Functional morphology of the cranial Retia mirabilia in the domestic mammals

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Introduction

Arterial retia mirabilia are fascinating structures that are known for more than 2000 years, since *Herophilus* (ca. 300 B.C.) described the rete mirabile that lies underneath the brain of the sheep. In the subsequent centuries, these vascular networks have been studied extensively by numerous famous anatomists such as *Galen, Leonardo da Vinci, Andreas Vesalius, Thomas Willis* and *John Hunter,* and to this day they have attracted the attention of many researchers. A review of the literature on this subject is given by *Legait* (1947), *Martinez* (1967) and *De Gutierrez-Mahoney and Schechter* (1972). However, many morphologic and functional characteristics of the retia mirabilia are still unclear or speculative.

In the present study, the location and the shape of the different cranial arterial retia mirabilia in the domestic mammalian species will be described, using the updated official terminology (*Simoens et al.,* 1979; Nomina Anatomica Veterinaria, 1983). In the discussion, a survey will be given of the various physiological functions assigned to these structures.

Material and Methods

The findings presented here result from the study of 5 horses, 10 ruminants (6 sheep, 2 goats and 2 oxen), 20 pigs, 5 dogs and 5 cats.

Corrosion casts of the cranial blood vessels were produced by injecting these vessels with different plastics based on methylmethacrylate. The commercially available plastics used, were: TECHNOVIT 7001 *(Kulzer & Co, Bad Homburg, BRD),* BATSON'S # 17 *(Polysciences Inc., Warrington, USA),* ARALDITE CY 223 *(Ciba-Geigy N.V., Dilbeek, Belgium)* and MERCOX *(Okenshoji Comp., Tokyo, Japan).* After setting of the resin, the specimens were macerated in a 20% KOH solution and subsequently in a 25% HCl solution. The vascular casts were then rinsed in destilled water, air-dried and appropriately dissected, whereafter they were studied macroscopically, stereomicroscopically and with the scanning electron microscope. For the latter procedure, the specimens were gold-sputtered and mounted on aluminum holders by conductive copper paint.

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[2] Dedicated to Prof. Dr. W. Mosimann at the occasion of his 65th birthday.

Morphological Results

Definition and general shape (fig. 1)

Arterial retia mirabilia are compact vascular networks which consist of numerous interanastomosing arteries that lie on the trajectory of certain arteries. They form well-defined clusters of closely intertwined vessels, and thereby they differ from the arterial networks (retia arteriosa) which are less dense, more variable in size and much more common.

In some cranial retia mirabilia, the parent artery has completely ramified at the level of the network, whereafter its branches converge again into a major artery that then splits up into arterioles and capillaries. This type of rete mirabile is called *bipolar*

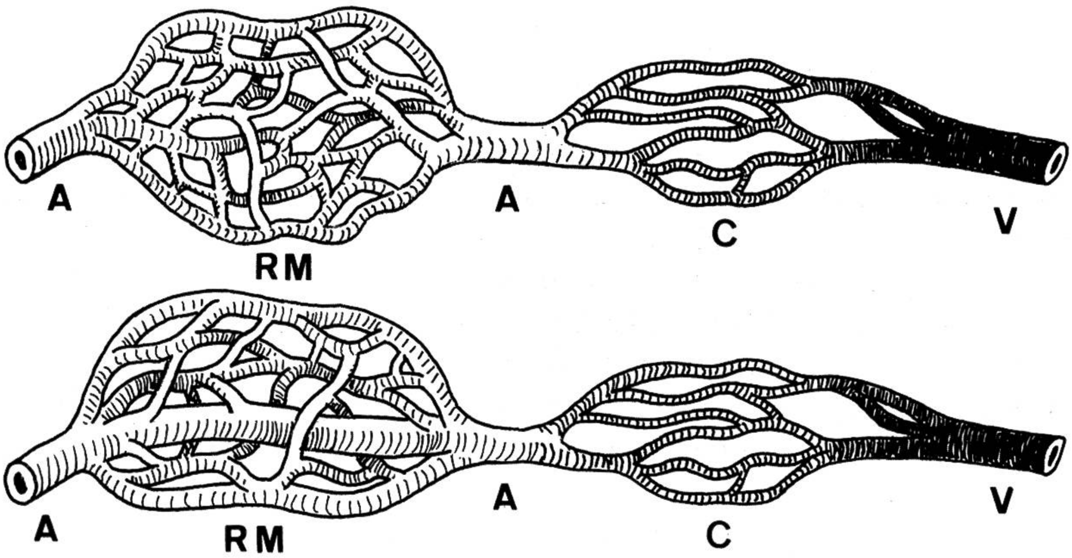


Fig. 1 Schematic drawing of the bipolar *(top)* and fascicular *(bottom)* types of retia mirabilia. The rete mirabile (RM) lies on the trajectory of an artery (A) which, beyond the rete, gives rise to capillaries (C) that unite again into veins (V)

