THE ARTERIAL BLOOD SUPPLY TO THE BOVINE BRAIN

Thesis for the Degree of Ph.D.
MICHIGAN STATE UNIVERSITY

Yahya Z. Abdelbaki

1964

THESIS

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THE ARTERIAL BLOOD SUPPLY

TO THE BOVINE BRAIN

By

Yahya Z. Abdelbaki

AN ABSTRACT OF A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
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Department of Anatomy

1964

ABSTRACT

THE ARTERIAL BLOOD SUPPLY TO
THE BOVINE BRAIN

by Yahya Z. Abdelbaki

The arrangement of the arterial blood vessels that contribute to the cerebral circulation varies in different species of animals. The bovine brain is supplied mainly by branches of the external carotid, occipital and vertebral arteries. A well-developed arterial plexus, rete mirabile, exists between these vessels and the circle of Willis. The internal carotid artery is rudimentary or lacking. The existence of such a vascular plexus at the base of the brain has been described by early anatomists. Recently investigators agreed on the fact that more information is required from anatomical and physiological studies before a satisfactory explanation for the existence of this arterial plexus is forthcoming.

This work was an attempt to elucidate the normal anatomical structure and distribution of the vessels that supply blood to the bovine brain. In this study various anatomical techniques were utilized. Macroscopic dissections of the arterial supply were conducted on fifteen adult

female animals, eight male and two female calves, and ten male fetal specimens.

This part of the study revealed that in the adult animals arterial blood was supplied to the brain through the carotid and vertebral systems. The carotid system included the condyloid branch of the occipital artery, the middle meningeal artery and anastomotic branches of the internal maxillary artery. The vertebral artery contributed to the cerebral circulation by anastomotic connections with the condyloid and basilar arteries. Before reaching the cerebral vessels, carotid and vertebral blood passed through a massive plexus of arterial anastomoses, the rete mirabile. This structure was bathed in the venous blood of the dural cavernous sinus at the base of the cranial cavity. From the dorsal surface of the rete mirabile two arteries emerged and formed a circulus arteriosus from which the regular pattern of cerebral, cerebellar and medullary arteries originated.

The basilar artery originated from the posterior border of the circulus arteriosus and not from the confluence of the vertebral arteries of both sides as is described in man and other species of animals. The internal carotid artery was lacking in all the adult specimens examined.

Dissections of calves revealed only one major difference from the adult animals: the internal carotid artery was shown to be undergoing various degrees of atrophy in different specimens. The internal carotid artery was

complete and patent in all the fetal specimens examined. The vessel was embedded in the fibrocartilagenous wall of the tympanic bulla. The later ossification of the wall of the bulla around the vessel is believed to limit the further development of the artery.

Cerebral angiographic studies were conducted on four heifer calves. A simple inexpensive speed cassette changer was developed to take rapid serial angiographs. In three clinically normal calves there was no cross circulation of blood between the two sides of the brain. Most of the vessels demonstrated by macroscopic dissections could be identified on the arteriographs. One case of carotid spasm due to the injection of opaque substance was encountered.

Microscopic study of the retial vessels revealed that the arteries were thin walled. The wall had a well-developed tunica adventitia which was covered on the outside by a continuous layer of endothelial cells. The tunica media was composed mainly of smooth muscle fibers and had a poorly developed, incomplete external elastic membrane. The tunica intima was thin and had a well-developed internal elastic membrane.

Differences among different authors concerning the nomenclature of blood vessels leading to the rete mirabile were discussed.

Various theories concerning the function of the rete mirabile were presented, and it was concluded that further investigation is needed to explain the existence of such a structure in certain species.

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The author is grateful to Dr. Thomas W. Jenkins, Department of Anatomy, for his help and guidance throughout the whole course of this study. Many thanks are due to Dr. M. Lois Calhoun, Head of the Department of Anatomy, for her kind assistance and patience.

The author also wishes to thank Dr. R. W. Davis, Head of the Department of Anatomy at Colorado State University, for his permission to utilize the time and facilities of the department for the completion of this study. He extends his gratitude to all the members of the Department of Anatomy at Colorado State University who contributed to this work through their stimulating discussions.

Particular thanks are offered to Dr. William D. Carlson and Dr. J. P. Morgan for their permission to use the facilities of the Radiology Department at Colorado State University.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

From the brain only arise our pleasures, laughter and jests, as well as our sorrow, pains, griefs, and tears. I hold that the brain is the most powerful organ in the body. Eyes, ears, tongue, hands and feet act in accordance with the discrement of the brain.

--Hippocrates

Under normal conditions the human brain contains small quantities of blood estimated at 2 per cent of the total blood volume in the body. The mean blood flow of the brain is about 12 per cent of the cardiac output (Nylin et al. 1956). For proper functioning the needs of brain tissue are critical. It has been estimated that in certain brain areas 20 seconds of ischemia will lead to neuronal death, so a constant flow of blood must be maintained. The blood supply to the brain in all mammals is assured by the carotid and vertebro-basilar systems. Normally these arterial routes supply different cerebral areas, but the two systems are connected also by anastomoses. In case of obstruction of one of the principal vessels circulation may be re-established by the accessory pathways. In addition true terminal arteries are few in the brain, so collateral circulation can sometimes supply the area that is deprived of its primary blood supply.

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The anatomy of the blood vessels to the brain has been known long and is well established, but new significance has been attached to it since vascular disturbances in man have been blamed for cerebral softening, cerebral atrophy, diffuse myelinating disorders and cystic degenerations. These conditions were demonstrated in experimental animals by simulated anoxemia (Courville 1959).

Another major factor that stimulated new interest in the study of cerebral vessels has been the great progress made in neurosurgery and the gratifying results due to the diagnostic value of cerebral angiography. The technique is still hazardous and is open to improvement. Nevertheless, it is increasing our knowledge about the vascular pattern of the cranial cavity. In man structures could be seen for the first time. An example is a transcerebral venous system which traverses the white matter of the cerebral hemispheres, consisting of fine veins which follow the course of the corona radiata. Their function and direction of blood flow are still unknown, but they seem to connect the cortical vascular system and the internal cerebral veins (Kaplan 1959).

The interest in the anatomy of the cerebral circulation in man makes it desirable to study further the anatomy of the cerebral circulation in domestic animals. There are certain peculiarities connected with this part of the animal body that are worthy of investigation. Certain facts should be considered before making such a study. First, the brain is

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is contained within a rigid box, the cranium; if the blood volume increases, it can do so only at the expense of the volume of the nerve tissue, the cerebral fluid, or both. Secondly, the internal carotid artery in man has a tortuous intracranial course known as the carotid siphon. A similar loop is seen in the vertebral artery between the atlas and the foramen magnum. The curvatures here are thought to dampen the transmitted arterial pulse as the arteries approach the brain. This anatomical feature varies among animal species. The horse and the dog have curvatures similar to those found in man. The cat, ruminants and the pig have more specialized mazes of arterial plexuses called retia mirabilia related to the external carotid arteries. The rete mirabile is highly developed in those species of animals in which the internal carotid artery is undergoing degeneration (cat), or has already degenerated (ox, sheep, goat and pig). Furthermore, the author finds that whether situated extracranially (cat), or intracranially at the base of the brain (ruminants and pig), it lies within a venous sinus. Interestingly enough, it is found in mammals as diverse as artiodactyla and cetacea (Walmsley 1938). Finally, the author could not find reference in the literature to cases of spontaneous cerebral hemorrhage in those animals which possess a carotid rete mirabile.

The existence of such vascular plexuses, especially the one at the base of the brain, has been known since the structure was described by Herophilus (350-290 B.C.). It

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was described in man as well as in animals by many anatomists; but it was not until the Renaissance that its existence in man became a matter of dispute as indicated by the work of Vesalius (1538), Winston (1659) and Willis (1664). Since then the few contributors to the literature on the same subject agreed on the fact that much more information is required from comparative anatomical and physiological studies before a satisfactory explanation for the existence of this special arterial plexus is forthcoming.

This work was another attempt to elucidate the normal anatomical structure of the blood vessels supplying the bovine brain with the hope it would throw some light on the mystery of the existence of the rete mirabile in the ox.

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REVIEW OF THE LITERATURE

The earliest study of the brain is generally conceded to be recorded in the ancient Egyptian surgical papyrus which was written in the 17th century B. C. and studied by Edwin Smith (Breasted 1930). In this treatise the word "brain" was recorded for the first time in human language. A thousand years later, Alcmaeon (500 B.C.) discovered the optic nerve and showed some curiosity about the distribution of the vessels to the brain (Singer 1925). Singer also stated that in the Hippocratic collection, Hippocrates (400 B.C.) in his treatise on anatomy mentioned that he cut open the skulls of goats to examine the brain. His description of the blood vessels to the brain was confusing: "To the brain there come many blood vessels; some are slender, but two are stout. One of these stouter blood vessels is said to come from the liver and the other from the spleen." (Singer thought this statement may be an alteration of an original which said that one came from the side corresponding to the liver and the other from the side of the spleen). Then Hippocrates mentioned that arteries contained air, an idea suggested from their emptiness in dead animals.

Another work in the Hippocratic collection indicated that channels pass from all organs to the brain, thence to the s

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the spinal marrow, thence to the kidney and finally to the generative organs. Clendening (1942) mentioned that Aristotle (350 B.C.) in his writings on parts of animals stated that: "In all animals the brain is without blood, and it does not contain any veins; and it is naturally cold to the touch."

Singer (1925) discussed Aristotle's refusal to attach great importance to the brain. Instead, he placed the seat of intelligence to the heart. He considered the brain simply an agent for cooling the heart. This concept was kept until the period of the great Alexandrians (300-250 B.C.), among whom Herophilus distinguished himself as a great anatomist. He definitely recognized the brain as the central organ of the nervous system and regarded it as the seat of intelligence. The term rete mirabile is a Latin translation of the title which he gave for the first time to that arterial plexus at the base of the brain. The fact that he described it shows that he dissected animals possessing this structure rather than human subjects. Singer further stated that Pelops (149 A.D.) was the first to study the distribution of vessels by inflating them with air. In his descriptions he stated:

> Among the arteries some went to the head and thereby vital spirit was brought to the base of the brain. Here the blood was minutely divided by the channels of the rete mirabile. In that mysterious organ the blood became charged with yet a third pneuma, the animal spirit, which was distributed by the nerves.

Leonardo da Vinci in his work on the human body collected by O'Malley and Saunders (1952) described the

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Fabrica

vertebral vessels as spinal channels that occupied the vertebral canals of the cervical region. He believed that these channels carried the animal spirit to the brachial plexus and through this medium conveyed the sense of touch to the brain and motor power to the nerves. He also described the rete mirabile as a plexus of vessels situated at the base of the brain. He found it in ruminants, most prominently in calves.

Singer (1925) and Saunders and O'Malley (1950) credited Berengario de Capri (1490) for the first illustrated anatomical book and for being the first anatomist to deny the existence of a rete mirabile below the human brain, thus contradicting Galen. Singer (1925) gave him credit for describing the choroid plexus composed of arteries and veins. Ask-Upmark (1935) credited Andreas Vesalius (1538) for being the first who denied the existence of any rete mirabile in the human skull.

In the Tabulae Sex (1538) in the plate on the arterial system, (Fig. 1), Vesalius illustrated the vital spirit as it ascends to the brain to be converted in the rete mirabile into a more refined and subtle substance, the animal spirit. Supposedly, this spirit, provided the nervous force necessary for motion and sensation and flowed through the nerves which he believed to contain minute channels.

In the second edition of the De Humani Corporis Fabrica (1555) Vesalius devoted the third book to the

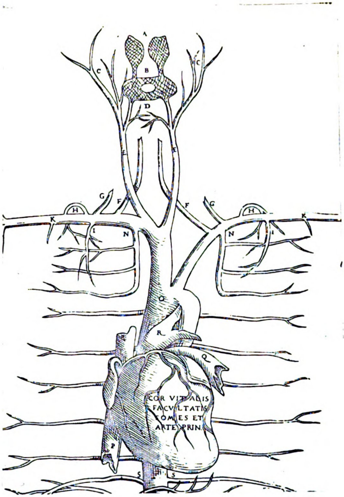

Fig. I (after Andreas Vesalius, The
Tabulae Sex I538)

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anatomy of the blood vessels. Being in a period when blood letting was in vogue for medical purposes, veins were more important than arteries. Singer (1925) mentioned that the vascular system displayed in that book is not basically human. It is combined from various animals and closely follows Galen, as he described the venous system of ungulates and the arterial system of apes.

