very complicated circuitry, possibly reflecting the important role of the cerebellum in swimming and the vestibulo-ocular reflex in these marine species (Ikenaga, 2013; Yopak, Lisney, Collin, & Montgomery, 2007). In contrast, the cerebellum is relatively small compared to the total size of the brain in lampreys, amphibians, and the majority of ray-finned fish (Hodos, 2009). Likewise, the cerebellum is small and resembles a thin flat plate in reptiles (Meek, 1992). Generally, the mammalian and avian cerebella are relatively large, roughly spherical in shape, and highly foliated (Hodos, 2009). Elephants have been reported to have the largest relative cerebellar size among mammals, which might be related to body size, cerebellar involvement in complex motor functions of the trunk, and/or the production of infrasonic vocalizations (Jacobs et al., 2014; Maseko et al., 2013; Maseko, Spocter, Haagensen, & Manger, 2012).

In mammals, the cerebellum is formed of an outer layer of gray matter, called the cerebellar cortex, and inner white matter. The cerebellar cortex has a uniform structure throughout the cerebellum and is formed of three layers (Hatten, 2020; Jacobs et al., 2014): (1) the superficial molecular layer, which contains two types of neurons: stellate cells and basket cells; (2) the middle Purkinje cell layer, which contains the cell bodies of Purkinje cells; and (3) the deep granular layer, which contains small granular cells, large Golgi Type II cells, Lugaro cells, and unipolar brush cells (Geurts, De Schutter, & Dieudonné, 2003; Mugnaini & Floris, 1994; Mugnaini, Sekerková, & Martina, 2011). The dendritic complexity of cerebellar neurons in mammals tends to increase with the cerebellar volume (Jacobs et al., 2014).

The cerebellum is one of the most studied parts of the nervous system. However, such studies are rarely performed in large animals, such as camels. The camel is a quadruped that lives in a harsh environment (sandy deserts) and walks on fine sand. Because camels evolved in such environments, sophisticated physiological adaptations have evolved, allowing them to cope with arid conditions (Montes, 2012). Camels have broad, flat, leathery pads with two toes on each foot. When camels place their feet on the ground, the pads spread, preventing the feet from sinking into the sand. When walking, camels move the 2 ft. of one side of their body together, followed by the 2 ft. of the other side. Descriptions of the gross morphology, cellular neurochemical organization, and arterial vascular architecture in camels have been thoroughly investigated by various research groups (Al Aiyani

et al., 2019; Attaai, Noreldin, Abdel-Maksoud, & Hussein, 2020; Ghaji, 1985). Herein, we investigated the neuronal morphology and several quantitative parameters of different types of neurons in the cerebellar cortex of camels and compared these neurons with their counterparts in other species. This study is a continuation of our previous findings in other camel brain regions (Al-Hussain, Albostanji, Mustafa, & Zaqout, 2021; Al-Hussain, Al-Saffar, & Zaqout, 2012; Zaqout, Al-Hussain, Al-Saffar, & El-Dwairi, 2012).

## 2 | MATERIALS AND METHODS

The brains of 10 camels (*Camelus dromedarius*) collected from local butcher shops were used in this study. No animals were sacrificed; therefore, Institutional Animal Care and Use Committee approval was waived. Camel brains ranging in age from 2 to 4 years were collected from butcher shops directly after sacrifice. They were kept for 2–4 hr in dd-H<sub>2</sub>O and transferred to the laboratory where the cerebella were dissected and preserved in 10% formalin solution for 2–3 months. Appropriate blocks of the cerebellar cortex were prepared and stained using the modified Golgi-Kopsch method, as described below.

Blocks were dissected from the cerebellar hemispheres and sectioned mostly in the parasagittal planes following the methods of Fox et al. and Braitenberg et al. (Braitenberg, Guglielmotti, & Sada, 1967; Davenport, 1960; Fox, Ubeda-Purkiss, Ihrig, & Biagioli, 1951). Briefly, the method described by Fox et al. (Fox et al., 1951) was performed by incubating 4-mm-thick blocks in a mixture of 3% zinc chromate and 2% formic acid for 7 days. The blocks were then removed from the chromate solution, dried without washing, and immersed in a 0.75% silver nitrate solution for another 7 days. Using the method presented by Braitenberg et al. (Davenport, 1960), 2-mm-thick blocks were cut, dried, and placed in a mixture of 3% potassium dichromate, 0.5% formaldehyde, and 12.5% sucrose for 12 days. They were then incubated in 0.75% silver nitrate solution for 7 days. The blocks of the two methods were removed from the silver nitrate and cut into 100- $\mu$ m-thick sections. The sections were collected and kept in absolute ethanol for 2 hr, transferred to xylene for 5 min, mounted on slides using DPX mounting medium, and covered with coverslips.

Well-impregnated neurons were studied (measured and photographed) using a Nikon and CETI light microscope with an oculometer. A Bel Photonic BioVid microscope was used to create images of the cells. Golgi methods are known to stain the cell body and the processes of neurons very well. The processes extended in

several focal planes and for more than one microscopic field; therefore, for each cell studied, images of several fields were taken to create a photomontage of the whole neuron. Adobe Photoshop CS5 Extended v12.0, and Microsoft Windows 7 Paint programs were used to combine the images.

