Anais da Academia Brasileira de Ciências (2018) 90(4): 3597-3606
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
http://dx.doi.org/10.1590/0001-3765201820180328
www.scielo.br/aabc | www.fb.com/aabcjournal

Neuroscience: unveiling the brain of *Saimiri collinsi* (Squirrel Monkey)

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Manuscript received on April 2, 2018; accepted for publication on May 2, 2018

ABSTRACT

Behavioral intelligence among non-human primates is a somewhat puzzling area to study, since it is closely linked to the morphology of the central nervous system. However, this morphology is still unknown to science in the case of *Saimiri collinsi.* As a means of assisting future studies on the social behavior of this species, we analyzed the brains of six adult females from the National Primate Center / Pará, which were sent to the Animal Morphological Research Laboratory at the Federal Rural University of Amazônia after death by natural causes. The animals were fixed in formaldehyde solution (10%) and dissected. The brains were covered externally by the dura mater, with long cerebral hemispheres, although there was a complete absence of gyri. The internal structures which form a part of the telencephalon, diencephalon, midbrain, hindbrain and myelencephalon were identified, with the exception of the mammillary bodies. This condition, when linked to the lissencephaly found in these individuals raises questions about the real learning abilities of this species.

Key words: animal behavior, brain morphology, cognition, encephalon, neuroanatomy, *Saimiri collinsi*.

INTRODUCTION

When assessing cognition and the consequent behavioral patterns of non-human primates, account should be taken on the ability to solve problems, which is directly linked to learning, and is a remarkable characteristic of human beings (Resende et al. 2008). However, the learning process does not only involve paying attention and memorizing facts and situations, but is also an important means of gathering information from new experiences. These have a strong influence on brain plasticity by inducing creative decision making regarding behavior. Moreover, they strengthen the skills needed to draw analogies between mental items, in order to obtain new meanings, from activities in the prefrontal cortex and association cortex (E. Ximendes, unpublished data).

In this context, the main organ is the brain, which is divided in three parts (the forebrain,

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midbrain and hindbrain) located in the cranial cavity (Samuelson 2007, Dyce et al. 2010). The size of the brain varies between species, and is larger in most developed mammals. However, before its different functions can be understood, it is necessary to have a better idea of its physical divisions and regions (Colville and Bassert 2010). This is a serious challenge, since there is a paucity of studies in the literature on brain morphology in general.

The brain morphology of *Saimiri collinsi* is intriguing and challenging, leading us to investigate its shape, and characterize if this species can also be used as a biological model for behavioral neuroscience purposes, since they are already widely used in biomedical research (Boinski 1999). Squirrel monkeys are small primates, weighing on average 1 kg, and its large groups (20 to 75 individuals) live in a wide variety of habitats, from primary forests to degraded forest remnants (Defler 2004). Thus, it becomes an easy prey for illegal trade, increasing biopiracy records (Jack 2007). However, little is known about the behavioral aspects and intelligence of these animals, factors that are intrinsically connected to the central nervous system.

On the above, it is essential to know the brain morphology of *Saimiri collinsi* in order to subsidize research involving cognitive aspects, as well as to corroborate studies regarding the preservation of the species.

MATERIALS AND METHODS

Six adult females of *Saimiri collinsi* were taken, after death by natural causes, from the National Primate Center (CENP) - PA, with the approval of the Animal Research Committee (CEPAN / IEC / SVS / MS) No 008/2010, frozen and sent to the Morphological Animal Research Laboratory (LaPMA) of the Federal Rural University of Amazonia (UFRA) - Belém / PA.

After being thawed under running water, the bodies were fixed by intramuscular and intracavity infusion by aqueous formaldehyde 10%, with subsequent immersion of the specimens in the same solution for a minimum timeframe of at least seven days. After this step, the samples were dissected.

After the period of fixation, the brains were accessed by two different techniques. In three specimens, we made an incision in the dermis that covers the skull, from the frontal region to the occipital region, completing a full cycle of 360 degrees above the external ears with subsequent folding of the skin, as well as in the cranial muscles that cover the frontal, parietal, occipital, and temporal bones. With the aid of needle-nose pliers, portions of bone were gradually withdrawn from each above-mentioned region, including the total exposure of the dorsal compartment and rostral and caudal side of the brain.