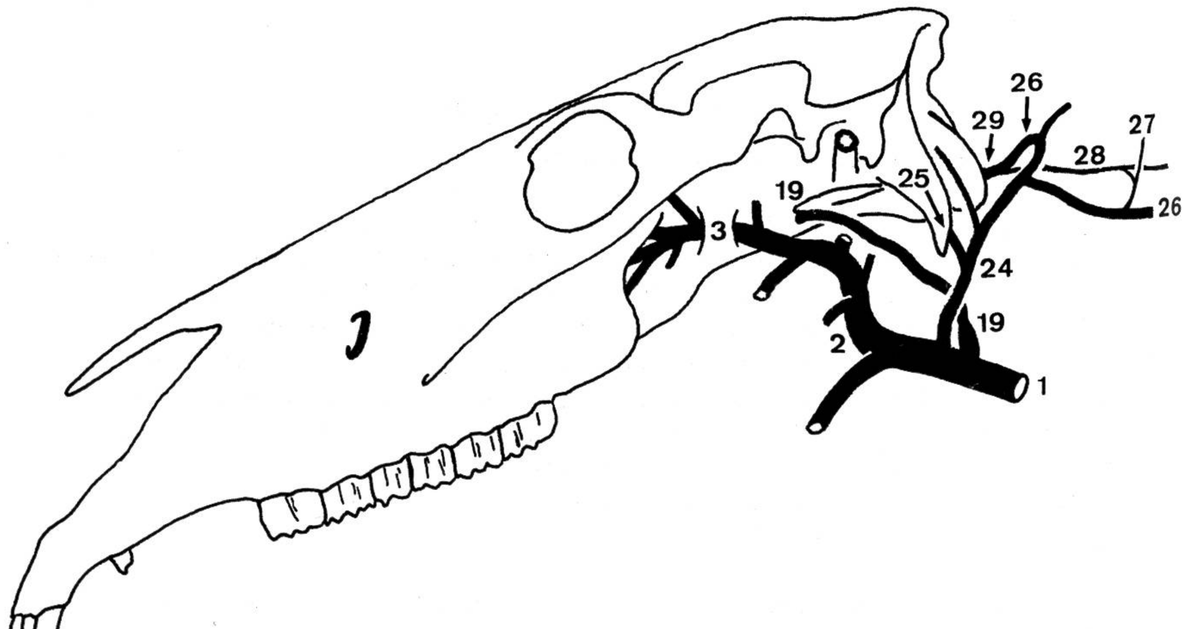


Fig. 2 Half-schematic drawing of the major arteries to the brain in the horse (left lateral view) (An index of the numbers used in all figures is listed at the end of the article)

because a large artery is present at the two poles of the network. In other cases, the parent artery continues through the center of the rete mirabile and thus it is encircled by a bundle of vessels. This type of rete mirabile is called *fascicular.*

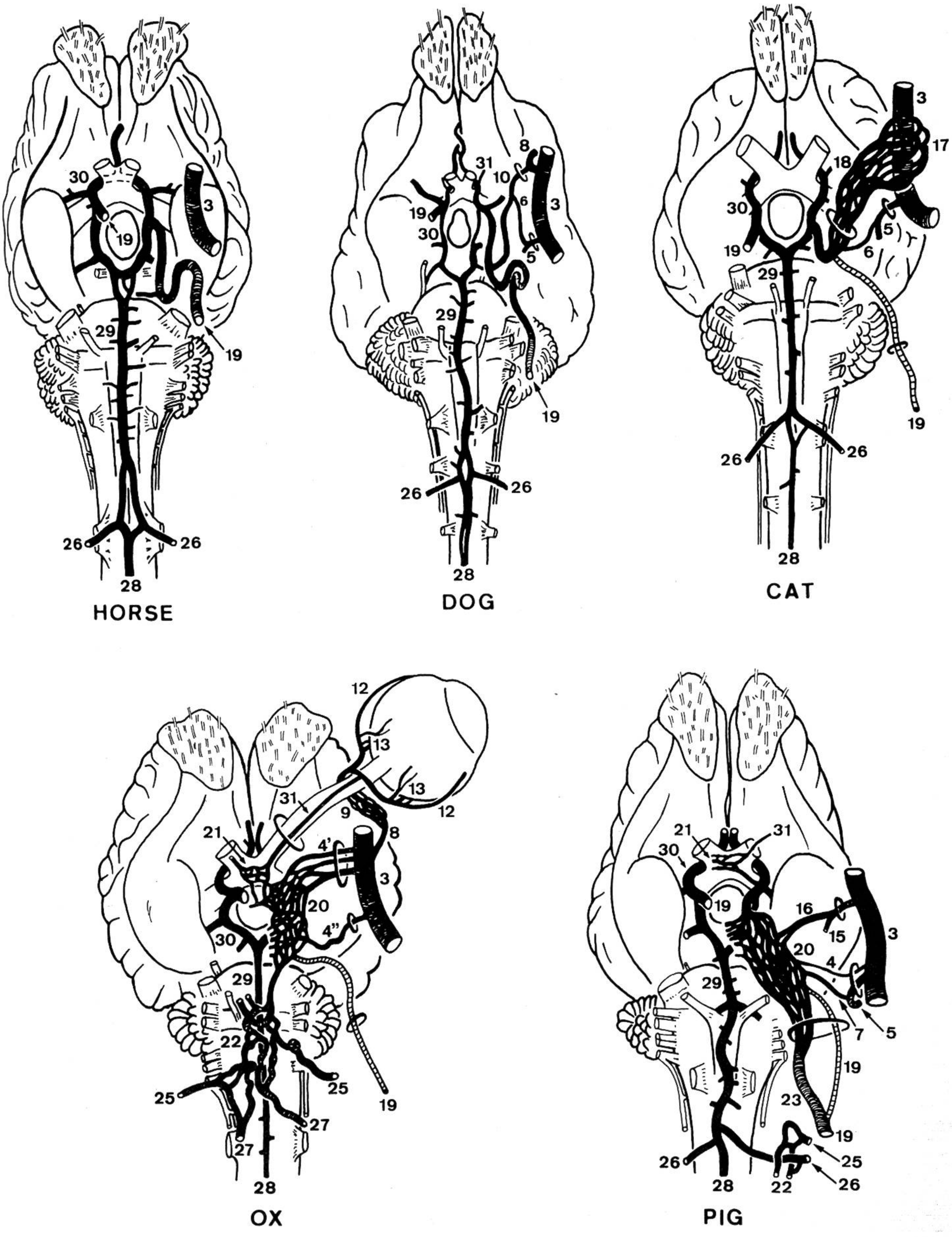


Fig. 3 Major arteries to the brain in the various species of domestic mammals (ventral view)

Position

In the heads of the various domestic mammals, arterial retia mirabilia are located along the course of certain major arteries to the brain and along some ocular arteries.

