STUDIES OF THE CAROTID RETE AND ITS ASSOCIATED ARTERIES

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(*Communicated by W. E. Le Gros Clark, F.R.S.—Received* 26 *November* 1952)

[Plates 12 to 19]

This work records an investigation of the anatomy of the cranial blood supply in various species of mammal. The findings were based on a study of radiographs of specimens injected with a radio-opaque mass and of casts of the vessels made by injection of neoprene latex, and on dissections of injected preparations.

A well-developed carotid rete was found to be present in the cat, sheep, goat, ox and pig, and a rudimentary form of this structure was found in the dog. In the cat the rete is situated extra-cranially, but in the other species it lies within the cranium in the cavernous sinus. There is no carotid rete in the rabbit or the rat.

The carotid rete consists of a compact network of intertwined, freely anastomosing arteries, and is related to the branches of the trigeminal nerve. When the rete is situated intracranially there is a variable degree of communication across the mid-line with the rete of the opposite side. Whether situated intracranially or extracranially the rete lies within a venous lake.

The presence of a well-developed carotid rete was associated with the non-persistence of, or a degenerating internal carotid artery.

A thin fibrous cord was the only remnant of this artery found in the cat. In the goat, sheep and pig the internal carotid artery was absent proximal to the rete, but the large trunk which connected the rete with the circle of Willis was identified as representing the still persisting distal segment of this artery. In the ox (a young animal) a similar trunk connecting the rete with the circle of Willis formed the continuation of a still persisting but relatively narrow proximal segment of the internal carotid artery.

The main vessels which may supply the carotid rete are the internal maxillary artery (usually via the ramus anastomoticus and the arteria anastomotica), the ascending pharyngeal artery, and the occipital artery. In the cat, sheep, goat and ox the chief vessel of supply is the internal maxillary artery, but in the pig it is the ascending pharyngeal artery. In the ox a substantial contribution is provided by the occipital artery.

Both the ramus anastomoticus and the arteria anastomotica form connexions between the external and internal carotid systems and they join one another within the cavernous sinus. It is at his site that the intracranial carotid rete is developed, but the extracranial carotid rete, seen in the cat, is situated around the internal maxillary artery at the site of origin of the arteria anastomotica of the artiodactyls. The variations in the situation of the carotid rete in different species is along the line of the arteria anastomotica. It is suggested that the arteria anastomotica and the ramus anastomoticus respectively are homologous with the recurrent meningeal and the middle meningeal arteries of the rabbit and man.

The arteries which supply the orbital and the ethmoidal regions are described and the homologies of the external ophthalmic artery are discussed. The great variability in the supply of these territories which was seen in the cat is thought to be associated with the presence of an extracranial carotid rete.

In spite of variations in different species of animal a basic pattern can be discerned in the major arteries supplying the head. It is suggested that this basic pattern is related to a primitive stapedial artery, and that the variations seen are due to modifications of the branches of this earlier vessel.

The circle of Willis was found to derive its blood supply from one or more of five sources: the internal carotid artery, the external carotid arterial system, the ascending pharyngeal artery, the vertebral artery (via the basilar artery) and the occipital artery. In the absence of an internal carotid artery the greatest contribution of blood passes to the circle of Willis through the carotid rete. An occipito-vertebral anastomosis seems to be of some importance in supplying the circle of Willis in the cat, pig, dog and rabbit. In the sheep, goat and ox the direction of the flow of blood in the basilar artery would appear to be away from and not towards the circle of Willis. In the pig the two anterior cerebral arteries anastomose in the mid-line and continue forward as a single vessel.

The peculiar structure of the vessels which compose the carotid rete suggests that this compact network has a haemodynamic significance, and since the rete lies in the pathway of the major artery or arteries which supply the brain, its existence and possible influence should be borne in mind when problems of the cerebral circulation are considered in species in which this structure is present.

Introduction

We first became interested in the carotid rete when we were considering the coiled arteries of the renal sinus whose unusual form appeared to be of haemodynamic significance (Trueta, Barclay, Daniel, Franklin & Prichard 1947, pp. 159–160). The need for a detailed anatomical investigation of the rete and its related vessels became apparent during angiographic studies of the cerebral circulation which showed that the rete was a very prominent feature in angiograms of those animals in which this structure is present. Apart from the question of the rete, a detailed knowledge of the cranial blood vessels of various species was also needed as a preliminary to a study of the vascular supply of the nose (Dawes 1952; Dawes & Prichard 1953). In the first instance we carried out an anatomical investigation in the cat, and then extended our study to other species as material became available.