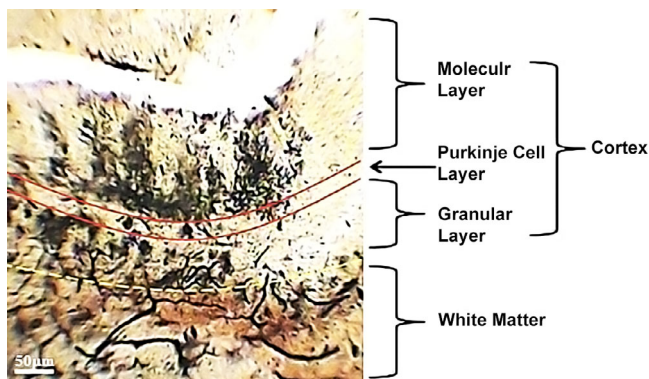
The following criteria were used to classify neurons in the cerebellar cortex: (1) position, shape, and size of the soma; (2) distribution and orientation of the dendrites; and (3) the course of the axon. The following quantitative measures were made: (a) mean diameter of the soma; (b) number of dendrites arising from the cell; (c) length of axons and longest dendrites for certain cells; and (d) for Purkinje cells, mean diameter of the smooth branches, diameter of spiny branches, and spine density. Microsoft Excel 2016 was used for the tabulation and analysis of the data, which were presented as mean  $\pm$  SD.

### 3 | RESULTS

Grossly, the cerebellar cortex easily differentiated from white matter. Three layers of the cerebellar cortex were observed (Figure 1). Purkinje cells were very well impregnated; they were arranged in a single row forming the Purkinje cell layer which was sandwiched between the molecular layers superficially and the granular layer deeply. The following is a description of these layers.

#### 3.1 | The molecular layer

Three types of neurons were distinguished according to their location in the molecular layer. The features are listed in Table 1.



**FIGURE 1** Photomicrograph showing the three layers of the camel cerebellar cortex and white matter

#### 3.1.1 | Upper stellate cells

These were found in the upper part of the molecular layer and had round or oval cell bodies that were directed horizontally or vertically (Figure 2). Their diameters ranged between 5.5 and 10.5  $\mu\text{m}$  ( $8.1 \pm 1.4$ ,  $n = 20$ ). Few dendrites were found to arise from the cell body and they were directed transversely, downwards (toward the white matter), or upward (toward the surface). The longest dendrites from these cells descended toward the white matter (a dendrite from an upper stellate cell was followed down for a distance of 70  $\mu\text{m}$ ). These dendrites showed several dendritic spines along their course, which were usually short and finger-like (Figure 2, insets a and b). Only the initial segments of the axons of these cells were stained.

#### 3.1.2 | Lower stellate cells

Present in the middle part of the molecular layer with oval-shaped cell bodies that are usually directed vertically (Figure 3). Their diameters ranged between 7 and 12.5  $\mu\text{m}$  ( $9.4 \pm 1.4$ ,  $n = 20$ ). Approximately, three to four dendrites emerged from the cell bodies of these cells and ran transversely or upwards in the transverse plane of the folium. The ascending dendrites were longer than the transverse ones, with the longest dendrite (seen in our study) traveling a distance of 85  $\mu\text{m}$ . These dendrites branched a few times and showed several dilated areas along their courses, which gave them a beaded appearance. Very few dendritic spines were observed, and these were usually short and finger-like. A single axon emerged from the axon hillocks. The axons of the lower stellate cells ran transversely and were well impregnated, enabling us to follow them for some distance (the longest was 225  $\mu\text{m}$ ). Initially, the axons were thin, but after some distance, their diameter increased notably to form transversal fibers (Figure 3). At various points along their courses, the axons gave off several axon collaterals that descended toward the Purkinje cell layer. The exact points of termination or participation in basket formation could not be determined. The descending axon collaterals showed a beaded appearance. The axons of these cells may have spines and may change their regular direction (Figure 4).

#### 3.1.3 | Basket cells

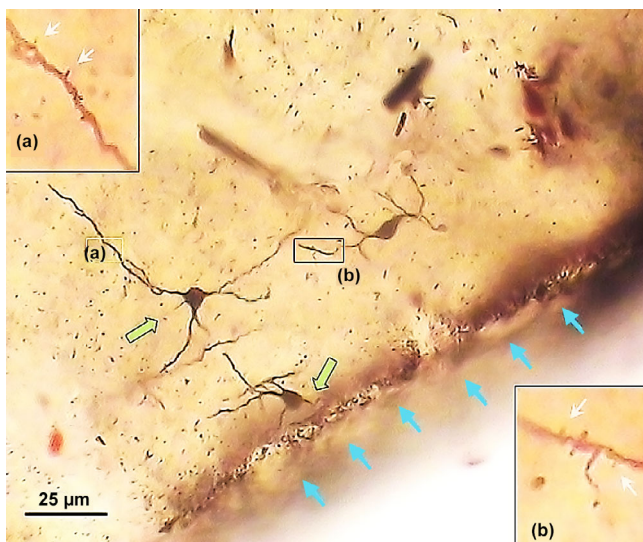
These cells were present in the lower part of the molecular layer, just above the Purkinje cell layer (Figure 5). They had round, oval, or triangular cell bodies. Their diameters ranged from 7.5 to 11.5  $\mu\text{m}$  ( $9.0 \pm 1.2$ ,  $n = 30$ ).



Feature	Cell		
	Upper stellate cells ( <i>n</i> = 20)	Lower stellate cells ( <i>n</i> = 20)	Basket cells ( <i>n</i> = 30)
Position in the layer	Upper part	Middle part	Lower part
Soma shape	Round, oval	Round, oval	Round, oval, triangular
Mean diameter of soma (SD)	8.1 $\mu$ m (1.4)	9.4 $\mu$ m (1.4)	9 $\mu$ m (1.2)
Number of dendrites	2–3	3–4	5–6
Direction of longest dendrite (distance)	Down (70 $\mu$ m)	Up (85 $\mu$ m)	Up (260 $\mu$ m)
Dendritic spines	+++	+	+
Axon	Short <sup>a</sup>	Long (225 $\mu$ m)	Long (300 $\mu$ m)
T-fibers	No <sup>a</sup>	Yes	Yes
Participate in basket formation	No	No	Yes