In plate 47 (Saunders and O'Malley 1950) Vesalius indicated that the carotid artery emptied largely into the dural sinuses. Furthermore, his drawing of the cerebral blood vessels fails to distinguish adequately between intracranial veins and arteries. In the seventh book of the Fabrica on the brain, Vesalius described an illustration of the base of the brain:

> In this figure we have depicted the exposed (pituitary) gland which received the phlegm from the brain. . . . . At the sides are portions of the sleep-inducing (carotid) arteries which are alleged to form a reticular plexus and which we have represented just as we have encountered them upon dissection. As these portions of the arteries are found to vary by the dissector, we have drawn variants of them. (Fig. 2)

Discussing the rete mirabile he stated:

> . . . . We have sketched the reticular plexus as it ought to be to agree with Galen's description in his book on the use of parts. Therefore A and B indicate the arteries entering the skull and then supposedly breaking up into the remarkable plexus. C and D are the branches into which the shoots of the plexuses are reunited and which correspond exactly in size to the arteries we indicated at A and B. (Fig. 3)

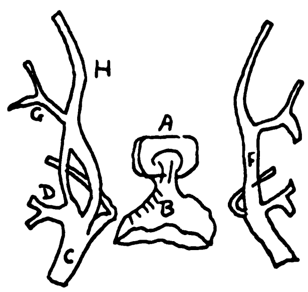

Fig. 2

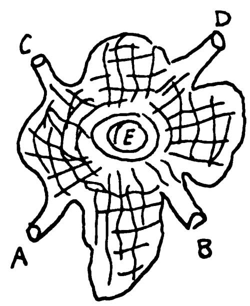

Fig. 3

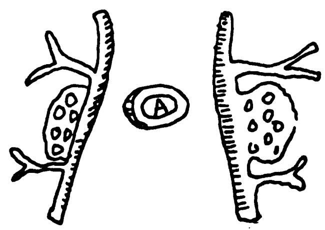

Fig. 4

(After Andreas Vesalius, plate 72 from the seventh book of the Fabrica)

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Vesalius then described another drawing:

> . . . . a series of arteries extending along the side of the gland (admitting the phelgm from the brain) which we have commonly observed in the heads of cattle and sheep. I am disposed to present this lest anyone should think we have concealed the fact that differences exist between these animals and man. In this figure A indicates the often mentioned gland; B and C, the position of the arteries where they first enter the skull. (Fig. 4)

Ask-Upmark (1935) considered Vesalius' courage to contradict Galen as the ardent spirit of a new era of thought. During the medieval period most authors have willingly followed the assertions of Galen, even though some divergent opinions were present, as may be seen in the description of the arteries to the brain given in the <u>Anatomia Magistri Micholai Physici</u> published in the 12th century,

> There are also arteries to the brain. Some say they enter the substance of the brain, others that they form an arterial net which closely surrounds the brain and supplies the pia mater and the dura mater.

This shows that as far as the rete mirabile is concerned, Vesalius was most certainly way ahead of his contemporary workers. During more than a century after the publication of the <u>Fabrica</u>, the existence of a human rete mirabile continued to be a controversial subject, as did the speculations about its functions.

Winston (1659) wrote:

> Vesalius denies it. . . . , Valvedra utterly denies it, and Laurentius had rather call the plexus choroides in the upper ventricles Rete Mirabilum. Howsoever the judgement (<u>sic</u>) of Vesalius may be questioned in giving in beastes (<u>sic</u>) and denying

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> it to men; because in men it is hardly found in regard of the thin spirits it containith, and after death are dissipated. Beasts have thicker and grosser spirits. Fallopius, Piccolhominger and Riolanus are all for it. Sylvius teacheth us the way how to find it. . . . this net which is not simple but as if diverse nets were flung on heaps together and cannot be separated. Here reside the animal spirits, which come from the heart, are elaborated and concocted then fly in plexus choroideum where they are perfected and poured forth into the third and fourth ventricles for their conservation.

Thomas Willis in his work on the brain (1684) confirmed Vesalius' view on the occurrence of the rete mirabile. He stressed the importance of a regulation against too sudden changes of the blood supply to the brain, and his comment on the arterial circle at the base of the brain is the first conception of a smooth and continuous cerebral blood supply.

> . . . . from thence a double benefit results because by this one and the same means care is taken both lest the brain should be defrauded of its due watering of the blood and also lest it should be overwhelmed by the too impetuous flowing of the swelling stream or torrent; as to the first lest that should happen, one of the carotides being obstructed, the other might supply the provision of both; then lest the blood rushing with too full a torrent, should drown the channels and little ponds of the brain, the flood is chastised or hindered by opposite emissiary, as it were a flood gate, and so is commanded to run back with an ebbing tide.

He further stated that no rete is present in man because:

> . . . . in an humane (<u>sic</u>) head where the generous affections and the great forces and ardors of the soul are stirred up, the approach of the blood to the confines of the brain ought to be free and expeditious; and it is behoveful for its river not to run in narrow and manifold divided rivulets,

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> which would scarce drive a mill, but always with a broad and open channel, such as might bear a ship under sail. And indeed, in this respect, a man differs from most brute beasts in which, the artery being divided into a thousand little shoots lest it should carry the blood with a fuller channel or more quick course than is requisite, makes the net-like infoldings, by which indeed it comes to pass that the blood slides into the brain very slowly and with a gentle and almost even stream.

Among the animals, the horse was considered most similar to man with regard to the cerebral blood supply. Willis continued:

> . . . . because magnanimous and fierce forces are convenient for this animal, born as it were for war and any dangerous attempts, and so there was need that the blood might ascend the brain in a free and plentiful course, and when occasion requires with a full torrent. The rete in a dog, fox, sheep, calf, stag and many four-footed beasts divides the torrent blood into small rivulets, its rapid course may be so far dulled or broken. For otherwise in labouring beasts, who go with their hands hanging down, and have but a weak brain, the more free influx of the blood might easily overthrow the fabric of the brain, and spoil the animal spirits.

He considered the rete to be larger in the grass-eaters than in a dog, cat and other flesh-eating or hotter brutes. On the occurrence of the rete in man he comments:

> If that be true, as some affirm that the wonderful net is sometimes also found in a humane brain, I believe it is only in those sort of men who being of a slender wit or unmoved disposition, and destitute of all force and ardor of the mind, are little better than dull working beasts in fortitude and wisdom.

After Willis the rete mirabile has been investigated repeatedly. Rapp (1827) was the only author since Willis who has made an attempt to find a general rule for the appearance of the rete mirabile in different species.

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Whereas Willis assumed a close connection with the mental abilities, Rapp maintained that the rete is present in animals where no vertebral artery is directed to the brain. This is erroneous, but the idea is nevertheless interesting. Hyrtl (1864) mentioned the existence of retia mirabilia in mammals and birds. Murie (1873) described wonderful nets connected with the cerebral and spinal systems of the whale. Tandler (1898, 1906) made repeated reference to the presence of the net in mammals.

Apart from the textbook descriptions, there has been very little information on the cerebral blood vessels in the ox in the recent literature.

Ask-Upmark (1935) concluded in his thesis on the carotid sinus that the rete mirabile was present in species of animals where the internal carotid artery was no longer the main source of blood to the brain. He also stated that the rete was particularly well developed in species where the external carotid was the main deliverer of the cerebral blood and less developed in species where the internal carotid still provided blood for the brain. He also believed that the hydrodynamic effect of the rete mirabile would probably keep pressure in the cerebral arteries at a convenient and fairly constant level.

Zhedenov (1937) discussed the obliteration of the internal carotid artery in cattle. He stated that the common carotid artery did not divide into internal and external carotid arteries but was continued directly as the

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external carotid. The internal carotid artery started to regress in the five-month fetus. From eight months to birth the blood vessel was still patent but its intracranial portion was hard to demonstrate. After birth the artery continued to regress, and at eight months only a small part of the vessel with an insignificant lumen remained. He also mentioned that there were no significant variations in the course of the internal carotid. There were wide variations in the time of obliteration. He found a patent internal carotid on the left side of a yearling Hereford bull and a two-year-old bull.

He believed that regression of the internal carotid artery was the result of growth of the rete mirabile and its arteries. Zhedenov divided the rete in the ox into two distinct parts, the rete mirabile orale and the rete mirabile aborale. The latter was well developed in a three-and-one-half-month-old fetus while the rete orale developed during the ninth prenatal month, reaching its typical full development only in the third postnatal month.

Walmsley (1938) stated that the retia of the ox have a structure similar to those of the whale. They do not, however, form the large vascular masses which are characteristic of the whale, but they are limited to relatively small plexuses that lie in the cranium and the anterior part of the vertebral canal. In the ox the vascular supply of the brain is derived mainly from the cranial rete which is supplied by vessels (vertebral, occi

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occipital and maxillary) which in some part of their course lie outside the bony protection of the axial skeleton, and in this respect the origins of the retia in the ox and the whale differ. In the whale the arteries which are destined for the brain are afforded the maximum possible protection by the axial skeleton, for as they lie in the retia they are successively within the thoracic vertebral canal and the cranium; as they pass from the thorax into the vertebral canal through the intervertebral foramina they are covered by the thick hypaxial muscles. Therefore he regarded this route of the cerebral arteries in the whale as an adequate adaptation to the unusual conditions determined by the habit of submergence. This includes the greatly prolonged intervals between respirations and increased pressure on the surface of the body when submerged. Walmsley then quoted Mackay (1886): "The generally accepted explanation of the use of these great retia is that they act as stores for oxygenated blood which is brought into use while the animal remains for a long time underneath the water."

Daniel et al. (1954) described the arrangement of the vessels related to the carotid rete in a four-month-old bovine calf. They described the rete as being more extensive than in other animals. The rete derived its blood supply from the internal maxillary artery via the arteria anastomotica and the ramus anastomoticus, from the occipital artery via the basi-sphenoidal arterial plexus, and from the internal carotid through a few small vessels.

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The specimen they examined had a complete internal carotid. It took its origin from the proximal portion of the occipital artery and passed through the carotid rete to join the circle of Willis.

The rete mirabile has been described in the common textbooks on anatomy of the domestic animals. Chauveau (1872) described the reseau admirabile as the rete mirabile of Galen.

> It appeared to be found on the carotid and vertebral arteries of animals which, in a state of nature, fed from the ground, the subject being to furnish an equable and prolonged supply of blood without the risk of check or hinderance and thus obviate the tendency to congestion of the brain during the dependent position of the head. This minute subdivision and subsequent reconstruction of an artery, with a like intention, is also observed in other creatures besides grazing animals. The vessels in the arm of the sloth are so disposed that the animal can remain suspended by its arms for long periods, and a similar arrangement is noted in the legs of birds, such as the swan, goose, etc., which stand for a long time. The same object is sometimes attained by great tortuosity. In the ox the reseau is a circular mass surrounding the sella turcica. The occipital arteries concur in its formation and pass into its posterior part.

Montane and Bourdelle (1917) stated that in ruminants as in other species of animals, the cerebral arterial supply terminates in trunks that will assure its circulation through the presence of the rete mirabile. They found that these arterial plexuses consisted of a complex anastomatic arrangement of ramifications of its forming arteries. They also stated that in the domestic ruminants, the rete mirabile is formed on both sides by branches coming from the maxillary artery which enters the cranium through the great

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great round foramen, "le trou grand rond" (the name they gave for the foramen orbitorotundum). The spheno-spinous artery also joins in the formation of the rete. The internal carotid artery is absent or atrophied at adult age in the ox and does not contribute much to the cerebral circulation. In the ox the occipital arteries join in the formation of the rete by a large branch which enters the posterior part of the arterial plexus. On the middle of the dorsal aspect of each side of the rete two single trunks penetrate the dura mater and anastomose with each other by transverse branches. These anastomoses give rise to an arterial circle around the pituitary gland, the circle of Willis, from which the anterior, middle and posterior cerebral arteries originate. According to Montane and Bourdelle the rete in the ox is formed by two lateral lobes that reunite by transverse anastomoses to form a circular mass around the pituitary gland.