In the other three specimens, a second brain extraction technique was employed, which involved removing the ventral part of the skull, after the displacement of the temporomandibular joints and the removal of the palatine bone, initially preserving the saddle-shaped sella turcica, to protect the hypophysis.

After the topographic analysis, the organ identification was carried out in the cranial cavity through photo documentation. One of the brains was removed while preserving optic nerves and eyeballs and then the meninges were extracted.

The nomenclature adopted was based on Veterinary Anatomy (International Committee on Veterinary Gross Anatomical Nomenclature 2017).

RESULTS AND DISCUSSION

With the opening and removal of the skullcap, we observed that the brain was covered by the meninges, while the outer part was the dura mater, which covered the arachnoid and pia mater (Figure 1a). These findings are observed in domestic mammals in general (Hildebrand and Goslow 2006) which have the same condition as the brain of *Cebus apella* (Marques et al. 2005) and *Saimiri sciureus* (Barcellos et al. 2011).

The *Saimiri collinsi* dura mater had some venous sinuses, according to the findings of Barcellos et al. (2011), which drew attention to the dorsal sagittal sinus (contained in the cerebral falx), the parietal sinus and temporal sinus, and those visualized from the dorsal to the lateral wall (Figure 1a).

The *ex situ* part of the brain consisted of two long cerebral hemispheres. These were separated by a longitudinal fissure, and occupied by the cerebral falx, compounding part of the telencephalon, which corroborates the findings of Barcellos et al. (2011) (Figure 1b). This basic condition is similar to that described in the literature regarding domestic animals (Konig and Liebich 2004, Prada 2014).

When it comes to the embryological division of the central nervous system, traditional opinions in the literature are that the telencephalon is formed from the forebrain (Machado 1993, Dyce et al. 2010). However, Nomina Anatomica Veterinaria (2017) and International Anatomical Nomenclature (human), state that only the cerebrum makes up the brain. Prada (2014), among other plausible assertions, argues that both the telencephalon and diencephalon are a part of the conformation of the brain, since these two regions are arranged in a rostral tentorium cerebelli, while the constituents of the brainstem (midbrain, pons and medulla oblongata) are arranged caudally inside the tentorium cerebelli.

Within this context, we analyzed each region, starting with the telencephalon, where we found that the cerebral hemispheres of *Saimiri collinsi* had a smooth surface (lissencephaly), which corroborated the prior findings of Barcellos et al. (2011) who macroscopically described the dura mater of the same species. In *Alouatta fusca* (Z. Bortolini, unpublished data), unlike *S. sciureus*, the gyri are present, although shallow and marked. However, in *Cebus libidinosus*, there is a mid-term condition where the cerebral convolutions of this species are compared with those of both *Alouatta fusca* (Z. Bortolini, unpublished data) and *Saimiri collinsi*. As in the case of *Cebus libidinosus* the frontal and occipital lobe are lissencephalic and the temporal and parietal lobes are gyrencephalic (Pereira-de-Paula et al. 2010).

Of the primate species, the one that effectively presents cerebral circumvolution is in fact the man, followed by the anthropoid primates (Marino 1998, Marino et al. 2004). Nevertheless, among mammals in general, the species that surpasses this condition in relation to anthropoid primates is not a primate, but an individual of the Order Cetacea: *Pontoporia blainvillei* (La Plata River Dolphin). In this species, in absolute terms, the telencephalon is smaller when compared to the human telencephalon, presenting dorsoventral flattening and a great number of convolutions (Gagliardo et al. 2017).

The classical literature points out that the cerebral sulci can help defining the cerebral lobes, and that the name was given because of the way they relate to the skull bones. Thus, the frontal lobe, parietal, temporal, occipital and the insula, which make up the fifth lobe, are located deep in the lateral sulcus, and have no correlation with the skull bones (Machado 1993). However, in the case of *Saimiri collinsi,* we cannot be guided by the grooves that border the lobes, since this species will then be shown to be lissencephalic. This lead us to question whether these animals, in fact, do not have an insula, since they also do not have a lateral sulcus, unlike what is described for *Pontoporia blainvillei*, in which the authors claim that such species has insular lobe, even though it is not visible on the surface of the encephalon (Gagliardo et al. 2017). Still, in *S. collinsi,* even without the presence of gyrus, the regions of the lobes, for example, can be detected by a correlation with the skull bones (Figure 1c, d).