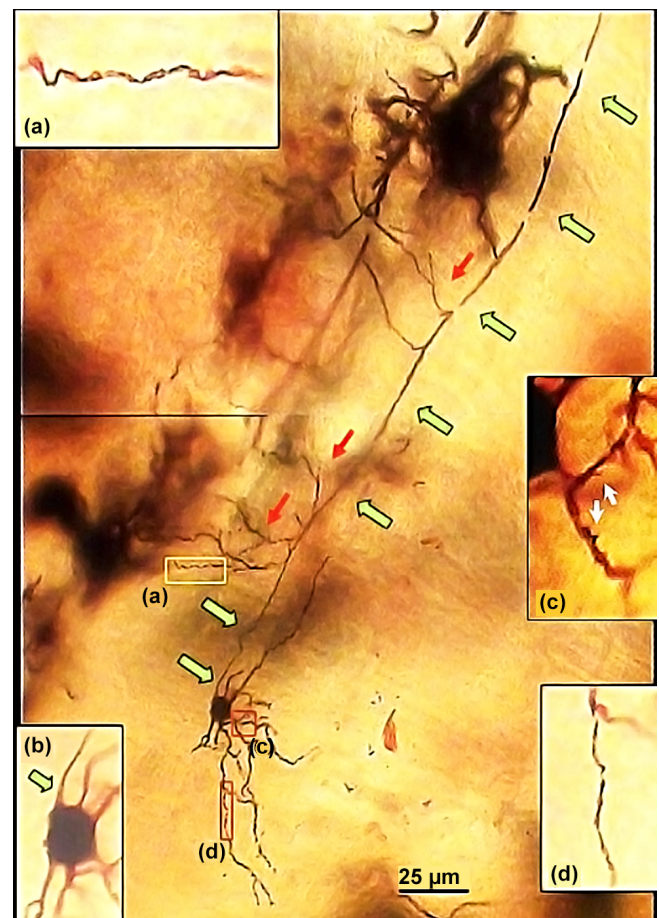
**TABLE 1** Comparison between the general features of the three types of cells in the molecular layer of the camel cerebellar cortex

<sup>a</sup>Assumed in this study.



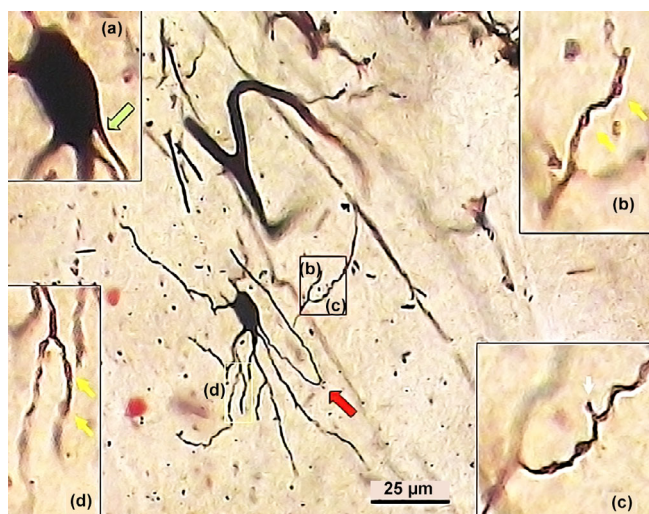
**FIGURE 2** Photomontage of three upper stellate cells in the upper part of the molecular layer. Pial surface indicated by blue arrows. The cell bodies are round or oval. Most of the dendrites are descending. Insets (a) and (b) show the short finger-like spines (white arrows) of the boxed dendrite. Green arrows indicate initial axonal segments

Approximately five to six dendrites arose from these cells and ran in a transverse or upward direction. The longest dendrites ascended (the maximum measured was 260  $\mu$ m long). The dendrites were beaded with few finger-like or drum-stick-shaped spines. The axons of these cells passed transversely. Each started thin and gradually thickened, forming transversal fibers (like the lower stellate cells). A transversal fiber arising from a basket cell was used in our study for a distance of 300  $\mu$ m. Along its course, it



**FIGURE 3** Photomontage of a lower stellate cell with a round cell body. The long axon of this cell (green arrows) has several descending collaterals (red arrows) that are beaded (inset a). Inset (b) shows the axon hillock. Most of the dendrites are ascending toward the pial surface. The dendrites show spines (inset c, white arrows) and are beaded (inset d)



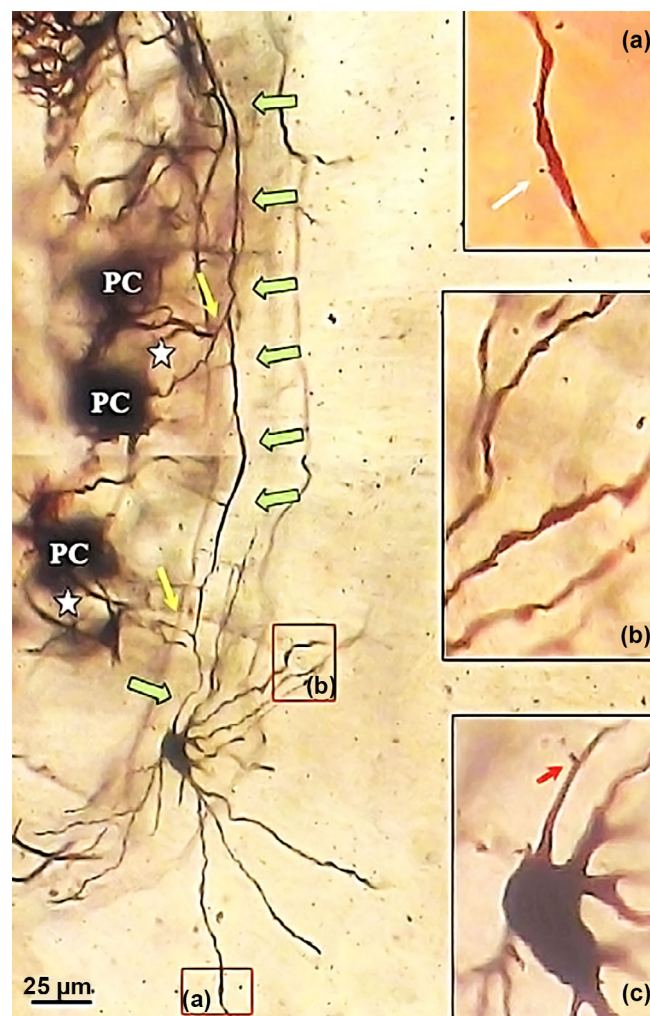


**FIGURE 4** Photomontage of a lower stellate cell with an oval cell body. The axon of this cell shows an unusual curve in its course (red arrow). The axon hillock is shown in inset (a, green arrow). A collateral can be seen descending from the axon. This collateral showed beads (inset b) and a spine (inset c, white arrow). Beads on the dendrites are shown in inset (d)