A. Retia mirabilia associated with arteries to the brain (figs. 2–9)

In general, the arterial blood to the brain is supplied by the unpaired basilar artery and the left and right internal carotid arteries. These three arteries form the cerebral arterial circle at the basal surface of the brain. The median basilar artery passes through the foramen magnum and is formed by the confluence of both vertebral arteries and the ventral spinal artery. The internal carotid arteries are the first major terminal branches of the common carotid arteries. The other terminal branches of the latter are the external carotid arteries which continue into the maxillary arteries and send primarily no branches to the brain.

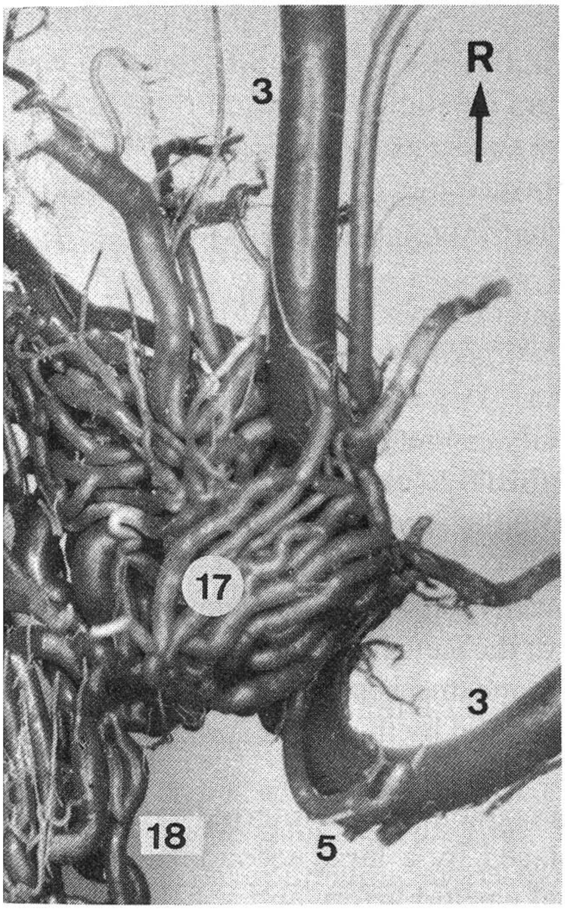
In many species, however, the extracranial segments of the internal carotid arteries regress and their intracranial sections are connected with large arterial retia mirabilia that are supplied by anastomotic branches of the maxillary arteries.

In the horse (figs. 2, 3), the general pattern is still present. The cerebral arterial circle is supplied by the basilar and internal carotid arteries, while the maxillary artery does not contribute to the brain vascularization.

In the dog (fig. 3), the internal carotid artery is sharply convoluted at the external carotid foramen. It receives a slender intracranial anastomosis that is formed by two small branches of the middle meningeal and the external ophthalmic arteries. These arteries are given off by the maxillary artery. The middle meningeal artery enters the skull via the foramen ovale, and the anastomotic branch of the external ophthalmic artery penetrates the fissura orbitalis. The arterial branches forming the intracranial anastomosis between the internal carotid and the maxillary arteries are sometimes tortuous and multiple. In these cases a rete arteriosum is formed that was correctly identified by *Jewell* (1952) as an arterial rete, whereas *Daniel et al.* (1953) and *Baker and Chapman* (1977) considered it as a rudimentary rete mirabile. However, this network is always very loose and therefore it should not be called a rete mirabile. Its occasional presence is nevertheless very interesting from a comparative point of view, because the corresponding vessels do indeed form a compact rete mirabile in other species.

In the cat (figs. 3, 4), the extracranial segment of the internal carotid artery obliterates and becomes vestigial. The intracranial section of the internal carotid artery, which enters the cerebral arterial circle, receives its blood through anastomoses with the

