A SYSTEMATIC STUDY OF THE BRAIN BASE ARTERIES IN CAPYBARA (*Hydrochoerus hydrochaeris*)

Sueli Hoff Reckziegel, Tânia Lindemann and Rui Campos

Departament of Morphological Sciences, Institute of Basic Health Sciences, Faculty of Veterinary Medicine,
Federal University of Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil.

ABSTRACT

Thirty specimens of *Hydrochoerus hydrochaeris* were injected with neoprene latex in order to study the distribution of vessels which compose the vertebro-basilar system and its derived branches in the encephalon. The right and left vertebral arteries anastomosed on the ventral surface of the encephalon to form the basilar artery, which gave rise to the caudal cerebellar (left and right, double and single) and middle cerebellar (both antimeres, single and double) as collaterals. The basilar artery splits into right and left terminal branches which gave rise to a series of arteries which included the rostral cerebellar arteries (right antimere, double and single; left antimere, double, single and triple), the caudal cerebral arteries (double, single and triple in both antimeres), the internal ophthalmic arteries (single in both antimeres), and the middle cerebral artery (single in the right antimere in all specimens and single and double in the left antimere). The ending branches of the terminal branches of the basilar artery were the rostral cerebral arteries (single or absent in both antimeres) with a rostral communicating artery (single or absent) between them. The arterial circle was derived solely from the vertebro-basilar system, since internal carotid arteries were absent in adults. The circle was closed rostrally in 90% of the specimens and open in 10%. In all cases, there was anastomosis of the circle with maxillary artery.

Key words: Brain vascularization, encephalic arteries, *Hydrochoeris hydrochaeris,* rodents

INTRODUCTION

Several authors [1,7,8] have described the encephalic irrigation in mammals. Tandler [8] asserted that the greatest differences in the types of encephalic irrigation in mammals occurred in rodents, although the genera *Cavia*, *Hydrochoerus* and *Dasyprocta* shared a similar encephalic irrigation.

In a study of the phylogeny of brain arteries De Vriese [3] classified the encephalic irrigation of vertebrates into one of three types: type I, in which brain irrigation is almost exclusively via the internal carotid arteries, type II, in which the encephalon is partially irrigated by the carotid and vertebro-basilar systems, with equal distribution between the two systems or a predominance of one of them, and type III, in which the encephalic irrigation is almost exclusively via the vertebro-basilar system. Examples of the three types include the chicken (*Gallus gallus*) [2], opossum (*Didelphis sp*.) [4,6,9] and capybara (*Hydrochoerus hydrochaeris*).

In this report we systematize and describe the vessels of the base of the capybara encephalon and determine which of them contribute to the formation of the arterial cerebral circle and its main branches. We also decribe the main structural and pattern variations in this species, and compare the tree types of encephalic irrigation in the classification by De Vriese [3].

MATERIAL AND METHODS

The encephala with a spinal chord segment from 30 *Hydrochoerus hydrochaeris* were studied. The specimens were from Pampa Safari, Taquara, RS, and were used under a licence granted by the Brazilian Institute of the Environment (IBAMA). The animals (15 M, 15 F) were anesthetized with chloral hydrate (30 mg/kg, i.p., Merck), followed by the administration of heparin (5000 UI; i.p., Liquemine-Roche). After opening the thoracic cavity, the brachial-encephalic

Correspondence to: Dr. Sueli Hoff Reckziegel
Departamento de Ciências Morfológicas, Instituto de Ciências Básicas da Saúde, Setor de Anatomia Animal, Faculdade de Medicina Veterinária, Universidade Federal do Rio Grande do Sul (UFRGS), Av. Bento Gonçalves, n º 9090, CEP: 91540-000, Porto Alegre, RS, Brasil. Tel: (55) (51) 3316 6924, Fax: (55) (51) 3316 7305, E-mail: preck@orion.ufrgs.br

trunk was cannulated and the subclavian and internal thoracic arteries were clamped. Subsequently, the vascular system was washed with saline solution and then filled with dyed latex (Neoprene, Artecola).

The pieces were cooled under running water for one hour, after which the neck was sectioned, the head skin removed and an opening made in the skull. The heads were then immersed in 20% formaldehyde for at least seven days. After this period, the encephala with a segment of spinal chord were removed, along with the dura mater, which was later detached to allow the observation and schematization of the encephalon arteries with the aid of a magnifying glass. The terminology used to name the arteries followed that of the *Nomina*

Anatomica Veterinaria [5]. For statistical analysis, the percentages and the test of two ratios with a normal distribution ($\alpha=5\%$) were used to compare differences between the sexes.