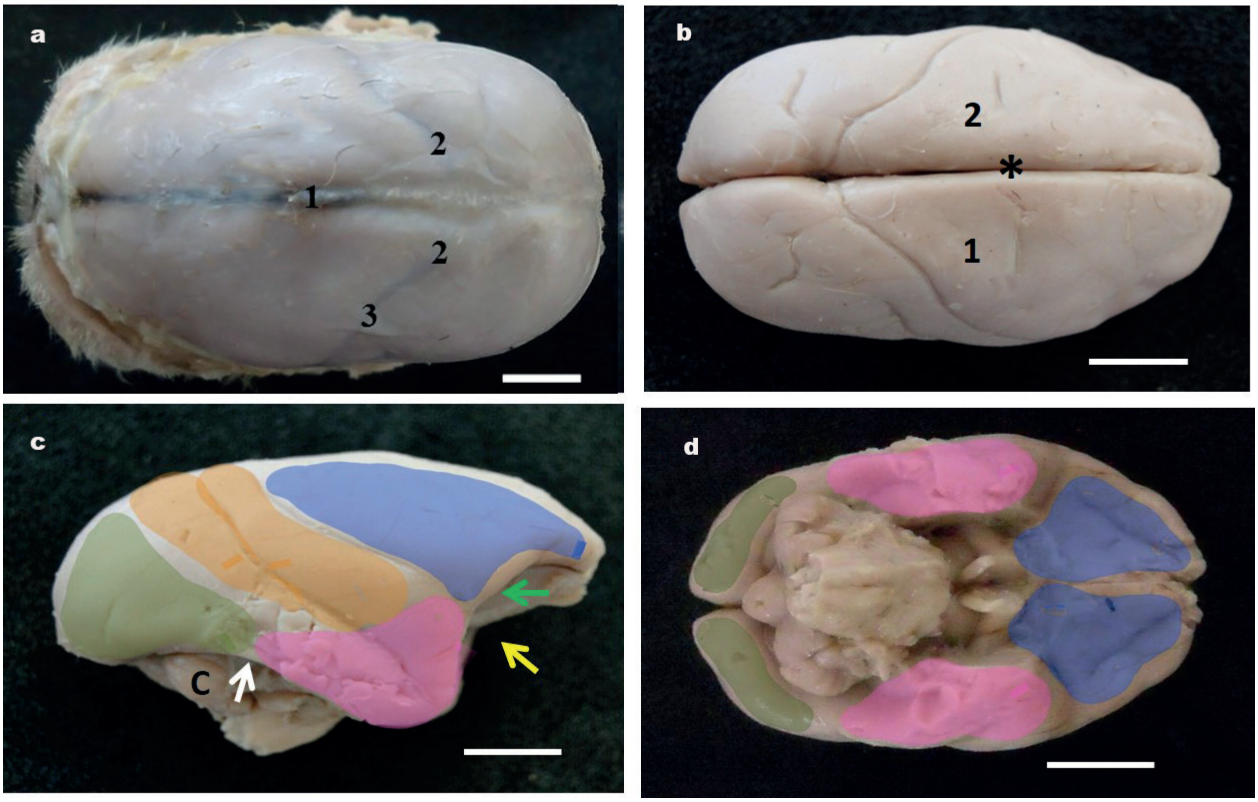

Figure 1 - Photomacrograph of the brain of *Saimiri collinsi.* **(a)** Dorsal view of the brain covered by dura mater in the cranial cavity after the removal of the temporal, frontal, parietal and a part of the occipital bones. Note the presence of the dorsal sagittal sinus (1), parietal bone (2) and temporal bone (3). **(b)** Dorsal view of the brain after the removal of the meninges, with a strong presence of longitudinal fissure (*) separating the right cerebral hemisphere (1) from the left cerebral hemisphere (2). **(c)** Side view of the brain without the meninges, which are observed the frontal lobes (blue), parietal (orange), temporal (pink) and occipital (gray), and the cerebellum (C). Note also the location of the nasal grooves (caudal - white arrow; cranial - green arrow), as well as ocular printing (yellow arrow). **(d)** Ventral view of the brain without the meninges, which are observed in the frontal lobes (blue), temporal (pink) and occipital (gray), and the bulb. Scale bar: 1cm.