gave off beaded descending collaterals in the direction of Purkinje cells. Unlike the similar collaterals of the lower stellate cells, those of the basket cells participated in the formation of a network around the cell bodies of Purkinje cells (basket formations, Figure 5). The axons of some basket cells showed a drumstick-shaped spine (Figure 5, inset c, thin red arrow).

### 3.2 | Purkinje cell layer

Purkinje cell bodies were arranged in a single row that formed the Purkinje cell layer. The cell bodies were large, and pear shaped with a diameter ranging from 19.5 to 36.5  $\mu\text{m}$  ( $27.7 \pm 3.5$ ,  $n = 45$ ). The dendrites of Purkinje cells showed extensive arborization, and the dendritic tree extended in the molecular layer from the upper pole of the Purkinje cell body to the pial surface (Figure 6a). The spread of the dendrites of Purkinje cells was only observed in the parasagittal sections. Sections cut in the longitudinal plane did not exhibit this feature. A single trunk arose from the soma. This primary dendritic trunk varied in length from 5 to 60  $\mu\text{m}$  ( $19.6 \pm 13.5$ ,  $n = 35$ ) and ranged in diameter from 4 to 12  $\mu\text{m}$  ( $7.7 \pm 1.8$ ,  $n = 30$ ). This trunk divided to give rise to secondary dendritic trunks with diameters ranging between 3 and 6  $\mu\text{m}$  ( $4.3 \pm 1.0$ ,  $n = 30$ ). These, in turn, gave rise to tertiary trunks with diameters ranging between 2 and 4  $\mu\text{m}$  ( $2.7 \pm 0.5$ ,  $n = 30$ ). All these dendritic trunks were devoid of spines and were therefore called smooth branches

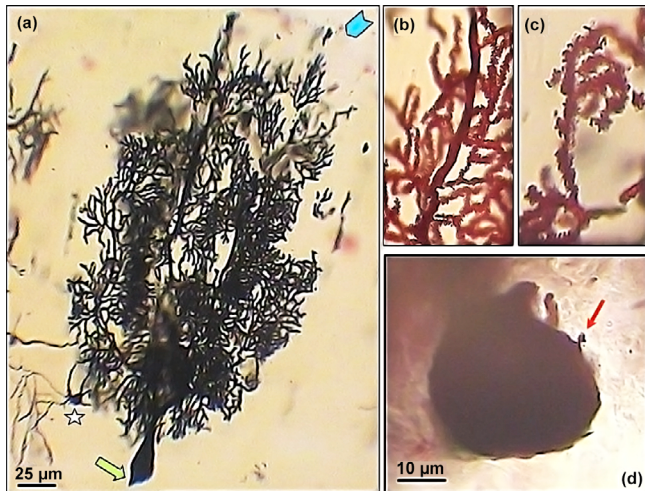


**FIGURE 5** Photomontage of a basket cell. The long axon of this cell (the transversal fiber, green arrows) passes over several Purkinje cells (PC). Two axon collaterals (yellow arrows) participate in basket formations (white stars). Dendrites show spines (inset a, white arrow) and beads (inset b). Inset (c) shows a spine on the axon (red arrow)

(Figure 6b). In this study, Purkinje cell dendrites showed no more than three generations of smooth branches (primary, secondary, and tertiary). Of the 37 Purkinje cells, 19 had 2 generations of smooth branches, and the rest had 3. Several narrow branchlets arose from all the generations of smooth branches. These branchlets passed in all directions and carried a high density of finger-like or drum-stick-shaped spines (Figure 6c). These spiny branchlets had a uniform diameter of 1  $\mu\text{m}$ , and the density of the spines ranged between 12 and 22/10  $\mu\text{m}$  ( $16 \pm 3$ ,  $n = 30$ ). Eventually, the smooth branches were terminated, dividing into spiny branchlets. The axons of Purkinje cells arose from the lower pole of the cell body or from the side of the cell, which was more common in this study. Only the initial segment of the



axon was stained, and we were not able to follow the axon for any considerable distance. In some cells, a spine was found on the soma (Figure 6d).