Fig. 4 Ventromedial view of the left Rete mirabile arteriae maxillaris of the cat (Corrosion cast, × 5)
Fig. 5 Ventral view of the cranial retia mirabilia of a neonatal calf (Corrosion cast, × 0.95)
Fig. 6 Ventral view of the cranial retia mirabilia of a fetal pig (Corrosion cast, × 5)
Fig. 7 Medial view of the left Rete mirabile epidurale caudale of the pig (Corrosion cast, × 4.5)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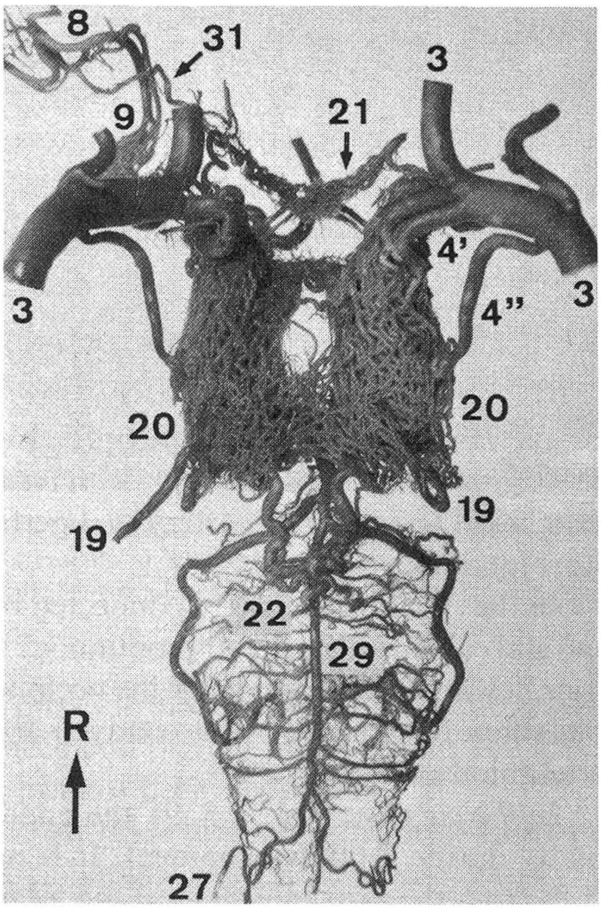
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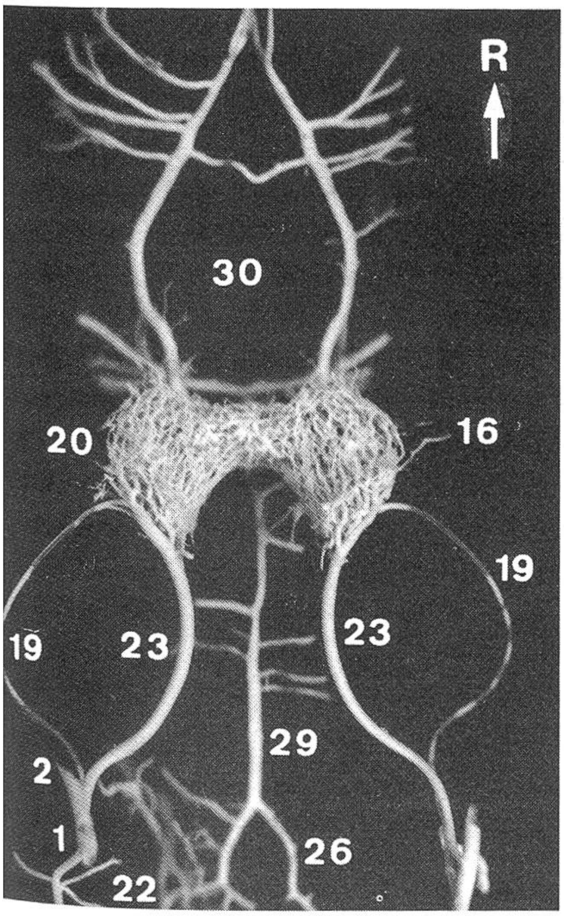
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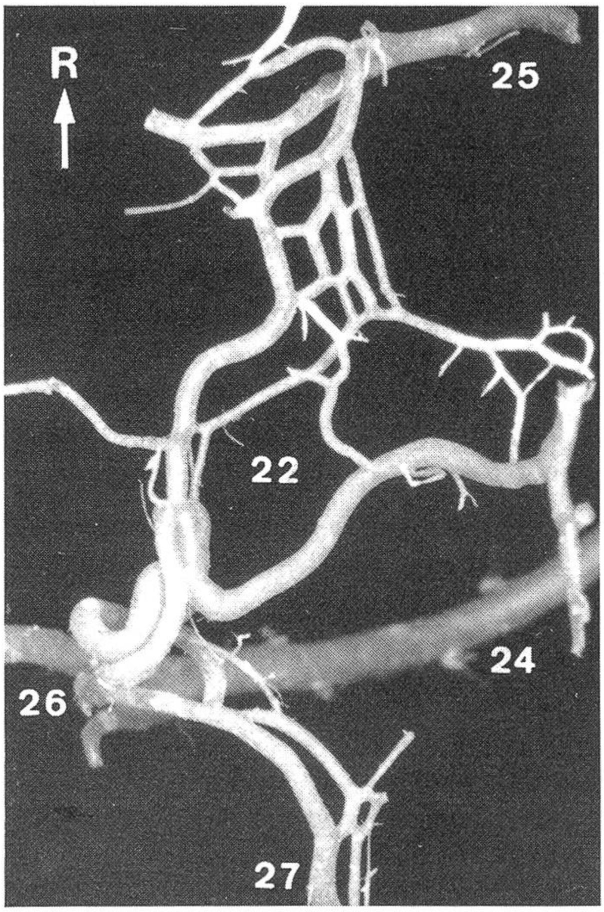
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maxillary artery. The latter is surrounded by a compact Rete mirabile a. maxillaris that lies extracranially. This rete is connected with the internal carotid artery via large and plexiform Rami retis that penetrate the fissura orbitalis. The Rami retis and the Rete mirabile lie inside the large venous cavernous sinus and the pterygoid plexus, respectively. An additional slender anastomosis is formed between the internal carotid artery and the middle meningeal artery which, like in the dog, enters the cranial cavity via the foramen ovale.

In the ruminants (figs. 3, 5), the extracranial segment of the internal carotid artery regresses as in the cat, and the intracranial portion of the internal carotid artery also receives its blood from the maxillary artery via a large rete mirabile. Unlike in the cat, however, this arterial network lies intracranially inside the cavernous sinus and is called the Rete mirabile epidurale rostrale. It is supplied by a caudal branch and several rostral branches of the maxillary artery that perforate the foramen ovale and the foramen orbitorotundum, respectively.

In the ox, this network is connected rostrally with the Rete chiasmaticum (see below) and caudally it is directly continuous with the Rete mirabile epidurale caudale. The latter lies at the basilar part of the occipital bone and is surrounded by the basilar venous sinus. It is formed by the condylar arteries and by the major spinal branches of the vertebral arteries.

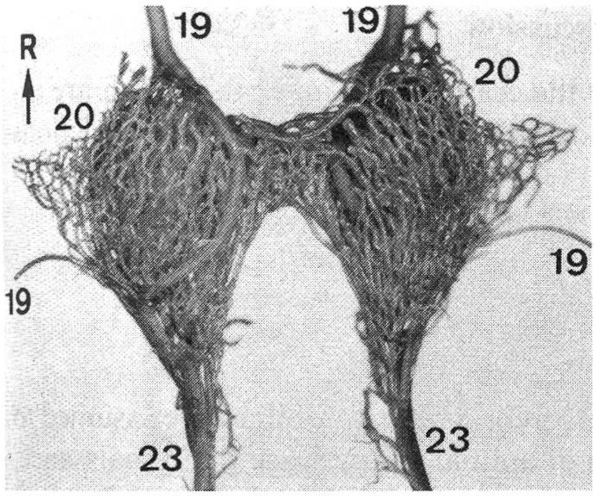
In the pig (figs. 3, 6, 7, 8, 9), the middle segment of the internal carotid artery regresses during fetal development. It is replaced by a large secondary branch which arises from the proximal stem of the internal carotid artery and splits up into a large Rete mirabile epidurale rostrale that lies at the foramen lacerum. This rete gives rise to the intracranial segment of the internal carotid artery and is located inside the plexiform sinus cavernosus, lying mostly intracranially and partly outside the cranial cavity. It receives additional but variable anastomoses from the maxillary artery. An inconstant slender anastomotic branch arises directly from the maxillary artery and penetrates the incisura ovalis, an often double branch is given off by the middle meningeal artery which enters the skull via the incisura spinosa, and one or more anastomotic branches arise from the rostral meningeal artery which enters the cranial cavity through the foramen orbitorotundum.