Regarding the circunvolutions, the analogy between the number of cortical reliefs (gyrus) and sulcus is expressed by the ability of these conformations to fit large surface areas within smaller spaces in the cranial cavity, as explained by R. O. Santos (Unpublished data), and leads to a greater capacity for learning and recognition in human primates. However, this condition apparently cannot be interpreted in the same way for *Saimiri collinsi,* which does not have these structures, characterized them as lissencephalic, as explained earlier (Figure 1b). However, Astumi and Nagasaka (2015), in their study of the persecution behavior of *Saimiri collinsi*, highlighted that this species follows patterns of movements aimed at specific goals, rather than simply following a similarity path. This leads us to ask whether they effectively trace a line of reasoning and how this procedure occurs.

According to Prada (2014), gyrencephalia, which is the most common condition in mammals, is established during the phylogenetic progression. However, this is not a "*sine qua non*" condition of evolution. This means that a lissencephalic species will not necessarily be considered less developed in evolutionary terms than a gyrencephalic species. However, it should be noted that, according to Gagliardo et al. (2017), encephalon areas that are

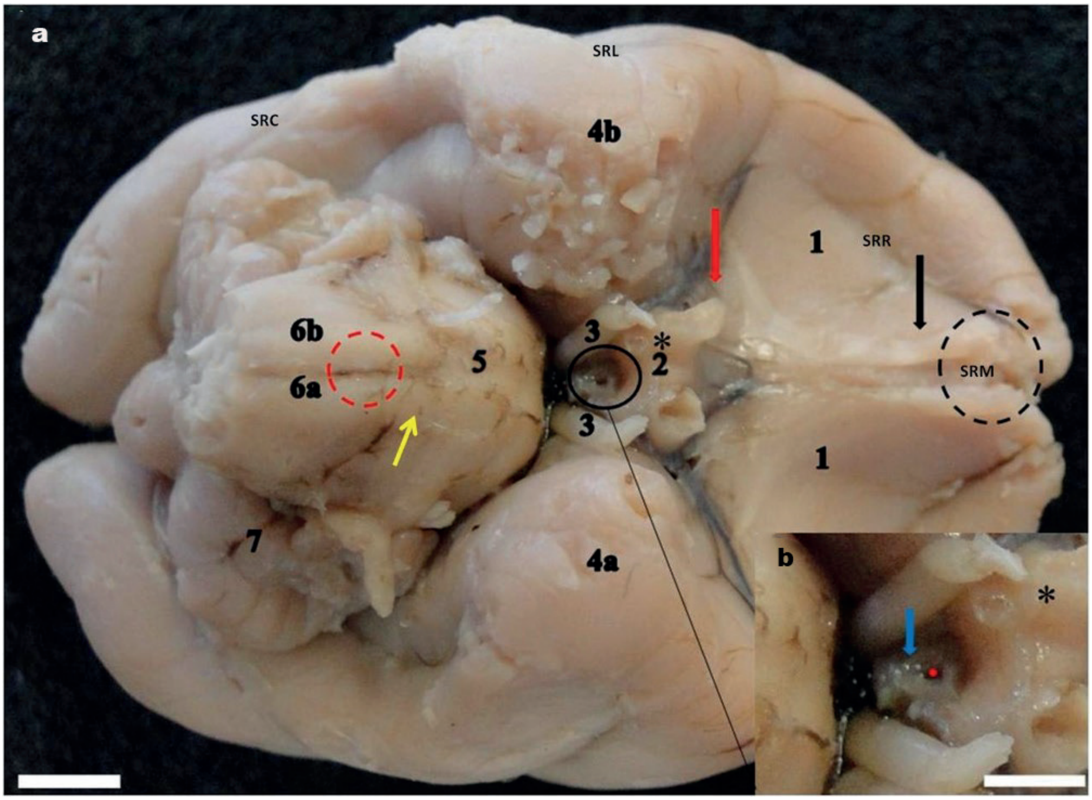

Figure 2 - Photomacrograph of the brain of *Saimiri collinsi*. **(a)** Ventral view of the brain, the rostral portion shows the olfactory bulb (black dashed circle) near the medial rhinal groove (SRM), the olfactory tract (black arrow) and the olfactory trigone (1), next to the rhinal rostral sulcus (SRR), followed by the optic nerve (red arrow), the optic chiasm (2) and optical tract (*), the region of the hypophyseal infundibulum (black circle) between the oculomotor nerves (3). Note the pyriform lobes on the left (4a) and right (4b) close to the lateral rhinal groove (SRL), the pons (5); the trapezoid body (yellow arrow) and left pyramids (6a) and right (6b) separated by the interpyramidal foss (red dashed circle). View the cerebellum (7), near the rhinal caudal sulcus (SRC). **(b)** View the cinereous tuber (blue arrow) surrounding the hypophyseal infundibulum (red dot) and the optic tract region (*). Scale bar: 1 cm.

more developed and with more gyri are closely related to some specific functions belonging to some species, such as the parietal and temporal lobes of *Pontoporia blainvillei*, which are larger than the others due to the great hearing capacity of this species.