Smith (1912) in his textbook A Manual of Veterinary Physiology discussed the functional reasons for the existence of the rete mirabile in ruminants. He stated that the great vascularity in the brain necessitates that the blood should pass to it with a degree of uniformity which will insure the carrying out of its functions. It must never be left without blood or immediate unconsciousness would occur. He mentioned that this is provided in the frequent arterial anastomoses presented by the circle of Willis and the rete mirabile of ruminants which insure that not only does

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does the blood enter with diminished velocity, but that if temporary obstruction occurs in one vessel its work is readily performed by the others. Then he added that the rete mirabile is considered by some to regulate the flow of blood to the brain when the head is depressed during grazing. He challenged this opinion by mentioning that the horse possesses no rete, and his head is depressed during grazing for more hours than are ruminants. He concluded that probably it has some other function to perform.

Ellenberger and Baum (1943) stated that in the cow the internal carotid artery is obliterated in its distal part. The proximal or cranial part originates from the "rete mirabile epidurale." Due to the lack of the distal part of the internal carotid artery, anastomotic branches leave the internal maxillary artery, pass through the foramen orbitorotundum and share in the formation of the rete mirabile. Other arteries that enter the rete on both sides are the middle meningeal, condyloid, and vertebral arteries. They also mentioned that in the bovine fetus, the internal carotid artery travels along the medial aspect of the tympanic bulla then enters the cranial cavity through the foramen lacerum. Finally it joins the rete mirabile which forms a circular network under the hypophysis cerebri. The rete extends caudad to the foramen magnum, where the vertebral arteries join it. According to these authors the condyloid arteries enter the cranial cavity through the foramen lacerum and unite with the meningeal branch of the occip

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occipital artery. Branches of the internal maxillary artery enter the cranium through the oval foramen and join the rete. Other branches pass through the foramen orbitorotundum and form the ophthalmic rete mirabile. One branch of this network passes forward and is called the internal ophthalmic artery. In front of the hypophysis one strong vessel emerges from the rete near the median plane. It penetrates the dura mater, extends to the subdural space, and is called the cerebral carotid artery which is the direct blood supply to the brain. As in the horse, the vessel gives a <u>ramus communicans nasalis</u> and a <u>ramus communicans caudalis</u>. The latter continues as the basilar artery. In the adult cow the blood supply to the rete mirabile and the brain is mainly through branches of the internal maxillary artery.

Sisson and Grossman (1953) defined the rete mirabile as an intercalated network in the course of an artery. The structure is mentioned in the description of the branches of the internal maxillary artery in the ox. They stated,

> Several branches which take the place of the internal carotid artery enter the cranial cavity through the foramen orbitorotundum. They concur with branches of the occipital, vertebral, middle meningeal, and condyloid arteries in the formation of an extensive rete mirabile cerebri on the cranial floor around the sella turcica. From each side of the rete an artery arises which is distributed in general like the internal carotid and basilar arteries of the horse.

It is mentioned that the arteries which concur in the formation of the rete may be termed the <u>arteriae retis mirabilis cerebralis</u>.

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MATERIALS AND METHODS

In this study the blood supply to the bovine brain was studied using different anatomical techniques. The animals used were clinically normal calves and adult cows. Some were injected with neoprene latex mass. Others were used for angiographic studies. Histological studies were made on tissues taken from non-injected animals.

Neoprene Latex Injection

The arrangement of the arteries that contributed to the normal cerebral circulation was studied in fifteen adult female animals, eight male and two female calves and ten male fetal specimens. The animals were anaesthetized using pentobarbital sodium, exanguinated from the common carotid artery, and 10 per cent formalin was then injected into the carcass via the same vessel. After twenty-four hours (maximum formaldehyde fixation is cited as being attainable in this period, Mendelsohn 1940), latex was introduced through the common carotid artery. Continuous, slow, steady pressure was found essential for successful results.

Some specimens were obtained from calves or cows shortly after their death. The head and neck were removed, and the arteries were flushed with physiologic saline solu

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solution followed by 10 per cent formalin. Twenty-four hours later latex was introduced into the common carotid artery, while pads of cotton were held firmly against the cut surface of the neck. On conclusion of the injection the vessels were ligated, and the head of the animal was placed in a solution of 10 per cent formalin with 1 per cent phenol. Some of the injected preparations were dissected in the usual manner. In a few, the brain with all of the cerebral vessels attached was dissected out of the cranial cavity. This was not easily accomplished if all the blood vessels were to be saved intact with their normal relationships to the rete mirabile. Other heads were macerated using a concentrated solution of sulfuric acid or sodium hydroxide. After maceration the specimens were kept under running water until all of the tissue debris was washed out. The latex casts of the blood vessels were kept in formalin for further study, at which time they were examined under water.

<u>Angiographic Studies</u>

Four heifer calves were used for this study. The animals were generously supplied by the Dairy Department at Colorado State University. At the same time, the calves were used for other survival experimental work. This limited the author to only one study on each animal to avoid the hazard of toxicity from the repeated injections of contrast medium.

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Rapid cerebral arteriographs were obtained by injecting a contrast medium, "Hypaque sodium 50 per cent," into the common carotid artery. The animals were anaesthetized using pentobarbital sodium. The skin of the neck was shaved and prepared in the usual manner for aseptic surgery. A skin incision about two inches long was made in the middle of the lateral aspect of the neck. The subcutaneous tissues were reflected and the sternocephalicus muscle was separated from the sternothyrohyoideus. The common carotid artery was located, brought out through the skin incision, and dissected away from the accompanying vagosympathetic trunk. A rolled piece of sterile gauze was looped loosely around the artery to keep it in place. Rapidly 20 ml. of the opaque mass was injected in the common carotid by one push of the plunger of the syringe, using a one-inch, sixteen-gauge hypodermic needle. A series of rapid radiographs of the head was started simultaneously with the injection. The simple cassette changer described below was devised to fulfill this purpose. With this technique it was possible to make five arteriographs in six seconds.

Cassette Changer

Due to the high cost of a commercial automatic speed cassette changer, a simple inexpensive device was prepared (Fig. 5). It consisted of a chute made of a wooden frame and masonite walls together with a wooden paddle with the injec

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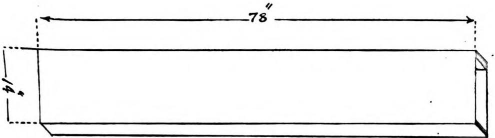

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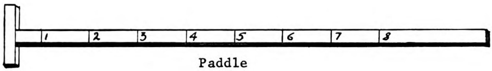

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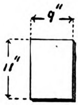
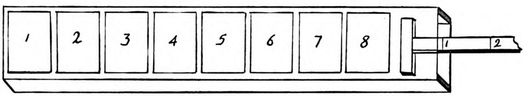
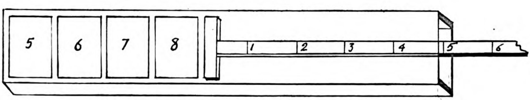


Cassette



Chute Loaded With Cassettes



Cassettes 1 - 4 Exposed
Cassette No. 5 Ready

Fig. 5. - Rapid Cassette Changer

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handle marked at regular nine-inch intervals. The chute could accommodate eight standard (9x11") cassettes.

After the chute was loaded with serially numbered cassettes, its upper side facing the X-ray tube was covered with sheets of lead, leaving only an area at one end of the chute equivalent to that of cassette number one directly under the cone of the X-ray machine.

The paddle was pushed in the other end of the chute, and the animal's head was placed on the area not covered by the lead sheets.

A team of three persons was required to perform the experiment (Fig. 6). Person A injected the contrast medium. Person B simultaneously pushed the cassettes into the chute while pushing the release button of the X-ray machine with his foot for each exposure. Person C received the cassettes containing the exposed film and kept them behind a lead-glass shield to protect them from scattered X-rays.

After the completion of the injection, the needle was withdrawn and gentle pressure applied on the site of penetration for about two or three minutes to seal the opening in the artery. The blood vessel was then returned to its place in the neck and the skin incision closed. The films were developed and studied for distribution of the cerebral blood vessels.

Histological Study

The arterial plexuses within the cavernous sinuses and their dural coverings were dissected out of the cranial


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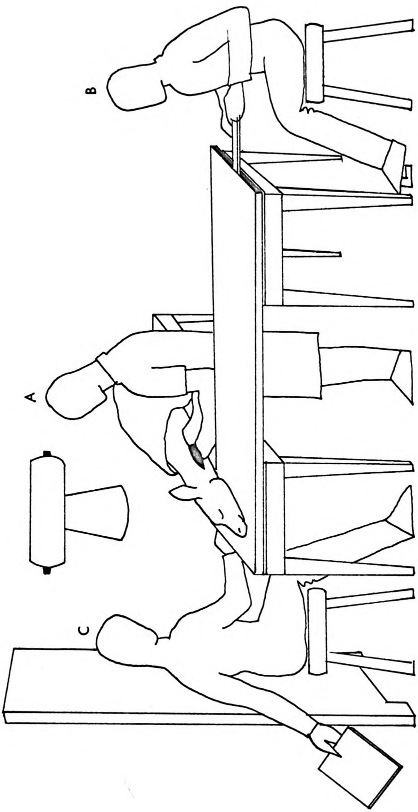

Fig. 6

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cavities of three recently killed calves and fixed in 10 per cent buffered formalin. They were processed in the routine way, embedded in paraffin, and sectioned at 6 microns.

Three staining techniques were used to differentiate various tissues: Weigert's resorcin-fuchsin stain to demonstrate elastic fibers, Van Gieson's stain to demonstrate collagenous fibers, and hematoxylin and eosin stain for general microscopic structure.

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RESULTS

I. The blood supply to the bovine brain

A. Adult

In the adult animals examined the common carotid arteries originated from the bicarotid trunk (*truncus bicaroticus*) about one to two inches cranial to the first rib and ventral to the trachea. Both the right and left arteries ascended along the neck accompanied by the vagosympathetic trunk dorsally, the recurrent laryngeal nerve ventrally, the internal jugular vein laterally and separated from the external jugular vein by the sterno-mastoideus muscle (Fig. 7). The right common carotid artery (*A. carotis communis dextra*) crossed the lateral surface of the trachea, then travelled craniad along its dorsolateral surface to the lateral wall of the pharynx. The left common carotid (*A. carotis communis sinistra*) crossed the trachea, then the oesophagus. At the level of the third cervical vertebra the artery acquired the lateral surface of the oesophagus and continued to the lateral wall of the pharynx. At the level of the paramastoid process both common carotids terminated by giving off the occipital artery (*A. occipitalis*), the external maxillary artery (*A. maxillaris externa*) and the external carotid artery (*A. carotis externa*) (Fig. 8). In three specimens the

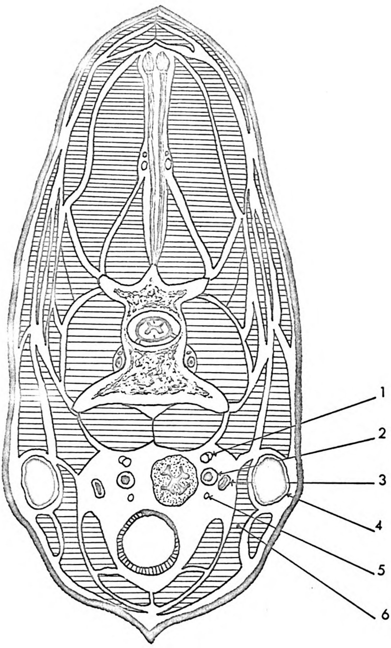


Fig. 7 (after D.R. Peterson)
Cross section of the neck in the middle cervical region

1. Vagosympathetic trunk
2. Common carotid a.
3. Internal jugular v.
4. External jugular v.
5. Recurrent laryngeal n.
6. Sternomastoideus m.