The pig possesses also a Rete mirabile epidurale caudale that has no direct connections with the rostral rete and lies at the level of the atlas. It is formed bilaterally by the condylar artery, the vertebral artery and its rostralmost Ramus spinalis. However, this caudal network is loose and has wide meshes, and therefore it is more a rete arteriosum rather than a rete mirabile.

B. Retia mirabilia associated with ocular arteries (figs. 3, 5, 10–13).

In the domestic ruminants and the pig, retia mirabilia can be found on three locations along certain arteries to the eye.

The *Rete chiasmaticum* (figs. 3, 5, 10, 11) forms an intracranial connection between the left and right internal ophthalmic arteries. It lies at the optic chiasma inside the rostral intercavernous sinus in the ox and inside the interophthalmic sinus in the pig. In the

8 

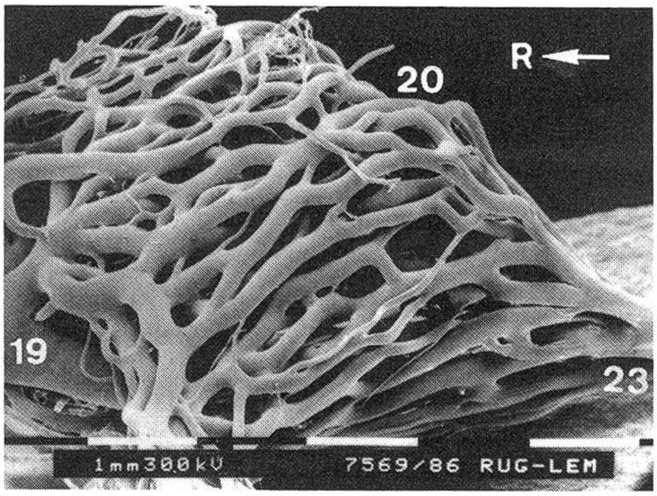
 9

Fig. 8 Dorsal view of both Retia mirabilia epiduralia rostralia of a fetal pig (Corrosion cast, × 6). The left rete has been partially dissected to show its fascicular arrangement
Fig. 9 Medial view of the right Rete mirabile epidurale rostrale of a fetal pig (Scanning electron microscopic picture of a corrosion cast, × 10)

ox it is large and compact, forming a true rete mirabile that has direct connections with the Rete mirabile epidurale rostrale. In the sheep and pig, it is much looser and it is a mere rete arteriosum, whereas in the goat it has not been observed.

The *Rete mirabile ophthalmicum* (figs. 3, 5, 10, 12) is located in the orbit along the course of the external ophthalmic artery in the ruminants. This rete is absent in the pig, although in some swine the external ophthalmic artery is locally accompanied by a few collateral branches which form a small and loose network.

Small *bulbar retia* (figs. 10, 13) are also present in the eyeball of the ruminants and the pig. They are situated at the origin of the short posterior ciliary arteries which arise from the long posterior ciliary arteries. These networks are variable in size and compactness, ranging from loose retia arteriosa to dense retia mirabilia.

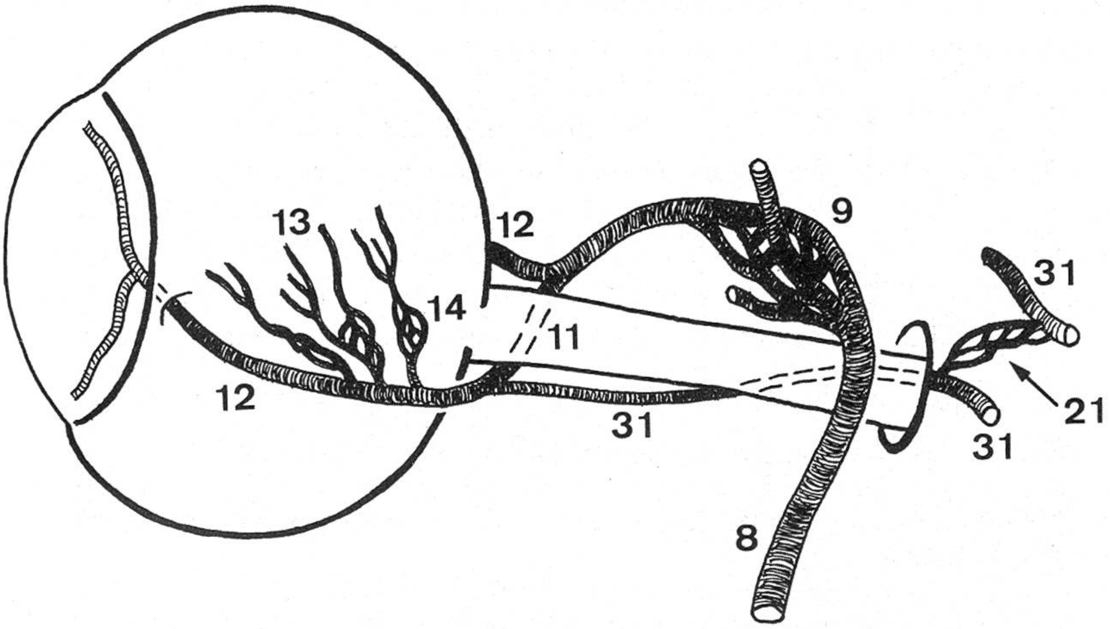


Fig. 10 Schematic drawing of the retia mirabilia associated with ocular arteries

Functional discussion

Several functions have been attributed to the cranial retia mirabilia which are associated with the arteries to the brain. The most important of these various functions will be discussed here.