This fact raises questions about communication between primates, since, according to Purves et al. (2004), as well as humans, animals are able to communicate in a specific manner by means of a "language." In man, this activity results from the participation of both the parietotemporal and frontal cortex, a fact that has not been established in animals.

In addition, according to Purves et al. (2004), the brain of non-human primates anthropoid, i.e. those that do not have a tail and resemble human beings (chimpanzees, gorillas and orangutans), have a greater morphological compatibility with the brains of man. This has led some authors to infer that this similarity also extends to the domain of language.

Regarding the macroscopic findings, ventrally forming the rhinencephalon, we can identify the structures related to olfaction: the olfactory bulb, olfactory tract, olfactory trigone and the piriform lobes. The first three of these were arranged in the ocular impression (Figure 2a), while the small olfactory bulb is compared to what is described for *Canis lupus* (Esteves et al. 2004), *Bradypus torquatus, Bradupus variegatus* (Ferreira et al. 2005) and *Dasypus novemcinctus* (Silva et al. 2007).

In support of what has been described in the traditional literature, primates in general are regarded as microsmatic, i.e. with a poorly developed sense of smell (Koeppen 2011). This would explain the small size of the structures related to smell in *Saimiri collinsi*, unlike, for example, dogs, in which such structures are more developed, since they are macrosmatic animals (Beccari 1943).

We also identified structures presented in the optical portion (optical nerve, optic chiasm, and optical treatment) (Figure 2a, b) which, along with the mammillary bodies and hypophysis, form a part of the diencephalon of *Saimiri collinsi* (Figure 2b).

The diencephalon of this species is restricted to a small ventral area, proportional to its brain size (Figure 2b). Its hypophysis performed in a similar way to that described for *Cebus apella* (Oliveira et al. 2007) (Figure 5), although it did not enable mammillary bodies to be identified. This structure, on the other hand, can be identified in *Cebus apella* (Oliveira et al. 2007), humans (Machado 1993, Dangelo and Fattini 2007) and *Alouatta fusca* (Z. Bortolini, unpublished data).

Mammillary bodies are important components of the limbic system (Vann and Nelson 2015, Lee 2016), since they are responsible for episodic memory (event memory) and spatial memory, as well as the location of an object or place. These memories are linked to strong emotions and enable animals to be engaged in useful survival activities such as finding food, other individuals or sexual partners (Vann 2010).