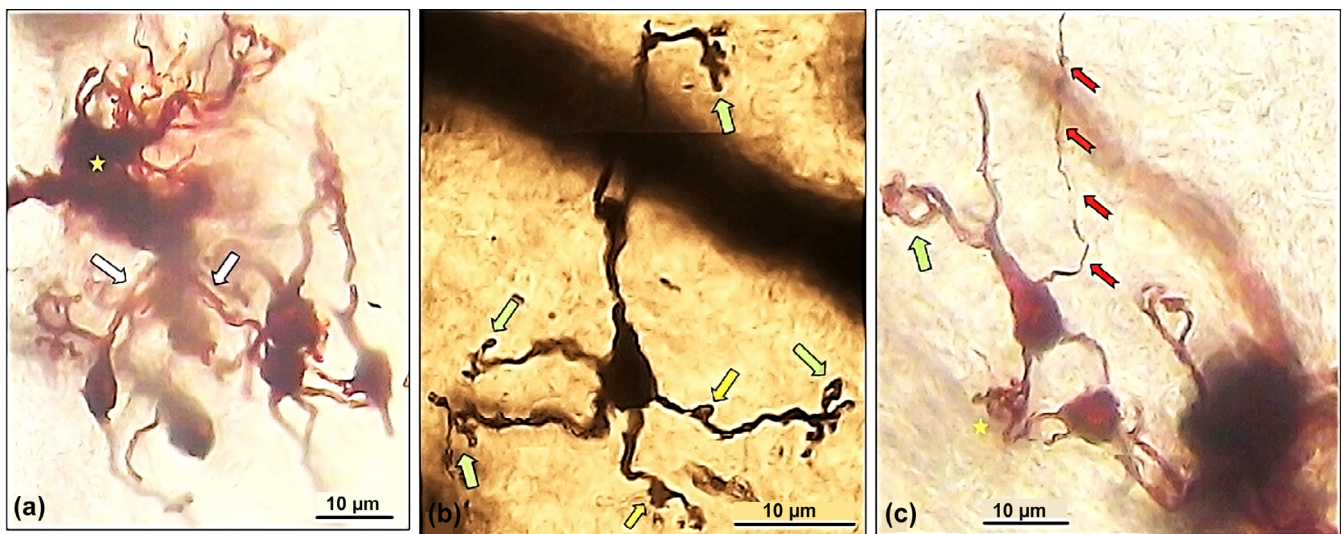
**FIGURE 6** Purkinje cells. (a) A photomontage of a Purkinje cell. Note the pear-shaped cell body. The axon hillock is apparent at the lower pole of the cell (green arrow). The dendritic tree of this cell is extensive and reaches the pial surface (blue arrow). The cell indicated by a star is a basket cell. (b) A magnified view of a spine-free smooth branch of the cell in (a) showing multiple spine-laden branchlets arising from it. (c) A spiny branchlet from the cell in (a) with a large number of spines. (d) A photomicrograph of a different Purkinje cell body showing a somatic spine (red arrow)

### 3.3 | Granular layer

The deepest layer of the cerebellar cortex is characterized by numerous darkly stained patches. Upon examination of these patches under higher magnification, they were observed to be formed of cell bodies and cell processes. The cell bodies were mostly those of granule cells, whereas the processes were from various sources. These processes converged to form cerebellar glomeruli (Figure 7). In the granular layer, four types of neurons were identified: granule cells, Golgi Type II cells, Lugaro cells, and unipolar brush cells.

#### 3.3.1 | Granule cells

These were small, round, or oval cells with diameters ranging from 4 to 7.5  $\mu\text{m}$  ( $5.7 \pm 0.9$ ,  $n = 60$ ), making them the smallest type of neurons in the camel cerebellar cortex. They were most abundant in the granular layer and were easily found in large numbers in all sections examined in this study. Several granule cells aggregated together to form a cell cluster (Figure 7a). Some granule cells were found to be isolated; however, we were unable to identify if these cells were truly isolated or if the other cells in the cluster did not stain well. Two to five dendrites emerged from the cell bodies. They were divided once or twice before terminating in expanded terminals that showed two to three finger-like projections giving each terminal a flower-like appearance (Figure 7b).

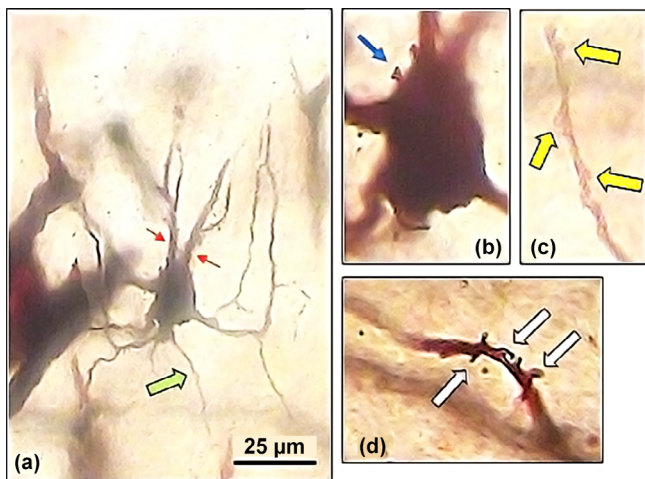


**FIGURE 7** Granule cells. (a) A photomicrograph of a cluster of six granule cells. Dendrites from two of these cells (white arrows) are passing to form part of a nearby cerebellar glomerulus (star). (b) A photomontage of a granule cell. The flower-like termination of the dendrites (green arrows) and appendages arising from the dendrites (yellow arrow) are seen. (c) A photomontage of two granule cells. A dendrite shows the flower-like ending (green arrow). The axon of one cell (red arrows) ascends toward the molecular layer. Dendrites from the two cells come together to form part of a glomerulus (star)

Appendages were also observed to arise directly from the dendrites of the shafts (Figure 7b). A single axon arose from the cell body and ascended toward the molecular layer (Figure 7c).

### 3.3.2 | Golgi Type II cells

These cells were larger in size than the granule cells (Figure 8). They were usually located in the upper or middle regions of the granular layer and very rarely in the lower part. They have an oval or, more commonly, a triangular cell body that ranged in diameter from 8.5 to 19.5  $\mu\text{m}$  ( $12.1 \pm 2.7$ ,  $n = 31$ ). The greatest length measured for these cells reached 25  $\mu\text{m}$ , which meant that Golgi cells might be as large as some of the Purkinje cells examined in this study. Some of these cells may have somatic appendages (Figure 8b). Usually four to six dendrites emerged from the cell body. Some of these ascended into the molecular layer and branched several times. Other dendrites passed transversely or descended in the granular layer and gave rise to several branches (Figure 8a). The dendrites of these cells may have protrusions, spines, and appendages (Figure 8d). The axons of these cells descended in the granular layer and formed plexuses that were localized to the granular layer. The axons of Golgi cells showed protrusions (Figure 8c).