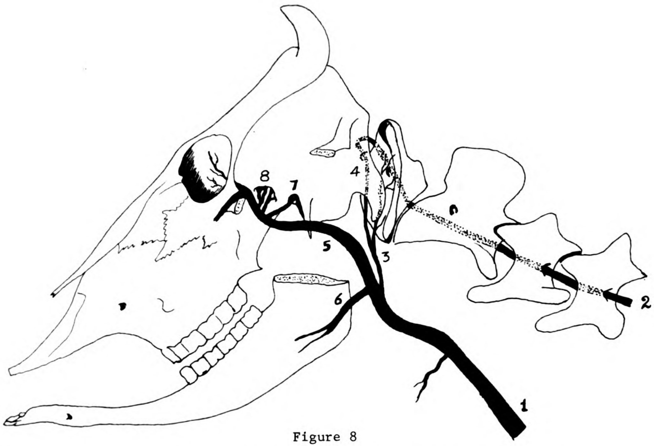


Figure 8

1.	Common carotid a.	5.	Internal maxillary a.
2.	Vertebral a.	6.	External maxillary a.
3.	Occipital a.	7.	Middle meningeal a.
4.	Condyloid a.	8.	Anastomotic arteries to the rete

pharyngeal artery (A. palatina ascendens) arose from the common carotid, while in twelve animals the artery had its origin in the proximal part of the occipital artery. The occipital and the external carotid arteries were the only terminal branches of the common carotid that contributed to the cerebral circulation.

1. The occipital artery (A. occipitalis)

This vessel arose from the dorsal surface of the common carotid artery, then ascended upward medial to the paramastoid process and entered the condyloid fossa where it divided into anterior and posterior branches. The posterior one (Ramus occipitalis) passed along the margin of the atlanto-occipital articulation and gave small twigs to the joint and the ventral straight muscles of the head. The anterior branch, the condyloid artery (A. condyloidea), entered the cranial cavity through the hypoglossal foramen; there it gave small twigs to the dura mater; then it curved backward and passed through the foramen magnum to the vertebral canal where it anastomosed with the terminal branches of the vertebral artery. With the contralateral vessels they formed a complex arterial plexus, the basisphenoidal plexus, which communicated with the posterior part of the rete mirabile (Fig. 9).

2. The external carotid artery (A. carotis externa)

This blood vessel was the direct continuation of the common carotid artery. It passed upward lateral to the

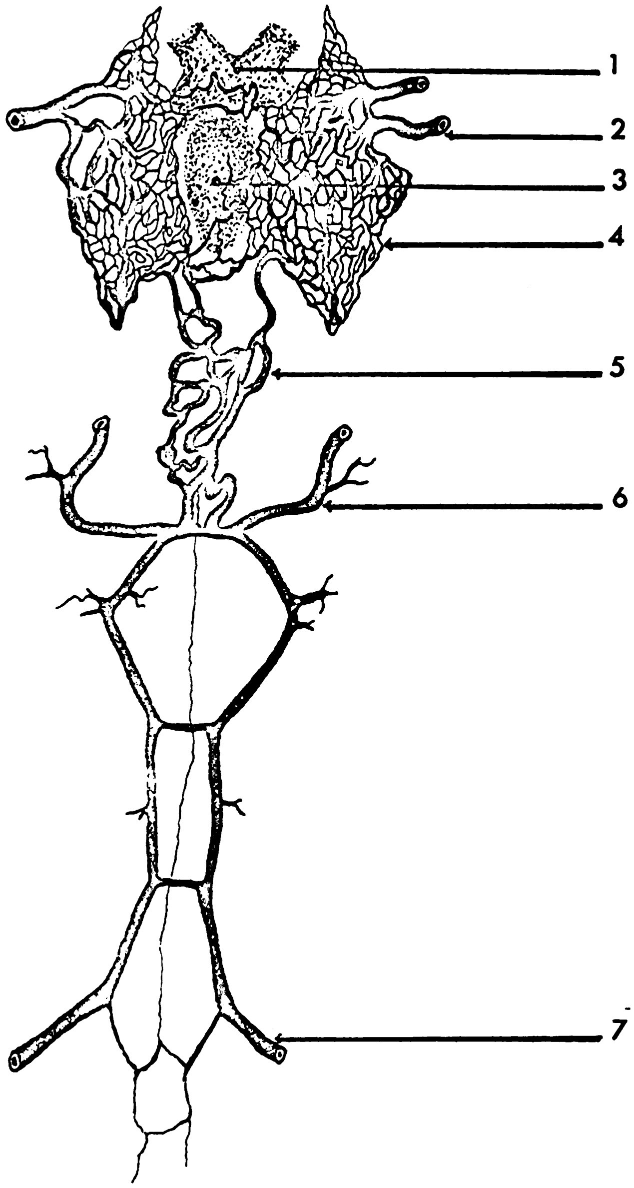


Fig. 9
Ventral view of the rete mirabile and associated arteries

1. Optic chiasma
2. Anastomotic a.
3. Hypophysis cerebri
4. Rete mirabile
5. Basisphenoidal plexus
6. Condyloid a.
7. Vertebral a.

great cornu of the hyoid bone to reach the posterior border of the ramus of the mandible. About one inch below the level of the mandibular articulation the artery divided into the superficial temporal and the internal maxillary arteries.

a. The superficial temporal artery (A. temporalis superficialis) was the smaller of the terminal branches of the external carotid. It gave branches to the frontal, temporal, auricular and cornual structures.

b. The internal maxillary artery (A. maxillaris interna): Due to the absence of an alar canal in the bovine skull the internal maxillary artery was completely extra-osseous. It lay first medial to the upper part of the ramus of the mandible. From there it extended forward to the pterygo-palatine fossa making a characteristic double curve (Fig. 8). The vessel ended in the maxillary recess by branching into the greater palatine and infraorbital arteries. On its course it gave the pterygoid, mandibular alveolar, deep temporal, buccinator, middle meningeal, anastomotic branches to the cerebral rete, and external ophthalmic arteries. The middle meningeal artery and the anastomotic branches to the rete supplied the bovine brain with blood usually carried by the internal carotid artery in man and other mammals where that vessel exists.

The middle meningeal artery (A. meningea media) arose from the dorsal surface of the internal maxillary artery at the beginning of its second curve. The vessel

entered the cranial cavity through the oval foramen where it was closely related to the mandibular division of the trigeminal nerve. Inside the cranial cavity the middle meningeal artery gave a branch to the dura mater, penetrated it and then entered the cavernous sinus. There it divided into two branches in seven specimens, three branches in five, four branches in one, and it did not branch at all until it got into the rete in two specimens.

In two animals the middle meningeal artery arose from a common trunk with the anastomotic branches to the rete. In both cases the trunk gave one middle meningeal artery that passed through the foramen ovale and one large anastomotic artery that entered the cranium through the foramen orbitorotundum. Inside the cranium the middle meningeal branch in both cases divided into three branches as it joined the posterior border of the rete.

Anastomotic arteries to the rete mirabile (<u>arteriae retis mirabilis cerebri</u>): Considering their size and mode of branching in the rete these vessels were the main source of blood to the cerebral plexus in all the adult specimens examined. They left the dorsal border of the summit of the second curve of the internal maxillary artery. The vessels had a short extraosseous course; then they entered the foramen orbitorotundum. As they emerged in the cranial cavity they entered the dura mater which was greatly thickened and then became entangled with both the ophthalmic and maxillary divisions of the trigeminal nerve. The arteries then

pierced the lateral wall of the cavernous sinus, entered the sinus and joined the anterior tip of the cerebral rete by fine branches. In eight animals there were three independent anastomotic arteries from the internal maxillary while five specimens showed only two. As mentioned previously, in two cases, there was only one large anastomotic artery that left the internal maxillary in a common trunk with the middle meningeal.

The cerebral rete mirabile: This massive plexus of arterial anastomoses is the meeting place for all sources of extracranial blood to the adult bovine brain. This structure is characterized by being completely bathed in a lake of venous blood in the dural cavernous sinus around the sella turcica on the floor of the cranial cavity. The retia lay on each side between the trigeminal nerve and the hypophysis cerebri. The right and left retia were joined together at both the anterior and posterior ends by communicating branches of the retial vessels; thus a ring made of anastomosing arteries was formed and surrounded the pituitary gland. Anteriorly, on each side, the retial mass extended under the optic chiasma and then tapered off to parallel the optic nerve (Fig. 10). The posterior communicating part of the rete was located at the level of the posterior border of the pons. At this point it received the large tortuous arteries of the basisphenoidal plexus. Laterally each lobe of the rete was closely related to the branches of the trigeminal nerve after these left the semilunar ganglion. The

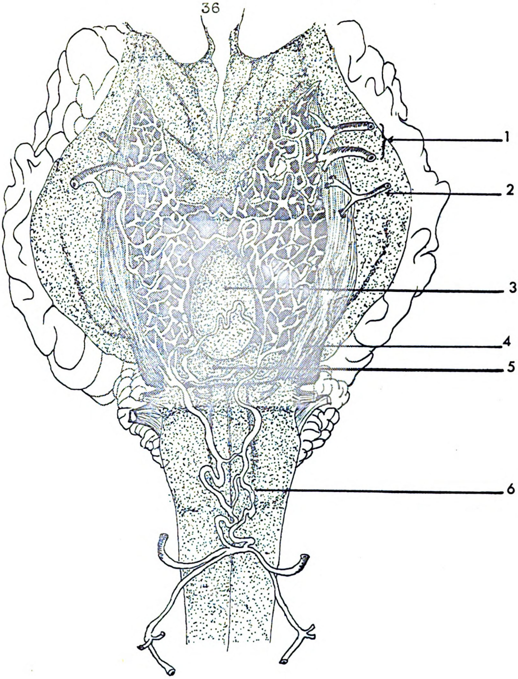


Fig. 10
Ventral surface of the brain and rete mirabile

1. Anastomotic aa.
2. Middle meningeal a.
3. Hypophysis cerebri
4. Fifth cranial nerve adherent to dura mater
5. Pons
6. Basisphenoidal plexus

most lateral retial arteries were found to adhere to the thickened dura forming the lateral wall of the cavernous sinus. Dorsally the rete was again adherent to the dura that formed the diaphragma sellae except where the hypophyseal stalk passed through the foramen diaphragmatis. Ventrally the plexus was covered by and adherent to the dural covering of the floor of the cranium.

The vessels which composed the rete for the most part were relatively uniform in calibre (0.5-2 mm in diameter). They were closely interwoven and anastomosed freely with one another to form a highly complex mass. In twelve specimens there was always a larger artery that traversed through the mass of the rete on each side. It ranged from $1\frac{1}{2}$ to 3 mm. in diameter. This vessel travelled anteriorly and dorsally, emerged out of the rete, and passed through an opening in the diaphragma sellae lateral to the foramen diaphragmatis. Then it divided into anterior and posterior branches which united with their homologues on the other side to form the circulus arteriosus at the base of the brain. In three specimens it was hard to find the main larger vessel in the retial mass. The emergent artery in those cases was formed by the mergence of several smaller retial vessels on the dorsal surface of the rete (Fig. 11). The distribution of the emergent artery in all specimens resembled the intracranial part of the internal carotid of animals lacking a cerebral rete.