The existence of a carotid rete in certain species of animal has been known since this structure was described by Galen, but it was not until the Renaissance period that the interest of anatomists in the 'rete mirabile' revived. At this period the presence of a carotid rete in man was a matter of dispute, as is indicated by the works of Vesalius (1538, table III; 1543, p. 621), Winston (1659, p. 242) and Willis (1664, pp. 53–63). At a later date John Hunter (1794, pp. 165, 179) and several others took an interest in the rete, but it was not until the end of the nineteenth century that an extensive comparative anatomical study of the arteries of the head and neck was made by Tandler (1899). This study included accounts of the carotid rete in several species.

Ask-Upmark (1935), in his account of the carotid sinus and the cerebral circulation, surveyed the literature on the carotid rete, and gave an account of his own dissections of a number of species. His researches, however, were not primarily directed towards the rete.

The best account of the carotid rete to date is that given by Davis & Story (1943) in their description of the carotid arterial system in the cat.

Material and methods

The animals used in this investigation were as follows:

Cat (*Felis domestica*)	20 adults, 3 kittens (a few weeks old)
Sheep (*Ovis aries*)	3 adults, 5 foetuses (near-term)
Goat (*Capra hircus*)	3 adults, 4 kids (a few weeks old)

Ox (*Bos taurus*)	1 calf (4 months old)
Pig (*Sus scrofa*)	1 adult, 8 piglets (4 new-born, 4 a few weeks old)
Dog (*Canis familiaris*)	11 adults
Rabbit (*Oryctolagus cuniculus*)	10 adults
Rat (*Rattus norvegicus*)	12 adults

Two main types of preparation were made. In some animals the cranial vessels were injected with radio-opaque masses for a radiographic study; in others casts of the vessels were made by injection with neoprene latex. Dissections of the head were carried out upon both types of preparation.

The animals were obtained shortly after death, having in most instances been killed by bleeding. Prior to injection the head was removed together with the adjacent portion of the neck. The injection mass was introduced into one or both common carotid arteries, and pads of cotton-wool were held firmly against the cut vertebra to prevent undue loss of the mass from the vertebral arteries.

The radio-opaque injection masses used were suspensions of barium sulphate or bismuth carbonate. These were introduced by syringe in amounts which varied according to the size of the animal. On completion of the injection a stereoscopic radiograph was taken of the whole head in the ventro-dorsal, lateral and oblique projections, and similar views were taken after removal of the lower jaw. Subsequently the head was divided by a saw-cut in the mid-line, and stereoscopic radiographs were taken of each half of the head in the lateral projection.

For injections of neoprene latex, glass cannulae were used and the mass was introduced from a pressure bottle at pressures ranging from 200 to 500 mm Hg. On conclusion of the injection the cannulated vessels were ligated and the head of the animal was immediately placed in an acidified fluid (either water or 10 % formol saline) so that the neoprene should set. Some of the neoprene preparations were dissected before the tissues were destroyed by maceration, or after the preparation had been partially macerated, to determine the relations of the vessels to other structures. For maceration of the tissues the head was placed in a covered bath containing concentrated hydrochloric acid which was kept at a warm temperature. After a few days the preparation was gently washed in running water for some hours, and if necessary was then transferred to a similar bath containing 10 % potassium hydroxide for the purpose of removing the remaining fat. It was given a final prolonged wash a day or two later, and the cast was then usually entirely free from tissue. The casts were examined under water. In some of the larger animals a magnified view was not always necessary, but generally the study of the vessels was made through a stereoscopic dissecting microscope.

It was found to be of great value to have the different types of preparation for study. The radiographic material made it possible to visualize the course of the vessels in relation to each other and to the bony structures, and to become familiar with the characteristic features of the course of individual vessels. From dissection of the injected preparations the relations of the vessels to the soft tissues could be determined. With the knowledge obtained from these preparations the individual vessels could be readily identified in the final neoprene casts, which in this as in other investigations proved to be an invaluable material for making a detailed study of the pattern and connexions of the vascular system.

In addition, a few heads (cat and sheep), some of which had been injected with a 2 % solution of Berlin blue, were used for a histological study of the carotid rete.