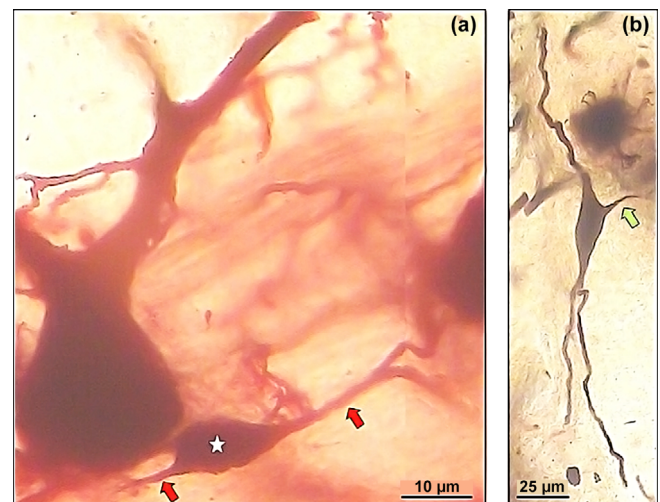
**FIGURE 8** Golgi cell. (a) A photomontage of a Golgi cell showing several dendrites arising from the cell body two of which (red arrows) are passing toward the molecular layer. The axon of this cell (green arrow) descends in the granular layer. (b) A magnified view of the cell body showing an appendage (blue arrow). (c) Magnified view showing axonal appendages (yellow arrows). (d) Dendritic spines (white arrows) in a magnified view

### 3.3.3 | Lugaro cells

These fusiform cells were horizontally directed; that is, their long axis was in the transverse plane of the folium; thus, they were only seen in the parasagittal sections (Figure 9). They were located deep to the Purkinje cell layer. Only a small number of cells were used in this study. Their diameters ranged between 8.5 and 19.5  $\mu\text{m}$  ( $12.2 \pm 3.5$ ,  $n = 10$ ). The two dendrites usually arose from the opposite poles of the cell body. These passed horizontally beneath the Purkinje cell layer, dividing a few times. The axons of these neurons descended in the granular layer. No spines or appendages were observed in any of these cells.

### 3.3.4 | Unipolar brush cells

These cells were rarely impregnated in this study (Figure 10). Only two cells were identified in this study. Two cells were found in the vermis. These cells had round or oval cell bodies. The diameters of these cells were 10 and 12.5  $\mu\text{m}$ . A single, short dendrite emerged from the cell body, which ended in an expanded tufted terminal (the brush). In one cell, a paint-brush-like expansion arose from the cell body. No impregnated axons were found in the two unipolar brush cells observed in this study.



**FIGURE 9** Lugaro cells. (a) A photomontage of a Lugaro cell. The fusiform cell body (star) is situated horizontally just beneath the Purkinje cell layer. Two dendrites (red arrows) arise from the opposite poles of the cell body to pass horizontally. (b) A photomontage of a different Lugaro cell showing the axon (green arrow) arising from the cell body passing downwards in the granular layer





**FIGURE 10** Photomicrograph of a unipolar brush cell in the vermis of the cerebellum. From the round cell body (yellow arrow), a single, short dendritic trunk emerged. This ended in an expanded brush-like terminal (blue arrow)

## 4 | DISCUSSION

Despite some drawbacks associated with Golgi staining, such as low reproducibility and the possibility of co-staining of glial cells and blood vessels, it remains an excellent method to study individual neurons as it completely stains neuronal cell bodies and processes including the spines (Zaqout & Kaindl, 2016). Based on the criteria used in this study, eight neuronal cell types were found in the cerebellar cortex of camels. Both similarities and differences were found between these neurons in camels and their counterparts in other species.

### 4.1 | Molecular layer

The “plexiform” or abundance of fibers in this layer is evident in this study. Our findings indicate that numerous transversal fibers derived from the lower stellate and basket cells (shown in the paramedian sections), and that parallel fibers (shown in longitudinal sections) derived from the axons of granule cells. This is in agreement with

previous studies on the cerebellar cortex of various species (Cajal, 2000; Fox, Hillman, Siegesmund, & Dutta, 1967; Johnston, 1902; Maseko et al., 2013). However, as shown in Table 1, the features of the cells changed in the deeper part of the molecular layer. Indeed, the number and length of the dendrites and the length of the axons increased, and the general direction of the dendrites was “down” for upper stellate cells and “up” for lower stellate and basket cells. The number of dendritic spines, on the other hand, became less. The axons of the lower stellate and basket cells formed T-fibers, but there was no evidence that the axons of the upper stellate cells formed these fibers. This was congruent with studies on other species (rats and primates) that have shown that the axons of upper stellate cells are short and do not form T-fibers (Fox et al., 1967; Nieuwenhuys, 1967; Sultan & Bower, 1998). Only the descending collaterals of the basket cell axons participated in basket formation. Based on the findings of previous studies conducted on the cerebellar cortex of humans and other vertebrates, including rats (Cajal, 2000; Sultan & Bower, 1998), we concluded that the level of a cell in the molecular layer is an important factor in determining its morphological features.

Various criteria have been used to classify neurons in the molecular layer of the cerebellar cortex (Table 2). The upper stellate cells in this study can be regarded as belonging to the first class of neuronal cells described previously (Rakic, 1972; Scheibel & Scheibel, 1954), whereas the lower stellate and basket cells can be considered to belong to the second class of neuronal cells described in previous reports (Rakic, 1972; Scheibel & Scheibel, 1954). The classification scheme used in this study was similar to that used by Fox et al. (Fox et al., 1967). These neurons were classified into three classes according to the length of the axon and whether or not they participated in basket formation. In elephants and some other large mammals, stellate cells were described as a single layer occupying the upper two-thirds of the molecular layer, while basket cells were located within the lower third of this layer (Jacobs et al., 2014; Maseko et al., 2013). No clear dendritic spines were found in either cell type of the molecular layer in the elephants (Maseko et al., 2013).