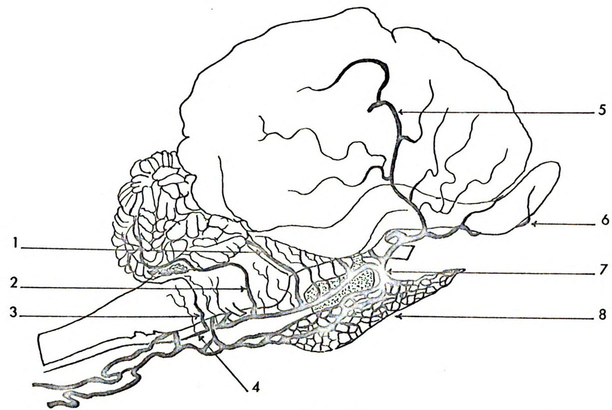


Fig. 11
Lateral view of the brain and cerebral vessels

1. Anterior cerebellar a.
2. Middle cerebellar a.
3. Posterior cerebellar a.
4. Basilar a.
5. Middle cerebral a.
6. Anterior cerebral a.
7. Emergent artery of the rete
8. Rete mirabile

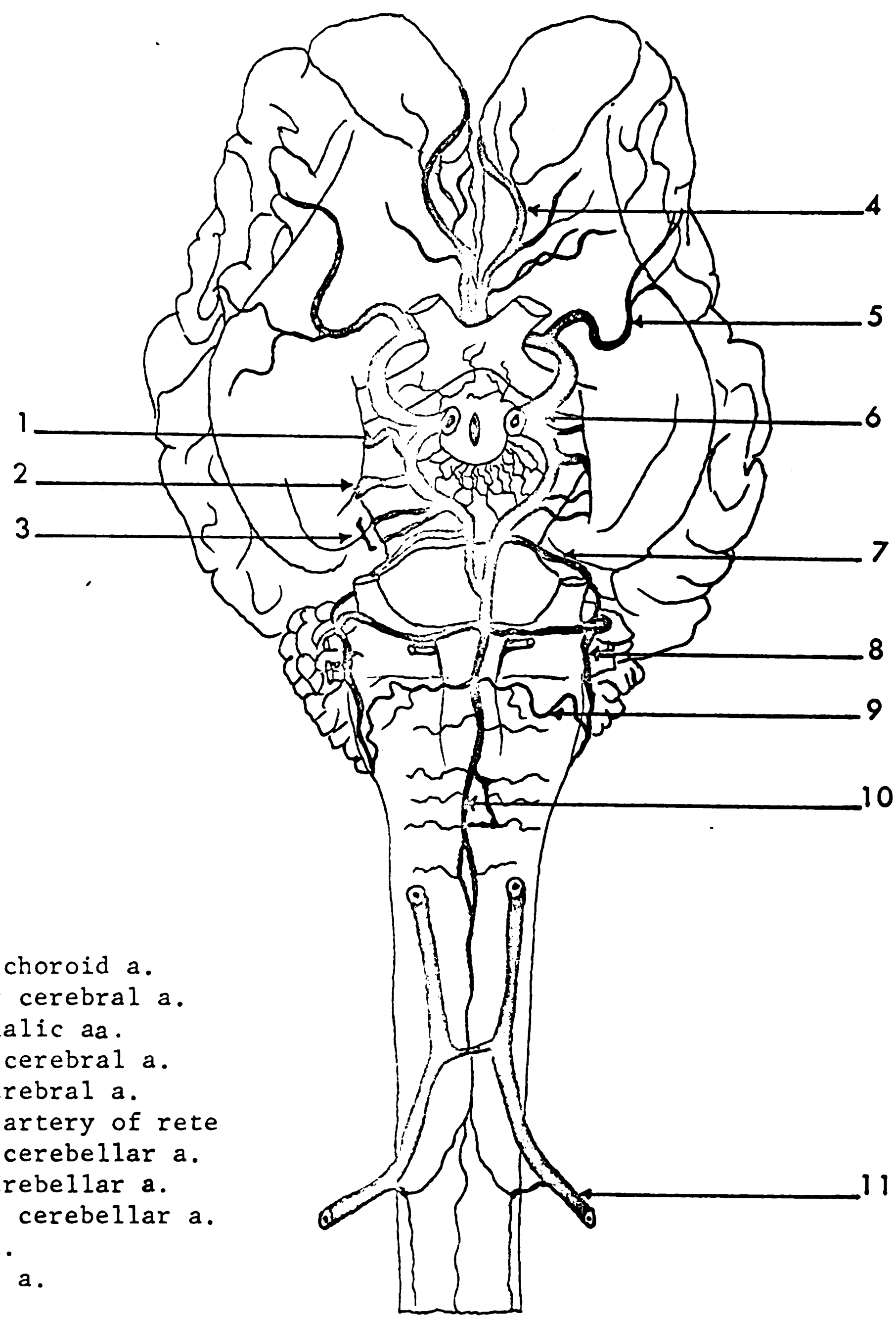
The vertebral artery (_A. vertebralis_)

This artery in the bovine specimens seemed to contribute to the cerebral circulation more than in any other animal with a rete mirabile. It originated from the costo-cervical artery at the level of the seventh cervical vertebra and extended along the neck in the transverse canal. On its way it gave branches to the intertransversalis muscle and, opposite each intervertebral foramen, a spinal branch to the spinal cord and meninges. The vessel entered the vertebral canal at the intervertebral foramen between the second and third cervical vertebrae. Unlike its homologue in man, the vertebral artery of the ox did not terminate by joining its counterpart of the opposite side to form the basilar artery. Instead it extended cranially on the floor of the vertebral canal where it joined the artery from the other side by a variable number of anastomotic branches. The polygonal patterns of these anastomoses were variable in all specimens examined. The artery then divided in the vertebral canal of the atlas into two branches. The larger of these branches left the canal through the intervertebral foramen of the atlas and ramified in the neck muscles, thus joining the occipital branch of the occipital artery. The second branch of the vertebral artery passed through the foramen magnum, and at the caudal border of the medulla oblongata it anastomosed with the condyloid artery to form the basisphenoidal arterial plexus, thus contributing to the posterior part of the rete mirabile.

The only connection between the vertebral and basilar arteries was at the level where the vertebral artery entered the vertebral canal between the second and third cervical vertebrae. There the vertebral artery gave the last spinal branch which divided into two fine twigs. The lateral and smaller twig extended caudad along the lateral surface of the spinal cord forming with its caudal counterparts the lateral spinal artery. The medial and comparatively larger twig crossed the ventral surface of the spinal cord, joined the vessel from the other side, and entered the caudal end of the basilar artery (Fig. 12).

The emergent cerebral artery of the rete (A. carotis cerebralis, Ellenberger and Baum, 1943)

This vessel differed from the intracranial part of the internal carotid of species of mammals lacking a cerebral rete because it carried both carotid and vertebral blood to the brain. The artery emerged from the dorsal surface of the rete near the median plane, crossed the cavernous sinus and penetrated the diaphragma sellae in front of the hypophysis cerebri. It then extended to the subdural space close to the hypophyseal stalk. At the caudal border of the optic tract it divided into two large branches. The anterior and larger branch passed laterad parallel to the optic tract, crossed it, and then curved mediad to reach the dorsal surface of the optic chiasma. There it joined its counterpart from the other side and formed the anterior communicating artery. The posterior branch of the cerebral artery of the



1. Anterior choroid a.
2. Posterior cerebral a.
3. Mesencephalic aa.
4. Anterior cerebral a.
5. Middle cerebral a.
6. Emerging artery of rete
7. Anterior cerebellar a.
8. Middle cerebellar a.
9. Posterior cerebellar a.
10. Basilar a.
11. Vertebral a.

Fig. 12

rete extended caudad and laterad to reach the midventral surface of the cerebral peduncle. It then turned mediad, crossed the pons close to the median plane and joined the artery from the other side at the caudal border of the pons. The anastomoses of the two vessels formed the posterior communicating artery and completed an arterial circle; the circulus arteriosus or the circle of Willis (Fig. 12).

The various arteries to the cerebral hemispheres, brain stem, cerebellum and medulla oblongata originated from the circulus arteriosus.

1. The anterior cerebral artery (A. cerebri oralis): This vessel originated from the anterior branch of the cerebral artery of the rete dorsal to the optic chiasma. In four specimens the artery arose from a common trunk with the artery of the other side, while in eleven specimens it had an independent origin. It passed forward on the medial olfactory striae, then entered the longitudinal fissure of the cerebrum, continued upwards and forwards along the genu of the corpus callosum, turned around the genu, followed the cingulate sulcus, then branched on the medial surface of the cerebral hemisphere and continued over the dorso-medial margin of the hemisphere. In the longitudinal fissure the arteries from both sides followed their course side by side with a variable number of anastomotic branches connecting them. In two animals the left anterior cerebral artery was larger than the right one and crossed the longitudinal fissure to supply the dorso-medial margin of the right

hemisphere. In one specimen there was an additional anterior cerebral artery; the vessel arose from the anterior communicating artery and terminated by supplying fine branches to the medial surfaces of both cerebral hemispheres.

2. The middle cerebral artery (A. cerebri media): This vessel was the largest of all the branches off the circulus arteriosus. It originated from the anterior branch of the cerebral artery of the rete mirabile at the level of the lateral angle of the optic chiasma. From the point of origin the vessel passed laterad in the lateral fossa where it gave a variable number of fine twigs that pierced the perforated substance. It then extended dorsad in front of the piriform lobe supplying fine branches to the anterior part of the area. The vessel became tortuous as it reached the lateral surface of the cerebral hemisphere. It then terminated by dividing into frontal, parietal and temporal branches. These branches left the tortuous stem of the artery at variable levels along its course. The author could not establish a definite pattern with which the different specimens could be identified.

3. The anterior choroid artery (A. choroidea oralis): This vessel had a variable origin. Out of thirty vessels examined in fifteen specimens, five arteries originated from the middle cerebral artery, seven from the anterior branch of the cerebral artery of the rete, twelve from the cerebral artery of the rete in the angle formed by its anterior and posterior branches, and six from the posterior branch

anterior to the origin of the posterior cerebral artery. The anterior choroid artery passed along the optic tract, crossed the lateral geniculate body, extended along the space between the hippocampus and the stria terminalis, entered the lateral ventricle and ended in the choroid plexus. The artery supplied the optic tract, the thalamus, the hippocampus and the caudate nucleus.

4. The posterior cerebral artery (A. cerebri aboralis): This vessel originated from the posterior branch of the cerebral artery of the rete anterior to the oculomotor nerve. The artery ascended dorsad across the cerebral peduncle, crossed the medial geniculate body, extended to the level of the splenium of the corpus callosum and supplied the tentorial surface of the cerebral hemisphere and the medial and lateral surfaces of the occipital lobe.

5. Mesencephalic arteries (Aa. mesencephalica): Two main vessels on each side took origin from the posterior branch of the cerebral artery of the rete just anterior to the occulomotor nerve. The vessels originated separately or from a common trunk. They crossed the cerebral peduncle, then branched repeatedly to form an elaborate arterial tree that covered the corpora quadrigemina. A branch from the anterior mesencephalic artery supplied the pineal body. Various fine vessels left the main mesencephalic vessels or the posterior branch of the cerebral artery of the rete and entered the cerebral peduncle.

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6. The anterior cerebellar artery (A. cerebelli oralis) (Superior cerebellar artery of the human brain): The artery originated from the posterior communicating artery of the circulus arteriosus. It passed laterad on the anterior border of the pons, directly below the oculomotor nerve of the same side and, after turning around the lateral side of the cerebral peduncle below the trochlear nerve, it reached the anterior surface of the cerebellum where it divided into a medial and a lateral branch. The medial branch supplied the antero-dorsal part of the vermis and the dorsal medullary velum. The lateral branch supplied the anterior surface of the cerebellar hemisphere.

7. The basilar artery (A. basilaris cerebri): This vessel was formed by the junction of the two posterior branches of the cerebral arteries of the rete mirabile at the posterior border of the pons. It extended caudad in the median groove on the ventral surface of the medulla oblongata; then it continued along the ventral median fissure of the spinal cord to the level where the vertebral artery entered the vertebral canal between the second and third cervical vertebrae. There the basilar artery received two small branches from the vertebral. Caudal to this anastomosis the basilar artery was continued as the ventral spinal artery. The basilar artery diminished rapidly in diameter from its point of origin caudad and attained a minimum diameter where the vertebral branches joined it.

The following collateral branches originated from the basilar artery:

a. The middle cerebellar artery (<u>A. cerebelli media</u>) (Anterior inferior cerebellar of the human brain): This vessel left the basilar artery at the posterior border of the pons or originated from the communicating branch just anterior to the origin of the basilar. The middle cerebellar artery was always larger than the posterior cerebellar. It left the basilar and passed in the groove between the pons and the trapezoid body to the root of the facial nerve. It then made a sharp turn backwards, descended along the lateral border of the trapezoid body, turned around the root of the acoustic nerve, and ascended dorsad to supply the posterior surface of the cerebellar hemisphere.

b. The posterior cerebellar artery (<u>A. cerebelli aboralis</u>) (Posterior inferior cerebellar of the human brain): This was a smaller vessel that left the basilar artery caudal to the trapezoid body. It crossed the ventral surface of the medulla oblongata and ascended dorsad between the roots of the acoustic and glossopharyngeal nerves. It then turned around the medulla oblongata to the postero-lateral boundary of the fourth ventricle, then terminated in the ventral and caudal parts of the vermis and the posterior surface of the cerebral hemisphere.

c. Medullary arteries (<u>Rami medullares</u>): These were seven to ten in number. They left the basilar artery along its course and were distributed to the medulla oblongata.