RESULTS

The irrigation of the encephalon of *H. hydrochaeris* was dependent only on the vertebral-basilar system, although it showed an anastomosis between the maxillary and internal ophthalmic arteries in both antimeres (Figs. 1- 4).
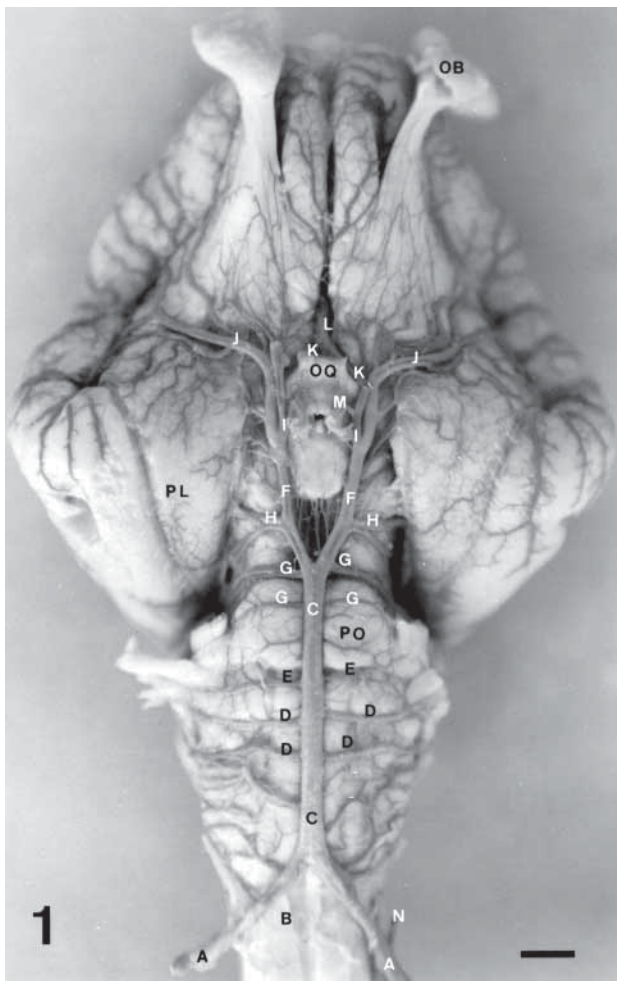

Figure 1. Ventral view of the brain base arteries of *H. hydrochaeris* without the hypophysis. A – vertebral artery, B – ventral spinal artery, C – basilar artery, D – caudal cerebellar artery, E – middle cerebellar artery, F – terminal branch of the basilar artery, G – rostral cerebellar artery, H – caudal cerebral artery, I – internal ophthalmic artery, J – middle cerebral artery, K – rostral cerebral artery, L – rostral communicating artery, M – anastomosis between the maxillary and the internal ophthalmic arteries, N – anastomosis between the occipital and the vertebral arteries, OB – olfactory bulb, PL – piriform lobe, OQ – optic chiasma. (Bar = 5 mm)
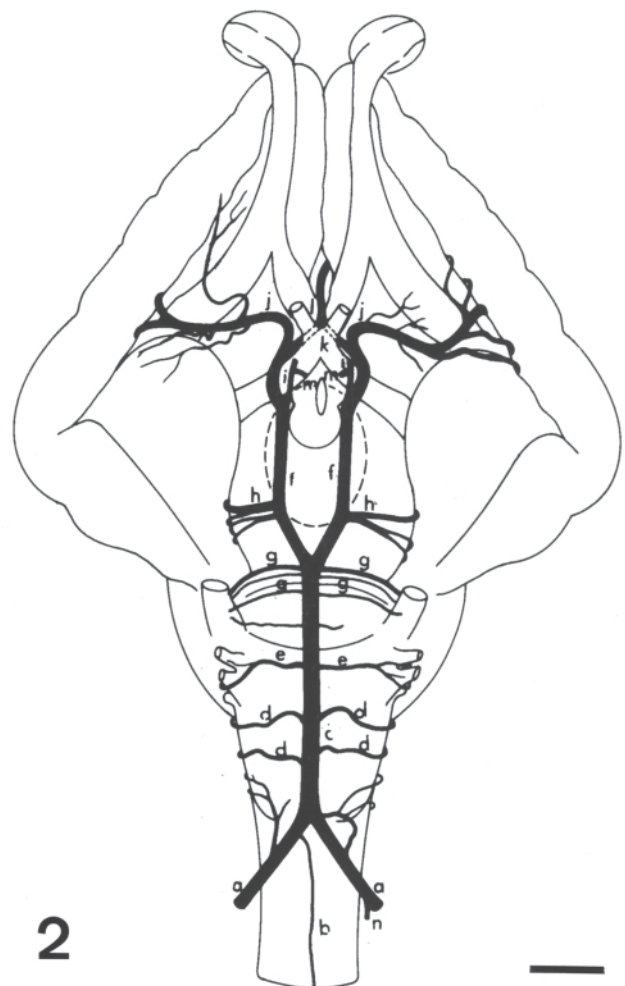