Historical

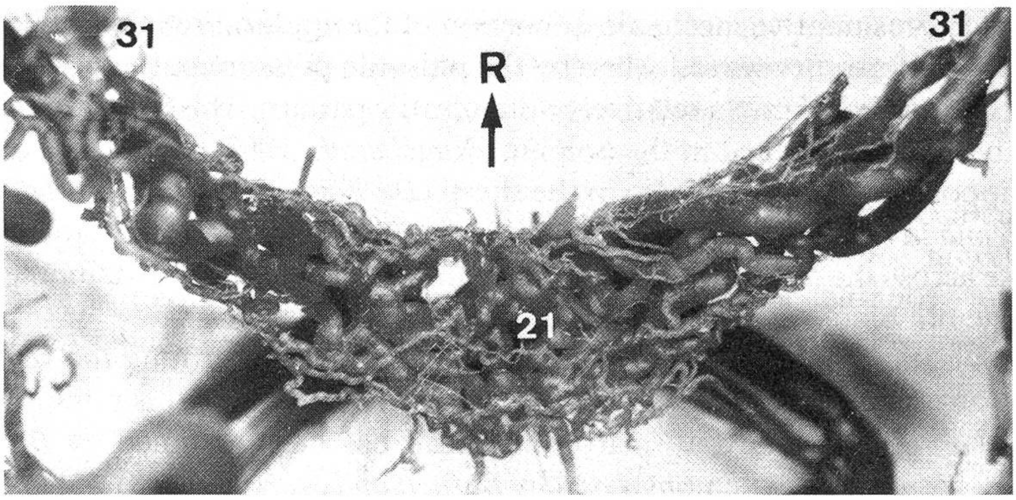
In the antique Galenic medical system, the cerebral retia mirabilia were assumed to transform the vital spirit into the higher form of animal spirit. Since the Renaissance, however, they were credited with a hydrodynamic role in retarding the blood flow and maintaining a smooth continuous blood supply to the brain (*Legait,* 1947; *De Gutierrez-Mahoney and Schechter,* 1972). In recent times, these mechanical functions are more precisely studied, defined and understood.

Mechanical

Many authors agree that the retia mirabilia offer a resistance to the blood stream, altering the hemodynamics of the blood reaching the brain. This vascular resistance is caused by the numerous small luminal diameters of the retial vessels, and can be increased by the narrowing effect of endothelial cushions which are observed in the ox and sheep (*De Boissezon,* 1941; *Legait,* 1947; *Uehara et al.,* 1978; *Khamas et al.,* 1984).

The retial vessels have also autoregulatory features as they dilate in response to systemic hypotension, arterial hypercapnia and isocapnic hypoxia (*Edelman et al.,* 1972; *Du Boulay et al.,* 1975). They also dilate in reaction to intravascular infusion of isopropylnoradrenaline (isoproterenol) and constrict when noradrenaline is injected (*Edelman et al.,* 1972), although the effects of adrenergic stimulation *in vitro* are negligible (*Dieguez et al.,* 1983: cited by *Ghoshal,* 1985). These observations were made by studying the Rete mirabile epidurale rostrale of the goat, and they may be correlated with the presence of epithelioid cells and an abundant innervation of the same rete in the sheep and ox, respectively (*De Boissezon,* 1941; *Legait,* 1947; *Khamas et al.,* 1984; *Ghoshal,* 1985). All these data suggest that the retial vasculature may regulate the cerebral blood flow, monitored by chemical, hormonal and neural factors.

Fig. 11 Ventral view of the rete chiasmaticum of the ox (Corrosion cast, × 6)
Fig. 12 Dorsal view of the left Rete mirabile ophthalmicum of the ox. The supraorbital artery (*) forms the direct continuation of the initial segment of the external ophthalmic artery beyond the rete (Corrosion cast, × 4.5)
Fig. 13 Caudolateral view of the choroidal vasculature at the lateral meridian of the left eye in the pig. The Retia bulbi are located on the trajectory of the short posterior ciliary arteries and are indicated by arrowheads (Scanning electron microscopic picture of a corrosion cast, × 18)



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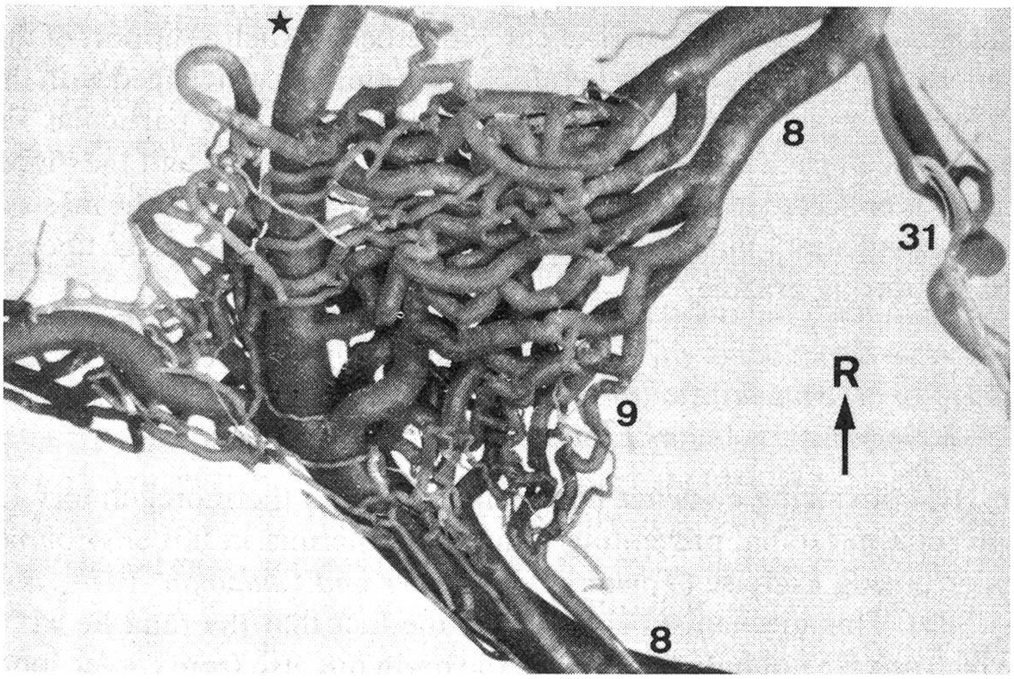