B. The Carotid and Vertebral Blood Supply in Calves

Fourteen calves were used to study the arrangements of the blood vessels that contributed to the cerebral circulation. Ten animals were used for neoprene latex injections while four were used alive for angiographic studies. The ages of the calves ranged from three days to four months.

Dissection of the latex injected calves revealed only one major difference from the adult specimens examined. This was the existence of an internal carotid artery undergoing various degrees of atrophy in different calves.

In a three-day-old calf, the vessel was complete and was well injected with the latex mass throughout its course. The artery arose from a common trunk with the occipital artery. It extended forward to the medial surface of the tympanic bulla where it was held in place by thick, fibrous connective tissue. From there it passed through the foramen lacerum, emerged in the cranial cavity and became tortuous as it joined the postero-lateral border of the rete mirabile. It continued rostrad in the rete, anastomosing freely with the retial vessels before it emerged from the dorso-medial surface of the plexus. The artery increased in diameter from a half a mm. where it entered the rete to $1\frac{1}{2}$ mm. as it emerged. It divided into an anterior and a posterior branch which anastomosed with their counterparts from the other side to form the characteristic circulus arteriosus. In a four-week-old calf the internal carotid exhibited the same arrangement as in the above specimen

except that it originated independently from the common carotid. As the artery approached the rete, it divided into three smaller branches which entered the posterior part of the plexus. The largest of the branches followed a course similar to that in the three-day-old calf. In two calves, eight and twelve weeks old, the internal carotid had a smaller lumen in its proximal part while the retial and emergent parts retained a size similar to that in the calves described above. A four-month-old calf demonstrated a more progressive atrophy of the internal carotid. The proximal part of the artery did not contain latex and was reduced to a ligamentous string which blended and faded in the fascia covering the tympanic bulla and the foramen lacerum. The retial and emerging parts of the internal carotid did not suffer any atrophy. They measured $1\frac{1}{2}$ mm. and 2 mm., respectively. In another four-month-old calf the proximal portion of the artery was less obvious and was hard to isolate from the surrounding fascia. Again in this animal the retial and emergent portions did not seem to suffer any change. They had a diameter of 1 mm. and $1\frac{1}{2}$ mm., respectively.

Cerebral Angiography:

Four living calves were used in this study. The results were limited because the animals were being used at the same time for other survival experiments. In one calf, the intracarotid injection of the opaque solution caused a spasm in the wall of the blood vessel at the site

of injection. This stopped the opaque material from ascending towards the cranial cavity (Fig. 13).

Among the other three animals one was six and two were eight weeks old. It was interesting to find that the internal carotid artery in the animals studied did not receive any of the opaque solution and so did not show in the angiographs. As stated above, gross dissection of calves in the same age group demonstrated regressing internal carotid arteries that could still be injected with latex. In one eight-week-old calf the occipital and vertebral arteries showed clearly in angiographs taken less than two seconds after intracarotid injection of the opaque solution. This demonstrated the effectiveness of the anastomotic connections between the carotid and vertebral systems in this animal (Fig. 14). In all three calves only one side of the rete received opaque material. The injected substance circulated only with the cerebral blood of the ipsiliateral side of the common carotid used. None of the three series of angiographs showed an indication of cross circulation from one side of the cranial cavity to the other (Fig. 15). Furthermore, the angiographs confirmed the information obtained from gross dissection of latex injected specimens. The internal maxillary artery showed its characteristic double curve. The middle meningeal artery and the anastomotic branches to the rete appeared as short connections between the second curve of the internal maxillary artery and the rete mirabile. The rete appeared as a fuzzy opaque

Fig. 13


Anastomoses
Vertebral and
Condyloid
Vertebral a.
Condyloid a.
Basisphenoidal plexus
2

Fig. 14

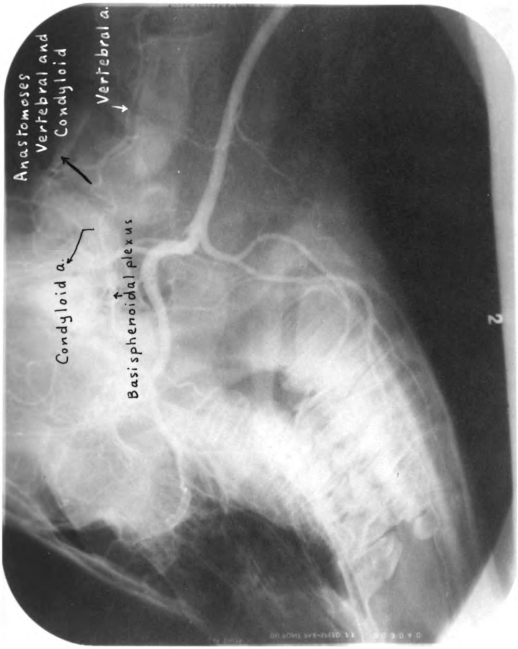
Anastomoses
Vertebral and
Condyloid
Vertebral a.
Condyloid a.
Basisphenoidal plexus
2

Fig. 14

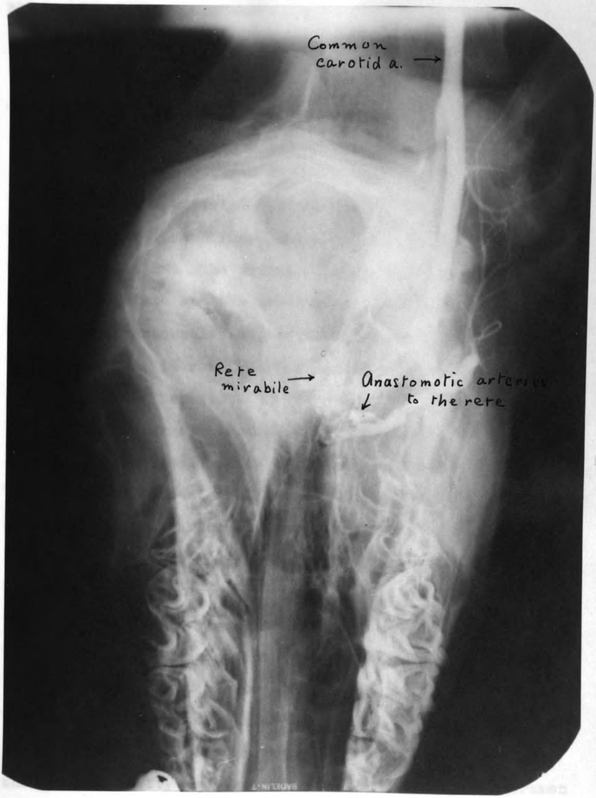

Fig. 15

Figure 15

shadow on the floor of the cranial cavity. The basiphenoidal plexus appeared in a lateral view as a sharp opaque line connecting the occipital-vertebral anastomosis to the posterior pole of the rete mirabile (Fig. 14).

C. The Cerebral Blood Supply in the Bovine Fetus

Ten formalin-fixed fetuses were injected with latex through the left ventricle of the heart. The youngest fetus was 18 cm long (crown rump length). The vertebral artery was well injected. The vessel entered the transverse canal between the sixth and the seventh cervical vertebrae and entered the vertebral canal between the second and third vertebrae where it ramified and anastomosed with its fellow artery on the other side.

The internal carotid artery branched from the common carotid at the level of the occipital condyles, then extended to the tympanic bulla where it became embedded in its medial wall. The artery crossed the narrow middle part of the foramen lacerum and embedded itself in a thick layer of connective tissue that joined the tympanic bulla to the lateral border of the basilar part of the occipital bone. The vessel then extended into the cartilagenous structure of the middle ear to the opening of the Eustachian tube. From there it continued in the direction of the tube for a short distance, turning medially back upon itself to enter the cranial cavity through the anterior part of the foramen lacerum. From there it continued rostrally and medially, penetrated the dura mater lateral to the hypophysis cerebri

and made a half circle around it. Just anterior to the hypophysis it received a communicating branch from the contralateral artery. The left internal carotid was completely filled with latex, while the right artery was only injected to the level of the hypophysis.

The occipital artery in this 18-cm fetus was well injected but seemed to lack anastomotic relationships with the vertebral artery.

The second fetus was 24 cm long. In that specimen the internal carotid extended to the tympanic bulla where it disappeared in its medial wall and then followed a course similar to the above specimen. After it entered the cranial cavity it penetrated the dura mater to join the posterior part of the lateral border of a tiny rete mirabile (3 mm wide x 3 mm long on each side). The structure was a miniature of the rete observed in adult specimens. It received two anastomotic branches from the internal maxillary artery. A small basisphenoidal plexus joined its posterior end, and the vertebral arteries on both sides showed the characteristic pattern of anastomoses. The rest of the fetuses (two 27 cm, two 36 cm, one 48 cm and three 53-55 cm long) had larger retia mirabilia (4x5 mm, 5x8 mm, 6x9 mm and 7x15 mm, respectively. The internal carotid was complete and contained latex in all the specimens examined. In all the specimens the vessel was completely embedded in dense fascia on the medial wall of the tympanic bulla.

D. Microscopic Structure of the Rete Mirabile

Transverse sections of the cerebral rete were studied. The arterial network was contained in the cavernous sinus which demonstrated a relatively thick wall made of dense fibrous connective tissue. The lateral sides of the sinus were greatly thickened by branches of the trigeminal nerve which were invested by dural tissue. The wall of the sinus was lined with a continuous layer of endothelium. In the region where the rete surrounded the hypophysis, the gland was also invested by a thin vascular dural covering. The retial arteries were suspended in the blood-filled cavity of the sinus. The central artery of the rete (remnant of the internal carotid artery) had a larger diameter than the vessels surrounding it. These decreased in size as they approached the dural wall of the sinus (Fig. 16). The arteries in general were thin walled for their caliber. For example, a central artery of the rete had a diameter of 3.45 mm and a wall 0.16 mm thick. The vessels had a well-developed tunica adventitia which was separated from the blood in the cavernous sinus by a continuous layer of endothelial cells. The tunica adventitia was composed of dense collagenous connective tissue. In most of the vessels it formed 50 per cent of the thickness of the wall (Fig. 17). It measured from 0.01 mm in small vessels to 0.10 mm in larger ones. Occasionally there were few elastic fibers scattered among the collagenous fibers. A few vessels contained adipose tissue that added to the thickness of the adventitia.

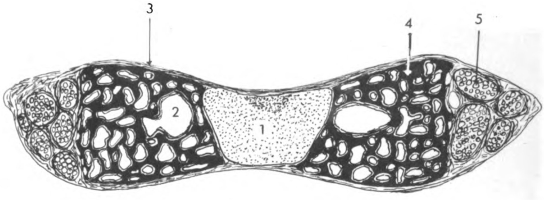

Fig. 16
Diagram of transverse section through the rete mirabile

1. Hypophysis cerebri
2. Central artery of the rete
3. Wall of cavernous sinus
4. Venous blood surrounding retial vessels
5. Nerve trunk; branches of fifth cranial nerve

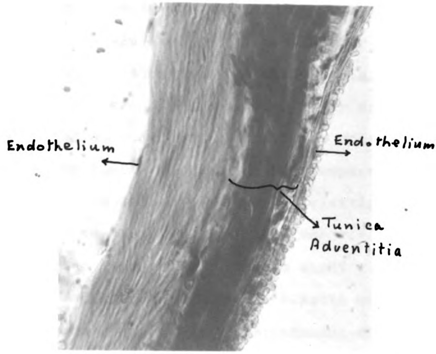

Fig. 17A
Photomicrograph of the wall of a retral artery 680 x

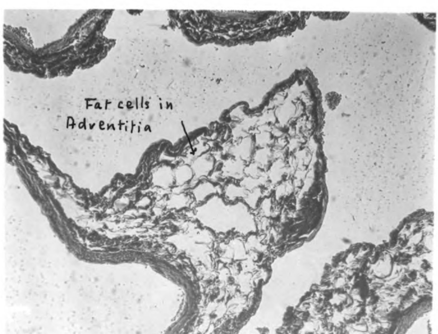

Fig. 17B
Photomicrograph of the wall of a retral artery 175 x

The tunica media was composed of smooth muscle fibers. In most of the vessels examined it was thinner than the tunica adventitia. It ranged from 0.009 mm in small arteries to 0.09 mm in larger vessels. The layer exhibited a poorly-developed external elastic membrane which was incomplete. The tunica intima was thin compared with the other layers of the wall. The internal elastic membrane was well developed in all of the blood vessels. It ranged from five microns in small arteries to eight microns in larger ones. Medial to the internal elastic membrane there was a thin intermediate layer of collagenous fibers. Innermost was a continuous layer of endothelial lining.