Figure 2. Schematic ventral view of the normal distribution of the brain base arteries in *H. hydrochaeris*. a – vertebral artery, b – ventral spinal artery, c – basilar artery, d – caudal cerebellar artery, e – middle cerebellar artery, f – terminal branch of basilar artery, g – rostral cerebellar artery, h – caudal cerebral artery, i – internal ophthalmic artery, j – middle cerebral artery, k – rostral cerebral artery, l – rostral communicating artery, m – anastomosis between the maxillary and the internal ophthalmic arteries, n – anastomosis between the occipital and the vertebral arteries. (Bar = 8 mm)

No internal carotid artery was present in any of the specimens examined. However, at the point in the common carotid artery where the internal carotid artery should arise, a fine fibrous chord was present in 33.3% of the specimens, and in 3.3% a small button was found on the left and right antimeres.

The vertebral arteries, which were branches of the subclavian arteries, ascended the neck via the transversal channel and penetrated the vertebral channel after passing through the alar and lateral vertebral foramena. On the ventral surface of the cervical spinal chord, these vessels crossed the foramen magnum and joined to form the basilar artery in 100% of the samples (Figs. 1 and 2).

The ventral spinal artery appeared as a fine vessel derived from the vertebral arteries immediately before the formation of the basilar artery and projected caudally in the median ventral fissure. This artery consisted of unified vessels derived from the right and left vertebral arteries in 86.7% of the specimens, from only the right vertebral artery branch in 6.7% of the cases, and from the left vertebral artery branch in a further 6.7%.

In all specimens, the basilar artery projected rostrally as a thick straight vessel to the ventral surface of the rhombencephalon, with no apparent change in diameter. At the rostral pontine sulcus, the artery divided into its left and right terminal branches. The basilar artery gave off several collateral branches to each antimere. These vessels showed a certain symmetry and generally formed right angles to this artery (Figs. 1 and 2). Of the main collateral branches, the caudal and middle cerebellar arteries are described below.

The caudal cerebellar artery originated from the initial third of the basilar artery and projected laterally to irrigate the most lateral caudal portion of the lateral cerebellar hemispheres and the caudal portion of the cerebellar vermis. In 60% of the cases, the right caudal cerebellar artery was double, while in 40%, it was single. The left caudal cerebellar artery was double in 53.3% of the samples and single in 46.7%.

The middle cerebellar artery originated in the middle third of the basilar artery and projected laterally to cross the roots of the facial and vestibulocochlear nerves until it reached the dorsolateral face of the lateral cerebellar hemispheres. The right branch of this vessel was single in 60% of the specimens and double in 40%. Its left branch was single in 76.6% of the cases and double in 23.2%.

The terminal branches of the basilar artery projected rostro-laterally at an angle of approximately 55 degrees. The rostral cerebellar artery arose near the bifurcation of the basilar artery and the caudal cerebral artery arose immediately thereafter, at the emergence of the oculomotor nerve. After giving off the second collateral branch, the terminal branches of the basilar artery continued almost parallel, with a subtle rostral divergence, to pass laterally close to the mamillary body and the hypophysis. At the tuber cinereo, which the internal carotid arteries reached during fetal life, the terminal branches bifurcated into an internal ophthalmic artery, which continued rostromedially, and a trunk, which turned rostrolaterally in an arch. The latter gave rise to the middle cerebral artery laterally and the rostral cerebral artery medialy.