According to Vaughan (1985), *Saimiri collinsi* is a primate species that is widely used as a biological model, despite the absence of a mammillary body, as shown by our findings. This would, for example, refute investigations into the Korsakoff syndrome, which results from a degeneration of the mammillary bodies as a result of chronic alcoholism and in which anterograde amnesia is the most important symptom (Machado 1993). It is also intriguing to think that this species might have its spatial memory impaired by the absence of mammillary bodies, since the home range of these primates in continuous forests is around 240 ha (Carretero-Pizón et al. 2009) and such range must count on some good spatial memory.

From a broader perspective, when composing the diencephalon, it might be better to observe the cinereous tube surrounding the infundibulum, which encloses the hypophysis (Figure 3b). With regard to the ventral view, the following were observed: pons, interpyramidal foss and cerebellum forming the metencephalon, and finally the medulla oblongata or bulb that comprises the myelencephalon, as found in mammals and primates in general (Dyce et al. 2010). On the basis of these findings, it could then define the brainstem, which consists of the midbrain, the pons and the bulb (Figure 3a).

Regarding the midbrain, for a better visualization of the cerebral peduncles (Figure 3a, b) it was necessary to partially withdraw the left and right piriform lobes (Figure 3a) and the pons (Figure 3b), this last one covering the interpeduncular fossa (Figure 3b). These structures were also observed in the brain of *Cebus apella* (Marques et al. 2005), *Bradypus torquatus* and *Bradypus variegatus* (Ferreira at al. 2005).

The middle cerebral hemispheres were separated, so that the telencephalon components could be identified: the corpus callosum and their portions (knee, fornix and splenium), corpus callosum sulcus, lateral ventricles (right and left), septum pellucidum and rostral commissure. Most of the parts of the diencephalon structure consists of pineal gland, III ventricle, interthalamic commissure (thalamus), hypothalamus, caudal