DISCUSSION

Mammals can be divided into two main classes in relation to the arrangement of the carotid arterial blood vessels that contribute to the cerebral circulation.

1. Animals in which the brain is supplied mainly by the internal carotid arteries. No rete mirabile is present. This group is represented by the horse and the dog.
2. Animals in which the brain is supplied mainly by the external carotid artery. The internal carotid is rudimentary or lacking. A well-developed rete mirabile is present. The cow, goat and sheep are good examples of this group.

Naturally there are transitional groups of animals between those two extreme patterns of cerebral arterial blood supply. In man, for example, the internal carotid and the vertebral arteries together are responsible for the cerebral blood supply in approximately equal proportions. In some lemurs the vertebral artery is the main vessel responsible for the cerebral circulation (Ask-Upmark 1935). Among the group of animals that has a well-developed rete mirabile, there are various species with the rete located intracranially (cow, camel, sheep, goat and pig) while in

others the rete is extracranial in position (cat). Whales have both intracranial and extracranial retia mirabilia.

The diversity of species among animals which have a rete mirabile makes the problem of finding a functional reason for the existence of a rete mirabile very challenging. It is present in ruminants, omnivores, carnivores and aquatic mammals. It is also absent from animals that belong to the same groups. This leads to a very logical question. Is there any factor common to all species in which the rete is present? One possibility is that animals of different orders and habitats assume the same morphological structure in order to fulfill analogous functions. This is called functional convergence and is best shown in the fishlike form of the body in aquatic mammals. This is unlikely to be the case in animals with a rete mirabile as they are completely unmatchable in their functional activities and as different as a whale, a camel, a leopard and an armadillo (Ask-Upmark 1935). The author believes that this is one of the delightful mysteries of the organizational pattern of the living body that will occupy the minds of many workers for some time.

Many early workers tried to find a reason for the existence of the cerebral rete in some animals and its absence in others. Vesalius (1538) and Winston (1659) believed that the blood carried the vital spirit to the rete mirabile to be refined into the animal spirit. This spirit they maintained provided the nervous force necessary

for motion and sensation. Willis (1684) then discussed a more reasonable function for the rete. He stressed the importance of a regulation against too sudden changes of the blood supply to the brain. He also believed that man and the horse because of their nature and spirit needed a free flow of blood to the brain, while in other animals the rete slowed the rapid course of the blood to avoid the overthrow of the fabric of the brain. Rapp (1827) thought that the rete existed in animals because they lacked the vertebral artery. Rapp's theory was the earliest record in the literature to associate the existence of the rete with the absence of a blood vessel. Actually most animals with a cerebral rete mirabile lack the internal carotid artery rather than the vertebral.

Chauveau (1872) theorized that the rete is naturally found in animals who feed from the ground and so furnish an equable and prolonged supply of blood without the tendency to congestion of the brain during the dependent position of the head.

MacKay (1886) gave a functional reason for the existence of the rete in the whale. He stated that they act as reservoirs for oxygenated blood which is brought into use while the animal remains for a long time underneath the water.

Ask-Upmark (1935) believed that the rete had a hydrodynamic effect that would probably keep pressure in the cerebral arteries at a convenient and constant level.

Daniel et al. (1954) suggested that the rete is of some hemodynamic significance in relation to the cerebral circulation. Both authors considered the fact that the rete lies within a venous lake may have a physiological significance. Goetz (1960) stated that the venous sinus around the rete mirabile in the giraffe acts as a pressure jacket especially when this animal lowers its head. Bell (1960) disagreed with Goetz and saw no relationship between the effect of the pressure exerted by the blood in the cavernous sinus and lowering of the head. The rete seems to have enough physical characteristics to slow down the flow of blood. On the other hand, the giraffe is a browsing animal that eats from the tops of the trees and only occasionally has to lower its head toward the ground. The author believes that the sudden narrowing of the blood vessels as they branch off the forming vessels of the rete would create increased resistance to the flow of blood. Ruch and Fulton (1960) stated that a decrease to half the radius of the lumen of a blood vessel would decrease the flow of blood to a sixteenth of the original value. They also mentioned that the rate of blood flow through the brain is affected by the cerebral vascular resistance. This resistance represented the resultant of all factors which impeded blood flow through the cerebral vessels among which were those factors which affected the caliber of the lumen of the blood vessels and the external pressure on them. All the above

discussions point out the fact that the rete mirabile could have a hemodynamic function.

The direct contact between the walls of the retial arteries and the venous blood in the cavernous sinus made the author think about some other functional significance for the rete mirabile. Many workers found that wherever arteries and veins were in close proximity, the venous blood returning from the surface of the body had a cooling effect on the arterial blood flowing towards the periphery. Hovarth <u>et al</u>. (1950) believed that cooling of the arterial blood could be due to heat transfer to the venous blood coursing in near by. Scholander and Schevill (1955) discussed two circulatory factors which would reduce the heat loss from the whale's fin. a) Slow rate of blood flow and b) precooling of the arterial blood by veins before it enters the fin. They mentioned that this was accomplished by the arterio-venous blood vascular bundles which are found at the base of the extremities in a variety of aquatic and terrestial mammals and birds. They stated that no matter what else these bundles do, they must exchange heat between the arteries and veins. The efficiency of heat exchange in a system like that was related to the rate of blood flow. The slower the flow, the more nearly identical would be the arterial and venous temperatures along the system. The author believes that the cerebral rete mirabile represents a most efficient heat exchange system. The small caliber of the retial arteries slows the flow of blood while the extensive anastomoses among the vessels increases the exposed

surface areas of their walls. Furthermore, the arterial walls are in direct contact with blood in the venous sinus. There remain a few questions that could not be answered:

1. Why would the brain need such a system?
2. Is the venous blood returning from the brain cool like blood returning from the skin of a limb or the fin of a whale? (The brain is one of the most actively metabolizing organs of the body and depends for its ultimate energy supply primarily upon the aerobic combustion of glucose, Ruch and Fulton 1960).
3. If the brain needs such a system for its normal function, why is it lacking from the cranial cavity of many animals?
4. What is different in those animals that necessitates the existence of such an arterial network along the course of their cerebral blood supply?

These are questions that need more refined research and investigation. Work should be done on the rate of flow of blood through the rete. The blood pressure before, inside and after the blood passed through the rete should be established. Temperatures of arterial blood at various levels in the cerebral circulation, and temperatures of the cerebral venous blood at various levels should be determined. These are problems which merit future investigation.

The Rete Mirabile in the Ox

The ox (Bos taurus) has an intracranial rete mirabile. Compared with other animals, the ox has a rete that is more extensive both in size and connections. In the sheep, goat and pig the rete is made of two separate lobes that may or may not be connected by very weak anastomoses (author's observations, Montane and Bourdelle 1917, Chauveau 1872 and Daniel et al. 1954). The rete in the cow is connected on both sides on its anterior and posterior borders by extensive communicating vessels, thus forming a large ring-like arterial plexus around the pituitary gland. Furthermore, it extends anteriorly parallel to the optic nerves, while the posterior border receives the elaborate basisphenoidal plexus. The rete in the ox has more extracranial connections than any of the other species mentioned above. It receives blood from the vertebral, occipital, middle meningeal arteries and the anastomotic branches of the internal maxillary. In sheep and goats the rete receives all its supply of blood from the internal maxillary artery (Baldwin and Bell 1960, Daniel et al. 1954). In the pig the rete derives almost its entire blood supply from the ascending pharyngeal (Daniel et al. 1954) or the internal carotid (Sisson and Grossman 1953). Apart from the abovementioned differences the cerebral rete in the ox shares other characteristics with retia of other animals. It was located in the cavernous sinus at the base of the brain around the hypophysis cerebri. It gave off two short blood

vessels which represented the intracranial portions of the internal carotids in animals lacking a cerebral rete. The emergent arteries formed the circle of Willis which is a characteristic structure in the cranial cavity of all mammals.

According to the basic pattern, there was an anterior cerebral, middle cerebral, posterior cerebral, anterior cerebellar, middle cerebellar, posterior cerebellar, basilar and ventral spinal arteries. There may be some little variation in size and distribution, but the general pattern was constant.

Due to the great development of the cerebral hemispheres in man and the location of the cerebellum below them, there were certain differences in both nomenclature and course of the cerebellar vessels in man and the ox. The anterior cerebellar artery in the ox was the homologue of the superior cerebellar artery of the human brain. In the ox the artery originated from the posterior communicating artery of the circle of Willis, while in man the homologous vessel originated from the basilar artery. The middle cerebellar of the ox was the anterior inferior cerebellar of man. The vessels originated from the basilar artery in both species. The posterior cerebellar artery in the ox represented the posterior inferior cerebellar artery in man. In the ox the vessel took origin from the basilar artery while in man it originated from the vertebral artery.

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Due to the great development of the cerebral hemispheres in man and the location of the cerebellum below them, there were certain differences in both nomenclature and course of the cerebellar vessels in man and the ox. The anterior cerebellar artery in the ox was the homologue of the superior cerebellar artery of the human brain. In the ox the artery originated from the posterior communicating artery of the circle of Willis, while in man the homologous vessel originated from the basilar artery. The middle cerebellar of the ox was the anterior inferior cerebellar of man. The vessels originated from the basilar artery in both species. The posterior cerebellar artery in the ox represented the posterior inferior cerebellar artery in man. In the ox the vessel took origin from the basilar artery while in man it originated from the vertebral artery.

The Basilar Artery

In the ox this vessel was formed by the confluence of the posterior branches of the cerebral arteries of the rete from both sides. It decreased in diameter as it extended caudad and reached its smallest caliber as it anastomosed with the vertebral artery. This peculiar configuration of the vessel may mean that the vessel actually carried blood away from the circle of Willis to the medulla and the spinal cord. In man the basilar artery is formed by the junction of the two vertebral arteries and ends by bifurcating into the two posterior cerebral arteries (Cunningham 1943). The vessel maintains its caliber during its short course. In the horse the basilar artery is formed by the union of the cerebral branches of the cerebrospinal arteries. The latter vessels are branches of the occipital arteries (Sisson and Grossman 1953).

Extracranial Arteries Supplying Blood to the Rete

There are some disagreements in the literature on naming certain extracranial arteries that contributed to the formation of the rete mirabile. Homologies of the vessels can be recognized in different animals by studying: a) the course of the vessels through bony foramina or soft tissues; b) their relationships to nerves; c) areas of distribution. The trigeminal nerve and its branches and the foramina at the base of the skull are useful guides. For example the foramen ovale is traversed in most species by the mandibular division

of the trigeminal nerve, and the artery which accompanies this nerve in different species of animals should be homologous. Sisson and Grossman (1953) called the vessel the middle meningeal as it is named in man. Ellenberger and Baum (1943) labelled it the caudal anastomotic branch to the rete. Daniel et al. (1954) gave it the name ramus anastomoticus in the cat, dog, sheep, goat, pig and ox. The foramen orbitorotundum in the cow was designated by that name by all authors except Daniel et al. (1954) who named it the orbital fissure. They also used the name arteria anastomotica to identify the vessel or vessels that accompanied the ophthalmic division of the trigeminal nerve through the foramen. Zhedenov (1937) named the same vessels arteria pro rete mirabile; Sisson and Grossman (1953), arteriae retis mirabilis cerebri; and Macleod (1958), arteries of the rete mirabile. Zhedenov (1937) later talked about the rete mirabile orale (the rete mirabile of other authors) and the rete mirabile aborale. He gave the latter name to the complex arterial plexus formed by the vertebral and condyloid arteries. Ellenberger and Baum (1943) included the same structure with the rete and called the combined network the epidural rete mirabile. Daniel et al. (1954) did recognize the condyloid artery. They mentioned it as the major branch of the occipital. This branch formed with the vertebral a large arterial plexus on the upper surface of the basisphenoid bone. They called it the basisphenoid arterial plexus.