The rostral cerebellar arteries originated from the terminal branches of the basilar artery, continued laterally along the pontino rostral sulcus, and then passed through the lateral and rostral faces of the lateral cerebellar hemispheres and through the rostral and dorsal faces of the cerebellar vermis. On the right, this artery was double in 56.7% of the cases and single in 43.3%, whereas on the left, it was double in 50% of the cases and single in 43.3%; in 6.7%, this artery was triple.

The caudal cerebral artery derived from the terminal branches of the basilar artery and projected laterally into the transversal sulcus, and then branched to the mesencephalon and the caudal pole of the brain hemispheres (Figs. 1 and 2). In the right antimere, this vessel was double in 56.7% of the specimens, single in 40% and triple in 3.3%. In the left antimere, it was single in 53.3%, double in 40% and triple in 6.7%.

The internal ophthalmic artery appeared as a middle-rostral projection of the terminal branches of the basilar artery close to the tuber cinereous and left the skull cavity along with the optical nerve (Figs. 3 and 4). Near its origin, this vessel received an anastomosis from the maxillary artery. To the right, these anastomosis occurred directly with the right terminal branch of the basilar artery in 3.3% of the specimens.
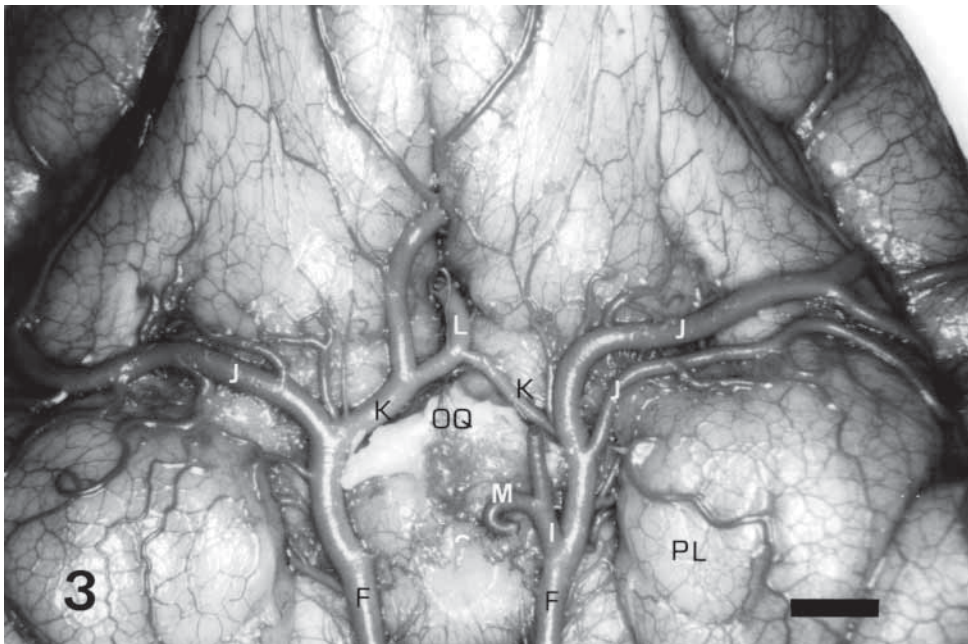
Figure 3. Ventral view of the brain of *H. hydrochaeris* showing the double left middle cerebral artery. F – terminal branch of the basilar artery, I – internal ophthalmic artery, J – middle cerebral artery, K – rostral cerebral artery, L – rostral communicating artery, M – anastomosis between the maxillary and the internal ophthalmic arteries, OQ – optic chiasma, PL – piriform lobe. (Bar = 3 mm).
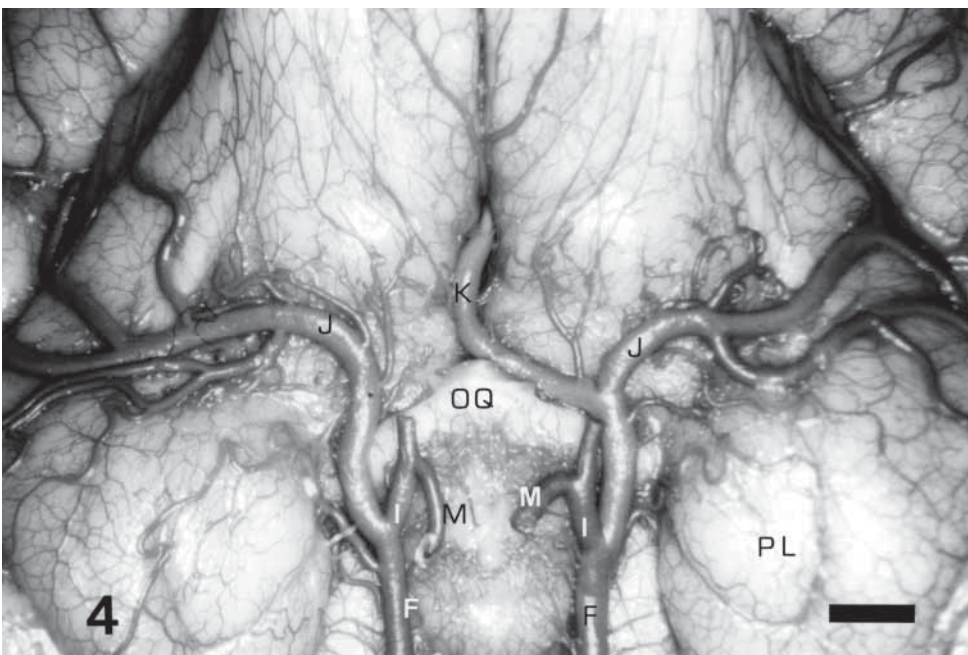