The presence of numerous spines on the dendrites of camel upper stellate cells has not been mentioned previously in other species. These spines may compensate for the shorter and fewer dendrites that emerged from these cells (compared to lower stellate and basket cells). The lower stellate and basket cells possessed fewer dendritic spines, but more dendrites that were longer than those of the upper stellate cells. Therefore, the density of spines and the number of dendrites may be considered as complementary features.

TABLE 2 Various schemes for the classification of cells in the molecular layer of the cerebellar cortex

Study					
Scheibel and Scheibel (Scheibel & Scheibel, 1954)		Rakic (Rakic, 1972)	Fox et al. (Fox et al., 1967)		This study
<i>Criteria</i>	Length of axon	Depth of cell in the molecular layer		<ul style="list-style-type: none"> <li>Length of axon</li> <li>Basket formation</li> </ul>	<ul style="list-style-type: none"> <li>Depth of cell</li> <li>Direction of dendrites</li> <li>Length of axon</li> <li>Basket formation</li> </ul>
<i>Cell classes</i>					
Class 1	Short axon stellate cells	Superficial stellate cells	Class 1	Upper stellate cells	Upper stellate cells
Class 2	Long axon stellate cells	Deep stellate cells	Class 2	Lower stellate cells	Lower stellate cells
			Class 3	Basket cells	Basket cells

The axons of the lower stellate and basket cells formed transversal fibers, which mostly gave off the descending collateral branches. The presence of ascending axonal collaterals is typical of these cells (Fox et al., 1967). For camels, however, the axons of basket cells only descended, and axons of only some lower stellate cells gave ascending collaterals. In addition, some axons, or collaterals, exhibited spines. The axons of the basket cell participated in the formation of a network around the cell bodies of Purkinje cells, similar to what has been described in other species (Cajal, 2000; Jacobs et al., 2014).

The presence of spines on the dendrites, and even axons, of the cells of this layer in such a perceptible manner indicated that they formed more synapses with parallel fibers. This suggests that these cells exerted a finer inhibitory control over the Purkinje cells. This is in line with the immunohistochemical findings, where the somata of both stellate and basket cells are intensely stained for parvalbumin and calretinin (Attaai et al., 2020; Maseko et al., 2013). This may give camels a better ability to coordinate their motor activity and balance, which is required because of its large size and ability to perform highly coordinated functions (carrying heavy loads while walking). To the best of our knowledge, no lower stellate cell (or any other cell) in the molecular layer of the cerebellum of any other species has been described as having a curved axon similar to that reported in this study (Figure 4).

## 4.2 | Purkinje cell layer

The Purkinje cells found in the cerebellar cortex of camels were generally similar to those of Purkinje cells described previously in birds and mammals (Cajal, 2000;

Fox et al., 1967; Jacobs et al., 2014; Maseko et al., 2013; Nieuwenhuys, 1967). In most cases, the soma size of these cells is directly proportional to the brain weight of the species (Lange, 1975). In our study, the Purkinje cell bodies in camels were large and pear shaped with a diameter ranging from 19.5 to 36.5  $\mu\text{m}$ . Despite using different quantification criteria, we believe this size is comparable to what has been described in elephants (Lange, 1975; Maseko et al., 2013).

Our findings are in agreement with a previous study on the primate cerebellar cortex in which smooth branches arise from the cell body and then spiny branchlets are given off (Fox et al., 1967). However, that study found that there were three generations of smooth branches in the primate cerebellar cortex. Two or three generations of smooth branches were found in camels. The spiny branchlets of the Purkinje cells of the camel were loaded with spines. The density of the spines averaged 17 spines/10  $\mu\text{m}$ . In primates, the density was found to be 15/10  $\mu\text{m}$  in macaque monkeys (*Macaca mulatta*) and 18/10  $\mu\text{m}$  in humans (Fox et al., 1967). The dendritic spine density of Purkinje cells was higher in camels than in monkeys.

In teleosts, the cerebellar efferent neurons, also known as eurydendroid cells, represent the neurons of the deep cerebellar nuclei and are distributed within the ganglionic layer that is equivalent to the Purkinje cell layer of other vertebrates (Ikenaga, 2013; Ikenaga, Yoshida, & Uematsu, 2006). Purkinje cells in most amphibians are scattered with simple dendritic trees that are not necessarily restricted to the sagittal plane (Nieuwenhuys, 1967). In reptiles, the Purkinje cell layer is variable in thickness and may reach up to five cells in thickness. The dendritic tree is more extensive than that in amphibians and is confined to a single plane. Except for the primary trunk, all dendrites were loaded with

spines. Similar to our observations in camels, Purkinje cells in birds and mammals become regularly arranged in a single layer throughout the cerebellum with extensive dendritic arborization spreading in the molecular layer confined to the sagittal plane (Jacobs et al., 2014; Nieuwenhuys, 1967). Immunohistochemically, it has been shown that somata, dendrites, and axons of Purkinje cells in camels are positive for calbindin and, to a lesser extent, parvalbumin (Attaai et al., 2020).

### 4.3 | Granular layer

Two types of cells in the granular layer of the camel cerebellar cortex were easily impregnated: granule and Golgi cells. The other two cell types, Lugaro and unipolar brush cells, were less impregnated. Nevertheless, these latter cells have been described in a previous study using crystal violet and immunohistochemical staining (Attaai et al., 2020). The teleostean, amphibian, reptilian, and avian cerebella have similar granule and Golgi cells in the granular layer of their cerebella (Cajal, 2000; Larsell, 1932; Nieuwenhuys, 1967). In addition, Lugaro cells have been described in teleosts and several mammals using the Golgi impregnation technique and in pigeons using immunohistochemical staining (Craciun, Gutierrez-Ibanez, Chan, Luksch, & Wylie, 2019; Jacobs et al., 2014; Puschina & Varaksin, 2002). Unipolar brush cells have been described immunohistochemically in chickens, pigeons, rats, guinea pigs, cats, and monkeys (Mugnaini et al., 2011; Takács, Markova, Borostyánkői, Görcs, & Hátori, 1999).