<u>The Internal Carotid Artery</u>

All authors agreed to the fact that the internal carotid artery is missing in the adult bovine animal. Zhedenov (1937) reported a patent internal carotid on the left side of both a yearling and a two-year-old bull. In calves the internal carotid exhibited varied degrees of regression. Zhedenov (1937) stated that regression of the internal carotid artery was the result of growth of the rete mirabile and its arteries. Later he contradicted this by saying the arteria pro rete develops after the regression of the internal carotid shortly after birth. The author agrees with Zhedenov that in a three-and-a-half-month fetus the rete was represented by two straight trunks. Furthermore, the author found that the internal carotid arteries were continuous with those trunks.

In the specimens examined in this study twelve adult animals had a central artery of the rete which, in the author's opinion and based on work reported here, is the remnant of the internal carotid artery. The central artery lost its identity in three adult specimens. It existed in all calves studied (three days to four months old). Zhedenov (1937) mentioned that, with increasing anastomoses of the rete, the part of the internal carotid artery in the rete loses its integrity and all that was left was the part from the rete to the brain. From Zhedenov's work and the work done in this study, a three-and-a-half-month fetus had two straight trunks which were considered by Zhedenov as the

beginning of the rete mirabile aborale, and in the specimens dissected by the author were continuous with the internal carotid arteries. Zhedenov then described a five-month fetus which did not develop a rete mirabile orale but had two fine arteriae pro rete (anastomotic arteries from the internal maxillary) which entered the internal carotid. The author believes that this finding should prove that the internal carotid artery is the parent vessel for most of the retial arteries.

Furthermore the author dissected a 24-cm-long fetus (crown rump length), which had the calculated age of four months, and found a rete mirabile surrounding the pituitary gland; this rete had the structure and relationships of a completely developed rete (both orale and aborale). Zhedenov stated that the rete orale started to develop in a six- to seven-and-a-half-month fetus, and it was still developing from eight months to birth. He may have meant a growth in size rather than development as he did not explain what a complete or fully developed rete orale was. The author believes that the rete mirabile was well developed structurally when it met the basisphenoidal plexus; it had both anterior and posterior anastomoses and received its anastomotic branches from the internal maxillary artery. The author found all those features in the rete of a four-month-old fetus.

The author believes that the peculiar course of the internal carotid artery through the medial wall of the

tympanic bulla could have a decisive role in causing regression of the vessel. As the fibro-cartilaginous wall of the fetal bulla ossifies completely it may limit further development of the artery which becomes embedded in its bony substance. Meanwhile anastomotic branches from the internal maxillary artery develop to maintain adequate blood supply to the developing brain. Those branches join the internal maxillary to the intracranial portion of the internal carotid. The extracranial portion regresses towards the point of origin from the common carotid artery. The existence of the free intracranial part in the rete of all calves examined and most of the adults, plus the presence of the ligamentous remnant of the artery between the tympanic bulla and common carotid in calves, lends support to the above conclusion.

Angiographic Studies

The main objective of this part of the study was to observe the normal route through which the blood flowed to the bovine brain. The inexpensive cassette changer developed by the author made it possible to take fast angiographs, thus recording the ascent of injected opaque material as it was carried by the blood stream in the common carotid artery. Circumstances permitted the successful injection of only three calves. From this limited experience, it was possible to conclude that in three calves under normal conditions of blood flow, no blood crossed from one side of the

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cranium to the other. One arteriograph showed the condyloid-vertebral anastomoses clearly. The arteries of the rete, the middle meningeal artery and the basisphenoidal plexus were also traced on radiographs. The author could not find any reference to cerebral angiography in the ox in the available literature.

One calf developed a carotid spasm, a condition experienced in human cerebral angiography. The reason could be a reaction of the arterial wall to trauma either from the needle or the opaque material. The animal did not suffer any permanent injury. Cerebral angiography seems to be safe in animals.

SUMMARY

In this study the normal structure and distribution of the arteries that supply blood to the bovine brain were studied by utilizing various anatomical techniques.

A. Macroscopic dissections of the arterial supply were conducted on fifteen adult female animals, eight male and two female calves, and ten male fetal specimens.

1. Arterial blood was supplied to the brain through the carotid and vertebral systems. The carotid system included the condyloid branch of the occipital artery, the middle meningeal artery and anastomotic branches of the internal maxillary artery. The vertebral artery contributed to the cerebral circulation by anastomotic connections with the condyloid and basilar arteries.
   The internal carotid artery was lacking in all the adult specimens studied.
2. Before reaching the cerebral vessels, carotid and vertebral blood passed through a massive plexus of arterial anastomoses, the rete mirabile. This structure was bathed in the

venous blood of the dural cavernous sinus at the base of the cranial cavity.

3. From the dorsal surface of the rete mirabile two arteries emerged and formed a circulus arteriosus from which the regular pattern of cerebral, cerebellar and medullary arteries originated.
4. The basilar artery originated from the posterior border of the circulus arteriosus and not from the confluence of the vertebral arteries of both sides as is described in man and other species of animals.
5. Macroscopic dissections of calves revealed only one major difference from the adult animals--the internal carotid artery was shown to be undergoing various degrees of atrophy in different specimens.
6. The internal carotid artery was complete and patent in all the fetal specimens examined. The vessel was embedded in the medial wall of the tympanic bulla. The later ossification of the wall of the bulla around the vessel is believed to limit the further development of the artery.

B. Cerebral angiographic studies were conducted on four heifer calves. A simple inexpensive speed cassette changer was developed. In three clinically normal

calves there was no cross circulation of blood between the two sides of the brain. Most of the vessels demonstrated by macroscopic dissections could be identified on the arteriographs. One case of carotid spasm was encountered.

C. Microscopic study of the retial vessels revealed that the arteries were thin walled. The wall had a well-developed tunica adventitia which was covered on the outside by a continuous layer of endothelial cells. The tunica media was composed mainly of smooth muscle fibers and had a poorly developed, incomplete external elastic membrane. The tunica intima was thin and had a well-developed internal elastic membrane.

D. Differences among different authors concerning the nomenclature of blood vessels leading to the rete mirabile were discussed.

E. Various theories concerning the function of the rete were presented, and it was concluded that further investigation is needed to explain the existence of such a structure in certain species.

LITERATURE CITED

L I T E R A T U R E
C I T E D

LITERATURE CITED

Ask-Upmark, E. 1935. The carotid sinus and the cerebral circulation. An anatomical and clinical investigation. Acta. Psychiat. Scand., Suppl. 6:1-374.

Baldwin, B. A. and F. R. Bell. 1960. The contribution of the carotid and vertebral arteries to the blood supply of cerebral cortex of sheep. J. Physiol. 151:9p.

Bell, F. R. 1960. Personal communication. Department of Physiology, Royal Veterinary College, London.

Breasted, James H. 1930. The Edwin Smith Surgical Papyrus. U. of Chicago Press.

Chauveau, A. 1872. The Comparative Anatomy of the Domesticated Animals. Translated by G. Fleming. W. R. Jenkins and Co., N.Y.

Clendening, L. 1942. Source Book of Medical History. Paul B. Hoeber Inc., N.Y.

Courville, C. B. 1959. Antenatal and paranatal circulatory disorders as cause of cerebral damage in early life. J. Neuropath. Exp. Neurol. 18:115-140.

Cunningham, D. J. 1943. Text-book of Anatomy. Edited by J. C. Brash and E. B. Jamieson. Oxford Univ. Press.

Daniel, P. M., J. D. Dawes, and M. L. Prichard. 1954. Studies of the carotid rete and its associated arteries. Phil. Trans. Roy. Soc. London, Ser. B. 237:173-208.

Ellenberger, W. and H. Baum. 1943. Handbuch der Vergleichenden Anatomie der Haustiere. Springer-Verlag, Berlin.

Goetz, C. 1960. Personal communication. Department of Surgery, Albert Einstein College of Medicine, Bronx, N.Y.

Hovarth, S. M., A. Rubin, and E. L. Foltz. 1950. Thermal gradiants in the vascular system. Amer. J. Physiol. 161:316-322.

Hyrtl J. 1864. Neue Wundernetze und Geflechte bei Vogeln und Sangetieren. Denkschr. Kais. Akad. Wiss. Wien. 22:113. (Quoted by Ask-Upmark 1935).

Kaplan, H. A. 1959. Trans-cerebral venous system. A.M.A. Arch. Neurol. 1:148-152.

MacKay, 1886. Proc. Glasgow Phil. Soc. 17:61. (Quoted by Walmsley 1938).

Macleod, W. M. 1958. Bovine Anatomy. Burgess Publ. Co., Minneapolis, Minn.

Mendelsohn, S. 1940. Embalming Fluids. Chemical Publ. Co., N.Y.

Montane, L. and E. Bourdelle. 1917. Anatomie Regionelle des Animaux Domestiques. J. B. Bailliere et Fils, Paris.

Murie, J. 1873. On the organization of the caaing whale, Globiocephalus melar. Trans. Zool. Soc. London. 4:238.

Nylin, G., H. Bomer, H. Jones, S. Headlund, and C. Rylander. 1956. Further studies of cerebral blood flow estimated with thorium B-labeled erythrocytes. Brit. Heart J. 18:385-392.

O'Malley, C. D. and J. B. Saunders. 1952. Leonardo da Vinci On the Human Body. Abelard H. Shuman Publ. Co., N.Y.

Peterson, D. R. 1958. Laboratory Guide to the Dissection and the Study of the Anatomy of the Domestic Ruminants. Oklahoma State Univ. Press.

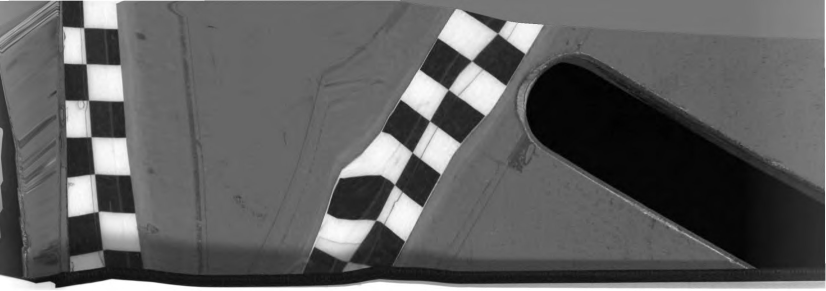
Rapp, 1827. Uber das Wundernetz. Meckels Arch. F. Anat. und Physiol. (Quoted by Ask-Upmark).

Ruch, T. C. and J. F. Fulton. 1960. Medical Physiology and Biophysics. W. B. Saunders Co., Philadelphia.

Saunders, J. B. and C. D. O'Malley. 1950. The Illustrations from the Works of Andreas Vesalius of Brussels. The World Publ. Co., Cleveland and New York.

Scholander, P. F. and W. F. Schevill. 1955. Counter current vascular heat exchange in the fins of whales. J. Appl. Physiol. 8:279-282.

Singer, C. 1925. The Evolution of Anatomy. Alfred A. Knopf Publ. Co., N.Y.



Sisson, S. and J. D. Grossman. 1953. The Anatomy of the Domestic Animals. W. B. Saunders Co., Philadelphia.

Smith, F. 1912. A Manual of Veterinary Physiology. Alexander Egar, Chicago.

Tandler, J. 1898. Zur vergleichenden Anatomie der Kopfarterien bei den Mammalia. Denkchr. Kais. Akad. Wiss. Wien. 67:677.

Tandler, J. 1906. Zur Entwicklungsgeschichte der arteriellen Wundernetz. Anat. Hefte. 31:235.

Vesalius, Andreas. 1538. The Tabulae Sex (Tabulae Anatomicae). Translated by Saunders and O'Malley, 1950. The World Publ. Co.

Vesalius, Andreas. 1555. de Humani Corporis Fabrica. The third book. Translated by Saunders and O'Malley, 1950. The World Publ. Co.

Walmsley, R. 1938. Some observations on the vascular system of the female finback. Contributions to Embryology, Carnegie Institution of Washington. XXVII, no. 166. Publ. 496:109-178.

Willis, Thomas. 1684. De Cerebri Anatome. London (Quoted by Ask-Upmark 1935).

Winston, Th. 1659. Anatomy lectures at Gresham Colledge. Daniel, London. (Quoted by Ask-Upmark 1935).

Zhedenov, V. N. 1937. On the question of the obliteration of the internal carotid artery in cattle. Arch. Anat. Hist. Emb. 16:490-508.