Figure 4. Ventral view of the brain of *H. hydrochaeris* showing the rostrally open arterial circle. F – terminal branch of the basilar artery, I – internal ophthalmic artery, J – middle cerebral artery, K – rostral cerebral artery, M – anastomosis between the maxillary and the internal ophthalmic arteries, OQ – optic chiasma, PL – piriform lobe. (Bar = 3 mm).

On the right, the internal ophthalmic artery was a collateral branch of the terminal branch in 96.7% of the cases, and in 3.3% of the cases it derived from the anastomosis between the terminal branch and the maxillary artery. On the left, this vessel originated from the terminal branch in 90% of the specimens, and from the anastomotic branch of the maxillary artery in 10% of the cases.

The middle cerebral artery derived as a collateral branch of the terminal branches of the basilar artery via the optic tract, then crossed the lateral fossa and distributed on the dorsolateral surface of the brain hemisphere. On the right, this vessel was single in all specimens, but had a double origin in 3.3% of the cases, forming an anastomosis 'island' immediately beyond its origin. On the left, this vessel was single in 96.7% of the cases and double in 3.3% (Fig. 3).

The rostral cerebral artery derived medially from the bifurcation of the terminal branch of the basilar artery and projected medio-rostrally towards the ventral longitudinal sulcus, where it

anastomosed with its contralateral homologous vessel to form the rostral communicating artery (Figs. 1- 3). In the right antimere, this artery was single in 93.3% of the cases and absent in 6.7%. In the left antimere, it was single in 96.7% of the cases and absent in 3.3%.

The rostral communicating artery was a median single vessel formed by the anastomosis of the right and left rostral cerebral arteries rostro-dorsal to the optic chiasma. This artery projected towards the ventral longitudinal sulcus, and branched off to supply the corpus callosum, the rostral olfactory areas and the rostral pole of the brain hemispheres. In 90% of the specimens, this artery was present as a single median vessel formed by the anastomosis of two well-developed rostral cerebral arteries in 43.3% of the cases. In 26.7% of the specimens, the left artery was well-developed and the right artery was very thin, whereas in 20%, the right artery was well-developed and the left artery was very thin. In 10% of the encephala, the rostral communicating artery was absent because of the atrophy of one of the rostral cerebral arteries (two cases in the right antimere and one in the left antimere) (Fig. 4). However, in all cases the persisting vessel bifurcated to irrigate the opposite antimere.

The special arrangement of the terminal branches of the basilar artery in the base of the encephalon gave rise to an arterial cerebral circle with unique characteristics because of the absence of internal carotid arteries. This circle extended rostrally from the rostral pontine sulcus up to the optic chiasm, where it usually closed to form the rostral communicating artery.

The cerebral arterial circle was supplied solely by the vertebral-basilar system. In all cases, the arterial cerebral circle was closed caudally; in 90%, it was also closed rostrally, while in 10% it remained open rostrally because of the absence of one of the rostral cerebral arteries.

There were no significant sex-related variations in the arrangement of the arteries described above.