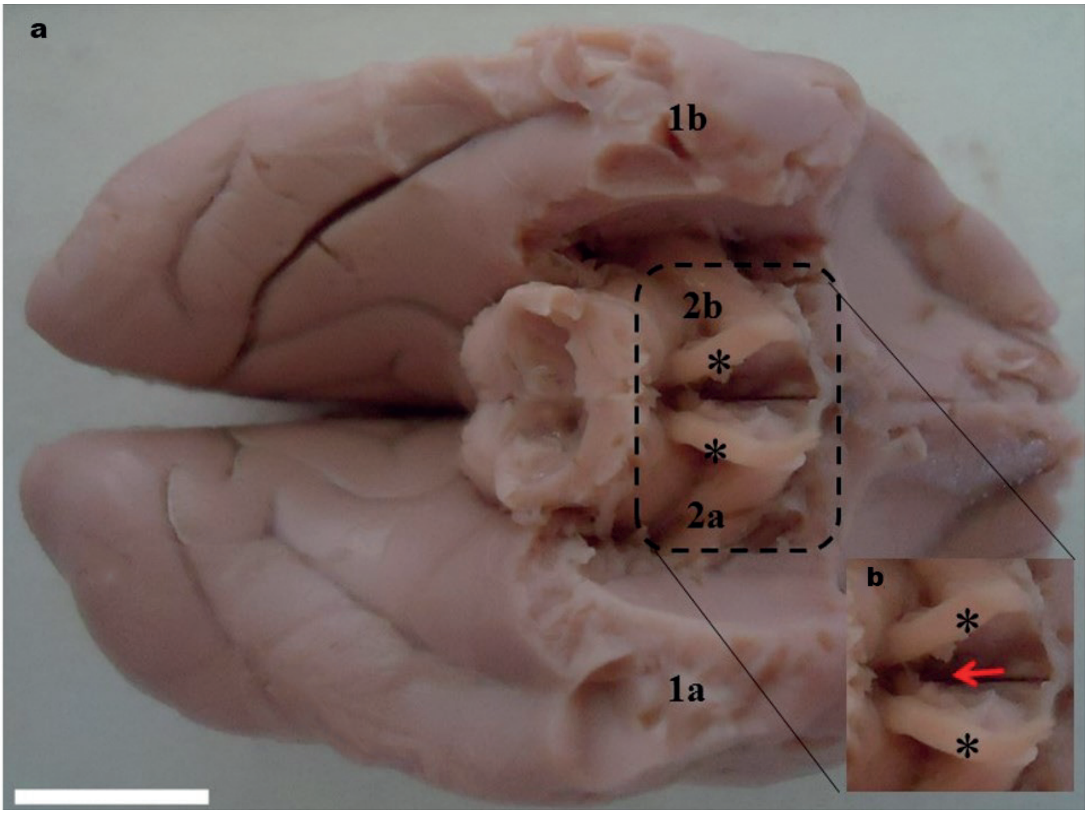

Figure 3 - Photomacrograph of the brain of *Saimiri collinsi.* **(a)** ventral view of the brain after the removal of a small portion of the left (1a) and right (1b) piriform lobes, as well as part of the cerebellum insertion for better visualization of the left cerebral peduncle (2a) and right (2b) and III pair of the cranial nerve (*). **(b)** enlarged view of cerebral peduncles and interpeduncular fossa (red arrow). Starting from the cerebral peduncles, the pair of cranial nerves III can be viewed (*). Scale bar: 1 cm.

commissure, optic chiasm, hypophysis, cerebral aqueduct, colliculus rostral and colliculus caudal; the two last partly belonging to the diencephalon and midbrain. In the metencephalon, we identified the pons and the cerebellum, and finally the medulla oblongata or bulb that constituted the myelencephalon. The IV ventricle, which was also identified, was found to occupy the metencephalon, like the myelencephalon (Figure 4).

This characteristic of brainstem formation, regarding the union of the midbrain with the bridge and the bulb, was also described in *Cebus apella* (Marques et al. 2010), revealing a neuroanatomic relationship between individuals of different species within the Cebidae family. All the findings mentioned above correspond to what is described not only for *Cebus apella,* but also for man and even other orders of animals, such as *Tamandua tetradactyla* and *Ovis aries* (Oliveira et al. 2007, R. Melul, unpublished data, A. C. Pádua, unpublished data).

In the median section, it was possible to identify the plexus choroid of the lateral ventricle (Figure 4), which is responsible for the production of cerebrospinal fluid. Its main function is to provide mechanical protection for the central nervous system, by covering the ventricles and thus reach the spinal cord (Fernández and Bernardini 2010).

The cerebellum was placed caudal-ventral to the cerebral hemispheres, which confirms the findings in *Cebus apella* (Oliveira et al. 2007),