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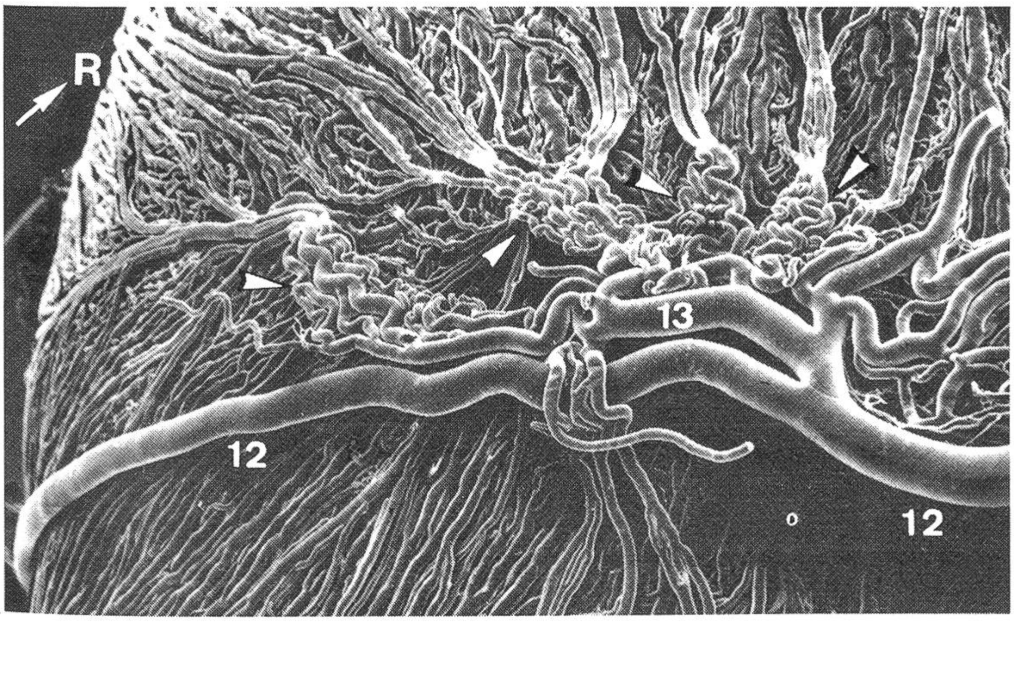

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Another presumptive mechanical function of the epidural retia mirabilia is damping the arterial pressure waves, whereby the pulsatile pressure pattern of the systemic arteries is transformed into a relatively nonpulsatile pattern. This pressure-damping effect has been demonstrated in the dolphin (*Nagel et al.,* 1968; *McFarland et al.,* 1979) and is supposed to be present also in the sheep (*De Boissezon,* 1941). In the goat, however, *Edelmann et al.* (1972) have found little damping in the transmission of the pressure pulse across the rete under ordinary conditions, although some damping did occur when systemic blood pressure reached hypertensive levels.

The pulsations of the retial arteries may also assist in returning the venous blood from the surrounding venous sinuses or plexuses. In the sheep, this pump-activity enhancing the venous blood return from the head has been assumed by *De Boissezon* (1941) and has later been demonstrated by *Barnett and Marsden* (1961). However, *Taylor* (1966) reasons that the lack of intravenous valves in close proximity to these venous spaces makes such a pump quite inefficient. Nonetheless, such a support of the return of cranial venous blood would be very helpful for the animals which feed with the head dependent (*Barnett and Marsden,* 1961). It may also explain the particular vascular arrangement in the horse where cranial retia mirabilia are absent and the blood from the cranial cavity is collected into venous sinuses which lie underneath the masseter muscle, whereby the masticatory muscle contractions apply a similar massage upon the cranial venous blood during grazing.

Thermoregulatory

Recently, convincing evidence has been given for a thermoregulatory function of the cranial retia mirabilia, preventing brain hyperthermia in hot environmental temperatures or during exercise (*Taylor,* 1966; *Baker and Chapman,* 1977; *Baker,* 1979; *Ghoshal,* 1985). This mechanism is based on the fact that the retia lie within venous sinuses which receive not only blood from the brain but also from cooler superficial cutaneous and mucosal areas such as the horns, mouth and nose (*Gillilan,* 1974; *Uehara et al.,* 1978; *Baker,* 1979). The veins in the horns are cooled by the ambient air, as *Taylor* (1966) has demonstrated in the goat, while the oral and nasal mucosal veins are cooled by panting during heat stress (*Baker,* 1979).

Heat can be transfered from the warm arterial blood in the retia mirabilia to the surrounding colder venous blood, whereby the afferent cerebral blood is cooled and the brain is protected from getting too warm (*Baker,* 1979). This heat exchange between the arterial retia mirabilia and the venous sinuses is quite efficient because of the considerable contact surface between the arterial and venous system and the countercurrent blood flow in the two systems (*Carlton and McKean,* 1977).

Baker and Chapman (1977) have demonstrated that dogs also have a similar brain-cooling which apparently occurs at the level of the arterial network formed by the anastomoses between the internal carotid and maxillary arteries. This network corresponds with the more complex retia mirabilia that are associated with the brain arteries in other species, in which higher rates of brain cooling can occur.