DISCUSSION

No internal carotid artery was observed in adult capybaras, as also reported for *Cavia cobaya, Sciurus* and *Arctomys* [8], *Sciurus, C. cobaya* and *C. aguti* [3], and *Hystrix cristata, H. leucura, Chincilla laniger, Myocastor coypu, Octodon degus, Thryonomys swinderianus, Bathyergus suillus, Cryptomys natalensis* and *Heterocephalus glaber* [1]. Tandler [8] reported the obliteration of the internal carotid artery in mammals, with a fibrous chord in only a few cases. This author also mentions thin fibrous vestiges of the internal carotid artery in the medial wall of the common carotid artery in *C. cobaya* at the site where the occipital artery emerges. In *Sciurus* and *Arctomys,* only the initial segment of the internal carotid artery close to the *bulla tympanica* is developed [8]. In *H. cristata, Lagostomus, Arctomys* and *Myoxus*, the cerebral portion of the internal carotid artery is rudimentary [3], as also found by Bugge [1] in *Cavia porcellus, Dolichotis patagona* and *Dasyprocta agutii*. Nilges [7] stated that in guinea pigs the internal carotid artery plays no part in the formation of the circle of Willis. This vessel enters the cranial cavity through the carotid canal and immediately leaves it as the ophthalmic artery which enters the orbit through the superior orbital fissure along with the ophthalmic nerve. In the orbit, branches of the ophthalmic artery anastomose with branches of the accessory ophthalmic artery. The latter artery enters the orbit together with the optic nerve. There are no large intracranial communications between the internal carotid artery and the circle of Willis. In adult capybara, the presence of fibrous chords and buttons on the wall of the common carotid arteries, where the origin of the internal carotid artery would normally be located, shows that a carotid encephalic irrigation existed during ontogenesis, and that the vertebro-basilar system gradually invaded the initial territory (which was exclusively carotid during embryo development), with consequent atrophy of the internal carotid arteries. As shown by De Vriese [3], the capybara has type III encephalic irrigation in which the vertebro-basilar system is the only source of cerebral irrigation, althoug during ontogenesis types I and II are present before becoming type III.

In all specimens, the vertebral arteries anastomosed to form a thick basilar artery. According to Tandler [8], the vertebral arteries are well-developed in all rodents and essential for brain irrigation, except for *Pedetes caffer*, in which these

arteries are rudimentary [3], a situation explained by the fact that this animal has a type II irrigation. In *Mus rattus*, the vertebral arteries are thicker than the internal carotid arteries, and in *Hystrix cristata, Lagostomus, Arctomys, Myoxus, Sciurus, C. cobaya* and *C. aguti*, the vertebral arteries are well-developed [3].Thus, the vertebral encephalic arterial system dominates the carotid system in rodents. Bugge [1] found that in *H. cristata, H. leucura, C. laniger, M. coypu, O. degus, T. swinderianus, B. suillus, C. natalensis* and *H. glaber*, the brain is supplied only by the vertebral arteries, while in *C. porcellus, D. patagona* and *D. agutii*, the brain is also supplied by the vertebral arteries, but there is a rudimentary internal carotid artery in these animals.

De Vriese [3] noted that the internal carotid artery is well-developed in the rat embryo, being divided into a cranial branch and a caudal branch, as in lower vertebrates. At the beginning of development, the vertebral arteries do not exist but they appear later and anastomose with the caudal terminal branch of the internal carotid artery. In adults, the branches of the basilar artery join the carotid trunk. There is then progressive atrophy of the posterior carotid cerebral system and secondary, progressive development of the vertebral system.

The internal carotid artery is absent in the adult guinea-pig, but is well-developed in the embryo. Considering the arrangement of the cerebral arteries in lower vertebrates, in which the circle of Willis is formed exclusively by internal carotid arteries connected caudally to a rudimentary vertebral arterial system, it is assumed that of the arteries which supply blood to the encephalon, the most ancient arteries are the internal carotid arteries. Compared to the carotid arteries, the vertebral arteries are a more recent development in brain irrigation. Thus, among rodents, the capybara is phylogenetically more evolved, in terms of brain irrigation. However, this does not mean that it is better adapted than animals with carotid or carotid-vertebro-basilar irrigation.