In primates, granule cells have been described as numerous cells with diameters ranging from 5 to 8  $\mu\text{m}$ . Each cell had several dendrites that ended in claw-like terminal expansions (Fox et al., 1967). In camels, the numerous granule cells had a similar size with two to four dendrites that terminated in a flower-like expansion. The claw-like terminals described in primates and other mammals are similar to the flower-like terminals found in camels (Fox et al., 1967; Jacobs et al., 2014). In both primates and camels, the granule cells were arranged in clusters and sent their dendrites to the cerebellar glomeruli and their axons toward the molecular layer.

The features of camel Golgi cells reported in the present study are quite similar to those reported previously in a study conducted on the rat and teleostian cerebella (Castejón & Sims, 1999). However, Golgi cells of primates are usually found near Purkinje cells or in the deep parts of the granular layer (Fox et al., 1967). They had stellate, polygonal, or triangular shapes. Their dendrites passed to the molecular and granular layers, and their axons formed plexuses. In this study, camel Golgi cells were

mostly located in the upper or middle parts and rarely in the deep parts of the granular layer. This is similar to the location of these cells in the cerebella of other mammals, including elephants (Jacobs et al., 2014; Maseko et al., 2013). They mostly have a triangular cell body that may possess appendages. Their dendrites also passed to the molecular and granular layers, but they showed several spines, protrusions, or appendages. Golgi cells in elephants and other large mammals have been considered the most complex cells in terms of the arrangement of dendritic arbors. However, no description of spines or protrusions has been provided (Jacobs et al., 2014; Maseko et al., 2013). No cells fitting the description of Golgi cells were found in the molecular layer of the camel cerebellar cortex, as described by Fox et al. (Fox et al., 1967).

Lugaro cells in camels are fusiform and horizontally directed along their long axis in the transverse plane of the folium, resembling the description of these cells in most previously studied large mammals (Jacobs et al., 2014). In elephants, however, two different types of Lugaro neurons have been described and are considered the largest neurons observed in the elephant cerebellar cortex (Maseko et al., 2013). Triangular cells were found immediately deep to the Purkinje cell layer at the same location as the Lugaro cells in camels. The fusiform cells, resembling Lugaro's somatic shape in camels, were located approximately 100  $\mu\text{m}$  into the granule cell layer. The dendritic organization of these cells is comparable to that of other mammals (Jacobs et al., 2014; Maseko et al., 2013). Two types of Lugaro cells have been described in the rat cerebellar cortex (Lainé & Axelrad, 2002). The first type was similar to that observed in camels. The second type was described with round cell bodies and variable locations in the granular layer and can be easily mistaken for a Golgi cell. Large interneurons of the granular layer have been differentiated in rats using different biological markers (Geurts, Timmermans, Shigemoto, & De Schutter, 2001). Due to the low number of impregnated Lugaro cells in this study, the presence of a second type of these cells in camels cannot be ruled out.

Although Fox et al. comprehensively described the primate cerebellum, unipolar brush cells were not mentioned (Fox et al., 1967). Subsequent authors believe that Fox mistook the unipolar brush cells for other types of cells, or that he considered the paint-brush-like terminal of these cells as artifacts (Mugnaini et al., 2011). Unipolar brush cells have been identified in various species (Mugnaini et al., 2011; Mugnaini & Floris, 1994). These cells can be identified more easily using electron microscopy or specific antibodies than with the Golgi method (Mugnaini et al., 2011). In these studies, various



morphological variations have been described for these cells. They may have two dendrites, each with its own paint-brush terminal. The single dendrite may have a branch, or the paint brush expansion may arise from the cell body directly. In our study, one of the cells had a single dendrite with a paint brush-like terminal and another paint brush expansion arising from the cell body. The other cell we found had a single dendrite with a paint brush terminal. Immunohistochemical studies have shown that most granular layer cells exhibit intense staining for calretinin (Attaai et al., 2020; Maseko et al., 2013).

## 5 | CONCLUSION

The present brain evolutionary study is pivotal to understanding the effect of environmental adaptation on brain structure organization. Eight types of neurons that are commonly described in the cerebellar cortex of various species were found in the cerebellar cortex of camels. These neurons have several features similar to their counterparts in other species. However, the interneurons of the molecular layer of camels (the upper and lower stellate cells and basket cells) seemed to have more dendrites and spines compared to their counterparts in other species. In addition, the large interneurons of the granular layer, Golgi cells, seemed to have the same dendritic branching pattern as other large mammals, but here we also described dense dendritic spines. The three types of cells in the molecular layer directly affect Purkinje cells, whereas Golgi cells affect the granule cells, which, in turn, affect Purkinje cells. The features of these interneurons in camels may have provided them with a better ability to control Purkinje cells (and ultimately the output from the cerebellar cortex), thus achieving a finer control of motor activity. In addition, the Purkinje cells of camels showed extensive ramification of the dendritic tree. This extensiveness seemed to be as dense as that of human Purkinje cells. Our results are an important follow-up to previous histochemical findings and should be investigated further with electron microscopic studies to identify the microstructure of the cerebellar cortical cells in camels.

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### CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

### AUTHOR CONTRIBUTIONS

**Saleh Al-Hussain:** Conceptualization; data curation; funding acquisition; investigation; methodology; project

administration; resources; supervision; writing - original draft. **Mustafa Yousuf:** Formal analysis; investigation; methodology; writing - original draft. **Ayat Banihani:** Formal analysis; investigation; methodology; software. **Sami Zaqout:** Methodology; resources; writing-review & editing. **Laiche Djouhri:** Resources; validation. **Ayman Mustafa:** Conceptualization; data curation; resources; supervision; validation; writing - original draft; writing-review & editing.

### DATA AVAILABILITY STATEMENT

The data sets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

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