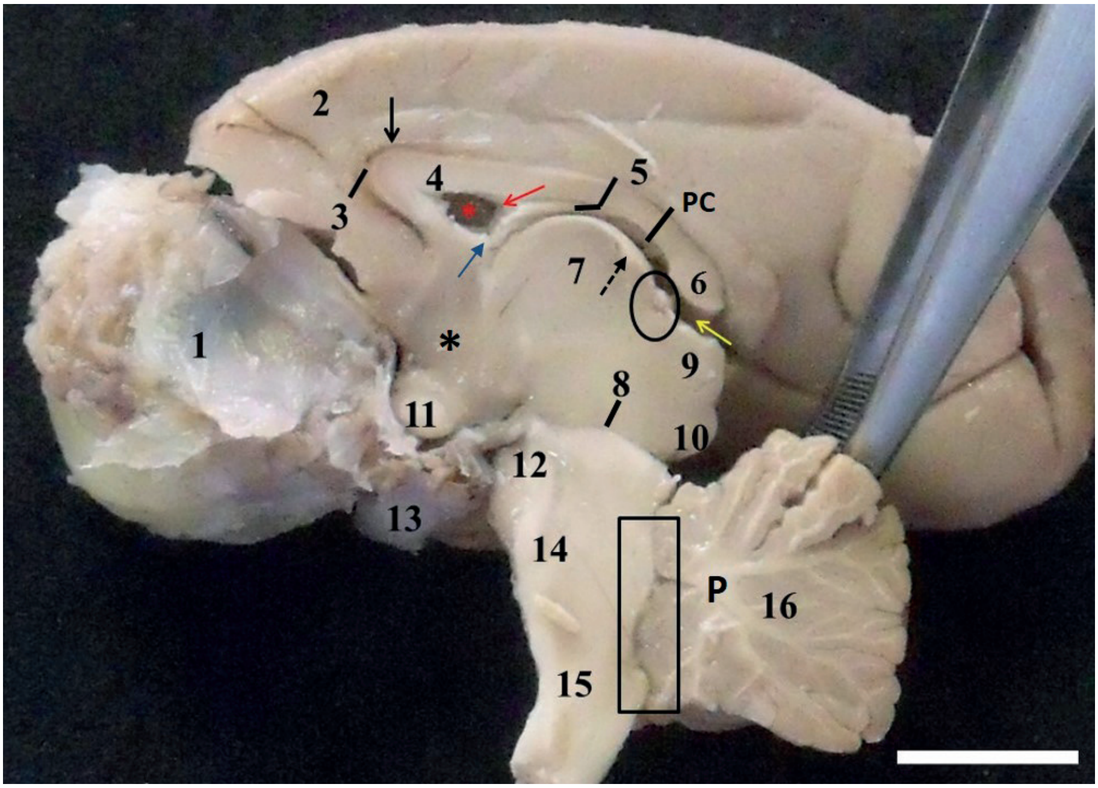

Figure 4 - Photomacrograph of the brain of *Saimiri collinsi.* Medial view of the brain showing the following structures: right ocular globe (1), right cerebral hemisphere (2), knee of the corpus callosum (3), corpus callosum sulcus (arrow), corpus callosum (4), right lateral ventricle (*), part septum pellucidum (red arrow), fornix (5), splenium of the corpus callosum (6), pineal (circle), III ventricle (yellow arrow), interthalamic commissure (thalamus) (7), cerebral aqueduct (8), rostral colliculus (9), caudal colliculus (10), making quadruplet bodies, optic chiasm (11), cerebral peduncle (12), hypophysis (13), pons (14), bulb (15), IV ventricle (rectangle) , cerebellum (16) with the middle cerebellar peduncle (P), hypothalamus (*), rostral commissure (blue arrow), caudal commissure (dashed arrow) and choroid plexus (CP). Scale bar: 1 cm.

which was proportionally developed, and unlike the brain, had several blades (cerebellar leaves) and sulcus (cerebellar fissures) as well as the cerebellum of *Alouatta fusca* (Z. Bortolini, unpublished data).

In a study of *Cebus apella*, by Oliveira et al. (2007), the authors erroneously call the cerebellar leaves of gyrus, contrary to what is recommended by the International Committee on Veterinary Gross Anatomical Nomenclature and expressed in the Nomina Anatomica Veterinaria (2017), and claim that these structures are responsible for carrying out complex and delicate movements such as the manipulation of tools and taking up semi-straight positions. However, like *Alouatta fusca* (Z. Bortolini, unpublished data), *Saimiri collinsi* also takes a bipedal posture in some situations, like when handling food (Auricchio 1995).

In this context of voluntary and automated movements, it should be emphasized that the cerebellum does not initiate movements effectively, although acts as an auxiliary aid in their planning and execution. This is because afferent sensory responses are triggered by the muscles of the front of the body and include physical, chemical and mechanical stimuli, involving the cerebellum and the centers motor system of the pyramidal and extrapyramidal (King 1993). Moreover, the cerebellum part of the unconscious and involuntary actions differs from the brain, since each hemisphere of the cerebellum acts directly on the lower motor neurons that correspond to the antimere (Prada 2014).

The structures found in the brain of the Squirrel Monkey (*Saimiri collinsi)* are similar to those described in several species of domestic and wild mammals. However, attention should be drawn to the absence of gyrus and mammillary bodies, which are generally found in the brains of mammals.

These two conditions lead us to question the real learning abilities of this species, since the sulcus and circunvolutions of the brain increased the cortical area composed of neurons, while the mammillary bodies play an important role in the formation and recall of episodic and spatial memory.

We undertook an anatomical description of the brain of *Saimiri collinsi,* which resulted in these intriguing findings. Thus, it is extremely important to also carry out a behavioral study of these animals, as well as to apply learning and memory tests that can correlate these responses to the morphology of the brain.

ACKNOWLEDGMENTS

To the Centro Nacional de Primatas (CENP/PA), for kindly providing the specimens used in this research.

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