In several rodent families, there is total or partial atrophy of the internal carotid artery associated with a strong mandible adapted to a modified temporal-mandibular joint with caudal-rostral movements and extremely well-developed muscles. In artiodactyls, the internal carotid artery forms a plexus or network associated with other facial vessels, and a brain carotid artery projects from this plexus. In ruminants, the mandible is also modified and adapted for the strong lateral movements of rumination. We speculate that the proximity of the route of the internal carotid artery to the deep chewing muscle movement during nibbling and ruminating could subject these primitive internal carotid arteries to frequent compressions, thereby impairing blood irrigation to the brain. As a result the vertebral system started to invade this area to compensate for a reduced brain irrigation in these rodents, whereas in artiodactyls, an alternative vascular network was developed. While attempting to explain this situation, Tandler [8] drew attention to the presence of a large *bulla tympanica* in rodents, which is even more developed in artiodactyls. Assuming that the *bulla tympanica* would be an obstruction to the path of the internal carotid artery in rodents, this obstruction would be even greater in artiodactyls. However, the latter do not have the vertebral system which aids encephalic irrigation.

According to Tandler [8] and De Vriese [3], the basilar artery is formed by the anastomosis of the vertebral arteries and subsequently bifucartes at the level of the pons into terminal branches known as the posterior communicating arteries. However, in *Sciurus, C. cobaya* and *C. aguti* [3], and in guinea pigs [7], only the basilar artery bifurcation into two branches is mentioned.

The caudal cerebral arteries are also known as the posterior cerebral arteries [3,7,8]. Tandler [8] and De Vriese [3] mentioned that these arteries are branches of the posterior communicating artery in *Arctomys*. Tandler [8] described the posterior cerebral arteries in *C. cobaya, Sciurus vulgaris, S. aureogaster* and *S. americanus* as branches of the posterior communicating artery. According to De Vriese [3], the posterior cerebral arteries in *H. cristata, Lagostomus* and *Myoxus* are branches of the posterior communicating artery, whereas in *Sciurus, C. cobaya* and *C. aguti*, they are branches of the terminal branches of the basilar artery, as also shown here. According to De Vriese [3], the posterior cerebral artery belongs morphologically to the carotid group, and also belongs to the vertebral domain because of the sequence of secondary vascular changes, which occurs in most rodents.

In the capybara, there was a complete and extreme progression of the vertebro-basilar system which, in the adult, incorporated the carotid system, to the point of completely eliminating its source (the internal carotid arteries). During this incorporation, the caudal terminal branches of the internal carotid arteries merged completely with the left and right terminal branches of the basilar artery, from which the caudal cerebral arteries currently derive. The rostral branches of the internal carotid arteries were integrated rostrally in this fusion, and their only vestige was the slight curve of the trunk which gave rise to the rostral and middle cerebral arteries, from which the internal ophthalmic artery also derived. The internal carotid arteries typically arrived at this point, lateral to the tuber cinereo and the hypophysis. Indeed, this trunk was nothing more than the rostral branch of these arteries, which represented the end of the basilar artery. With regard to the ontogeny of type III animals, it remains to be determined at which stage of embryonic development in the capybara these changes are completed, or whether they occur after birth.

According to Tandler [8], the (internal) ophthalmic artery varies in its origin. This vessel arise from the internal carotid artery, before the emergence of the cerebral arteries, at exactly the point where the internal carotid arteries split into cerebral arteries, or it may originate from the anterior branch of the internal carotid artery. In *Sciurus*, this vessel emerges from the origin of the middle cerebral artery, whereas in *C. cobaya* it is a branch of the posterior communicating artery [8]. The middle cerebral artery in *C. cobaya* is derived from the common trunk of the cerebral arteries, whereas in *S. vulgaris, S. aureogaster, S. americanus* and *Arctomys marmota*, it emerges from the posterior communicating artery [8]. However, De Vriese [3] stated that in *H. cristata, Lagostomus, Arctomys* and *Myoxus*, the middle cerebral artery derived from the posterior communicating artery, whereas in *Sciurus, C. cobaya* and *C. aguti*, it is projected from a branch of the basilar artery bifurcation, a conclusion consistent with our findings.