Such a vascular thermoregulation is impossible in the horse because cranial retia mirabilia are lacking in the equine species. In this animal, however, profound cooling of the body may occur by profuse sweating, a phenomenon that is lacking in the other domestic animals which have cranial retia mirabilia.

The physiological meaning of the retia mirabilia associated with the ocular arteries in mammals is scarcely studied in the literature. There is some evidence, however, that they also have a thermoregulatory function similar to that of the above-mentioned cranial retia mirabilia.

In the sheep, *Ohale and Ghoshal* (1982) found indications suggesting that the arterial blood to the retina is cooled by passing through the Rete mirabile ophthalmicum. In this rete, heat is transfered to the surrounding ophthalmic venous plexus which contains cooled blood draining from the nasal area. *Carlton and McKean* (1977) ascribe the same role to the orbital retia mirabilia in some wild ruminants.

According to the latter authors, the orbital retia could also interfere with the thermoregulation of the brain, because they lie inside the ophthalmic venous plexus which discharges into the cavernous sinus. Consequently, the arterial network could warm the orbital venous plexus before this blood reaches the cavernous sinus. So, during cold stress, the ocular retia could moderate the dumping of very cold venous blood into the intracranial sinus and thus prevent extreme brain hypothermia.

A different mechanism of thermoregulation of the brain has been demonstrated in the birds which have a Rete mirabile ophthalmicum. This avian rete is surrounded by a venous plexus containing blood returning from the evaporative surfaces of the head, and forms an important collateral circulation for the intracranial arterial system. It acts as a vascular heat exchanger by which brain temperatures are maintained below body temperature (*Kilgore et al.,* 1979). It exchanges not only heat with the surrounding venous plexus but also blood gases, increasing the level of oxygen and decreasing the amount of carbon dioxide in the arterial blood to the avian brain (*Bernstein et al.,* 1984). There is no evidence that these special functions of the avian Rete mirabile ophthalmicum occur also in the mammals, which have a quite different arrangement of the cranial vasculature.

A final paragraph should be dedicated here to the human retia mirabilia. Although for many centuries it was thought that man has cerebral retia mirabilia, *Vesalius* and many scientists after him have demonstrated that these structures are absent in the human species (*Legait,* 1947; *Du Boulay et al.,* 1975; *McFarland et al.,* 1979).

However, in recent times the term Rete mirabile has been used again in human medicine for indicating cerebral vascular networks seen radiographically along with congenital malformations or due to pathological alterations of the circulatory system. These vascular networks have some resemblance with the retia mirabilia of the lower species, but they have too important ontogenic and anatomical differences to be considered as true retia mirabilia (*De Gutierrez-Mahoney and Schechter,* 1972; *Picard et al.,* 1972; *Du Boulay et al.,* 1973).

Summary

The cranial retia mirabilia of the various domestic mammals are studied by means of vascular corrosion casts. A comparative anatomical description is given of these compact arterial networks which are associated with certain arteries to the brain and some arteries to the eyes. The various mechanical and the thermoregulatory functions attributed to these retia are discussed and commented.

Zusammenfassung

Die kranialen Wundernetze der Haussäugetiere sind anhand von Gefässabgüssen untersucht worden. Diese Retia mirabilia befinden sich im Verlauf von bestimmten Hauptarterien zum Gehirn und von einzelnen Augenarterien und sie werden vergleichend-anatomisch beschrieben. Die verschiedenen mechanischen und thermoregulierenden Funktionen, die man ihnen zuerkannt hat, werden diskutiert.

Résumé

Les réseaux admirables crâniens des mammifères domestiques ont été étudiés au moyen de moulages vasculaires. Une description anatomique comparative est donnée de ces réseaux artériels compacts qui sont localisés le long de certaines artères vers le cerveau et de quelques artères oculaires. Les diverses fonctions mécaniques et thermorégulatrices attribuées à ces retia mirabilia sont discutées.

Riassunto

Le reti mirabili craniali dei mammiferi domestici sono state studiate per mezzo di infiltrazioni vascolari. È data una descrizione anatomica comparativa di queste reti arteriose compatte. Esse sono localizzate lungo certe arterie verso il cervello e qualche arteria oculare. Le diverse funzioni meccaniche e termoregolatrici attribuite a queste reti mirabili sono discusse.

Literature

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Numbers used in the illustrations*

1. A. CAROTIS COMMUNIS
2. A. CAROTIS EXTERNA
3. A. MAXILLARIS
4. Ramus ad rete mirabile epidurale rostrale (su)
4.′ Rami rostrales ad rete mirabile epidurale rostrale (Ru)
4.″ Ramus caudalis ad rete mirabile epidurale rostrale (Ru)
5. A. meningea media
6. Ramus anastomoticus cum a. carotide interna (Car)
7. Ramus ad rete mirabile epidurale rostrale (su)
8. A. ophthalmica externa
9. Rete mirabile ophthalmicum (Ru)
10. Ramus anastomoticus cum a. carotide interna (ca)
11. Ramus anastomoticus cum a. ophthalmica interna
12. Aa. ciliares posteriores longae
13. Aa. ciliares posteriores breves
14. Retia bulbi (Ru, su)
15. A. meningea rostralis (su)
16. Ramus ad rete mirabile epidurale rostrale (su)
17. Rete mirabile a. maxillaris (fe)
18. Rami retis (fe)
19. A. CAROTIS INTERNA
20. Rete mirabile epidurale rostrale (Ru, su)
21. Rete chiasmaticum (bo, ov, su)
22. Rete mirabile epidurale caudale (bo, su)
23. Ramus ad rete mirabile epidurale rostrale (su)
24. A. occipitalis
25. A. condylaris
26. A. VERTEBRALIS
27. Rami spinales
28. A. spinalis ventralis
29. A. basilaris
30. CIRCULUS ARTERIOSUS CEREBRI
31. A. ophthalmica interna

* In all pictures the rostral direction is indicated by (R←)

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