Tandler [8] referred to the rostral cerebral artery as the corpus callosum artery or anterior cerebral artery. He also mentioned that in *S. vulgaris, S. aureogaster, S. americanus* and *A. marmota* the corpus callosum arteries were the final branches of each posterior communicating artery, which merged to form the arterial circle. In *C. cobaya*, the anterior cerebral arteries derived from the common trunk of the posterior communicating artery and eventually formed a closed arterial circle. According to De Vriese [3], in *H. cristata, Lagostomus, Arctomys* and *Myoxus*, the anterior cerebral arteries were the ends of the posterior communicating arteries, which were joined by an anterior communicating artery. In *Sciurus, C. cobaya* and *C. aguti*, these anterior cerebral arteries were the ends of the branches derived from the bifurcation of the basilar artery which merged to form a single median artery. Morphologically, in all mammals, the anterior cerebral arteries are anastomosed to form a single median artery, or are united by one or more transversal arteries. During the initial stages of ontogeny in the rabbit, both anterior cerebral arteries run ventrally and in parallel to the forebrain, with no intercommunications. These arteries are later interlinked by an arterial network to form an anterior communicating artery. This network becomes one or more transversal arteries and, eventually, a single median artery appears, as in capybaras. De Vriese [3] questioned wether these rostral communicating arteries, the transversal vessels or the single median vessels mean a higher or lower degree of evolution.

At the site of origin of the internal ophthalmic artery in *S. americanus* and S. *aureogaster*, there is a vessel which continues caudally, passing through the rotundum foramen, to anastomose with the maxillary artery [8], whereas in *A. marmota* and *C. cobaya*, as well as in our findings, the internal ophthalmic artery anastomoses with the maxillary artery. Based on our observations, we infer that in capybara the anastomosis of the internal ophthalmic artery with the maxillary artery is possibly a source of compensation. In the case of a vascular accident causing partial interruption of the blood supply via the vertebro-basilar system, blood flow via the maxillary artery may compensate for the reduced flow towards the arterial circle. Although we observed the anastomosis mentioned above in all specimens, blood flow would obviously not be directed towards the arterial circle, but towards the internal ophthalmic artery. This assertion is based

on the fact that the anastomosis is thinner than the vessels coming from the vertebro-basilar system. However, this situation could be reversed if there was an interruption of the blood flow in a terminal branch of the basilar artery, which would cause a progressive increase in the width of the anastomosis, thus allowing blood to reach the circle via the maxillary artery.

According to Tandler [8], the arterial circle is always closed in rodents, and possibly in all mammals. This is not consistent with our results, as we found an open arterial circle in 10% of the specimens examined. We conclude that the number of specimens used by Tandler [8] was not sufficient to provide a true indication of the patterns and asymmetries of this vessel system.

As shown here, the cerebral circulation of the capybara originated solely from the vertebro-basilar system which gave rise to all of the arteries that irrigated the encephalon. This organization is typical of the type III irrigation of De Vriese's classification. The arterial circle was formed by the terminal basilar rami and was closed rostrally in 90% of the cases and open in only 10%.

Type I irrigation occurs in fish, reptiles and birds. Campos *et al.* [2] claimed that the arteries that supply the brain of *Gallus gallus* arose from branches from the right and left cerebral carotid arteries, i.e., the carotid systems in all specimens studied. These arteries left the carotid canal and projected ventro-caudally to the hypophysis where they were interconnected transversally by a rather large vessel which formed an intercarotid anastomosis. The absence of a communication between the two rostral cerebral arteries in this species means there is no arterial circle as found in mammals. The caudal ramus of the right and left cerebral carotid arteries runs caudally and forms the basilar artery which then decreases in calibre. Interestingly, the intercarotid anastomosis is stable and thick, and supplies blood to the entire carotid system. Such an anastomosis thus provides a perfect substitute for the arterial circle in *Gallus gallus*.

Voris [8] and Gillilan [4], in describing the type II encephalic irrigation of *Didelphis virginiana*, indicated that the blood supply to the brain was shared by the carotid and the vertebro-basilar systems. However, they disagreed on the limits of these two systems. For Voris [9], the caudal cerebral artery belonged to the carotid system, whereas Gillilan [4] stated that this vessel was already incorporated in the vertebro-basilar system.

Lindemann *et al.* [5] showed that in *Didelphis albiventris* the carotic system formed by the right and left internal carotid arteries contributed most to the encephalic irrigation compared to the vertebro-basilar system, since the former reached the caudal cerebral artery [9]. This author also stated that the arterial circle was closed rostrally in 96.7% of the brains and open in only 3.3%. According to Voris [9] and Gillilan [4], the arterial circle is open in all cases. This division between the two systems classifies these species as having the type II irrigation of De Vriese's classification [3].

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