CAT, *Felis domestica*

(Figures 1; 10 to 13, plate 12; 14, 15, plate 13)

In the cat the carotid rete is situated outside the skull, and for this reason we term it an extracranial rete (rather than a 'rete externum' in the terminology of Davis & Story 1943) to distinguish it from the intracranial rete of the artiodactyls examined. Although most of our findings agree with the account given by Davis & Story (1943), we have in no specimen found the 'rete internum' described by these authors.

The carotid rete

The extracranial rete is a tightly packed network of interlacing arterial vessels through which blood is transmitted from the external carotid arterial system to the circle of Willis, to the orbit, and to the ethmoidal region of the nose (see figures 10 to 15). The rete is wrapped around the internal maxillary artery as the latter crosses the medial pterygoid muscle (figure 13). It is closely related to the branches of the trigeminal nerve, and in fact the maxillary division of this nerve passes directly through it. The rete is shaped like a pyramid, with a base situated antero-laterally, and three sides, forming respectively an inferior, a supero-lateral, and a supero-medial surface.* The base is concave and is closely applied to the muscle cone of the orbit, and the apex lies at the origin of the rete from the internal maxillary artery. The inferior surface rests upon the medial pterygoid muscle, the supero-lateral surface is adjacent to the temporalis muscle, and the supero-medial surface lies immediately beneath the base of the skull.

The vessels which compose the rete are for the most part relatively uniform in calibre (casts of these vessels measuring 200 to 300μ in diameter). They are closely intertwined and anastomose freely with one another (figures 13, 15). The whole structure lies in a venous lake which receives blood from the orbital veins and cerebral sinuses and drains through a venous plexus (the pterygoid plexus) into the facial and jugular veins.

The rete is supplied by short branches of the internal maxillary artery which courses through the midst of it as a single large vessel (figure 1). These arteries which supply the rete approximate in calibre to the vessels which form the body of the rete. The most proximal of the afferent arteries to the rete is fairly constant in position and arises at an acute angle from the superior surface of the maxillary artery (figure 13) directly beneath the foramen rotundum. This artery breaks up to form the vessels of the supero-lateral and supero-medial surfaces of the rete. Other arteries of supply arise from the lateral and medial surfaces of the internal maxillary artery, and form a tunnel for the maxillary nerve (figure 14) before freely anastomosing with other vessels of the rete. The angle at which the afferent arteries to the rete are given off from the internal maxillary artery increases until

* The descriptive terms of orientation conventionally used in human anatomy have been employed throughout in this account.

in the case of the most distal ones it is greater than a right angle. The vessels of the inferior surface of the rete are derived from a short trunk arising from the inferior surface of the internal maxillary artery approximately midway along its course within the rete. This inferior portion of the rete receives, in addition, a branch from the proximal part of the inferior dental artery (figures 1; 11, plate 12). The mandibular nerve (including its motor division) passes between the branch of the inferior dental artery which supplies the rete and the internal maxillary artery.

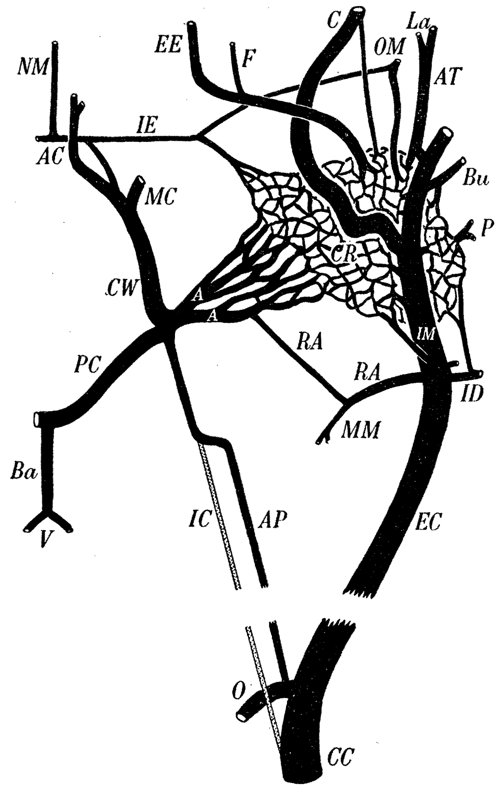


FIGURE 1. Cat (*Felis domestica*). Schema of the carotid rete and its associated arteries. That part of the internal carotid artery which degenerates soon after birth is indicated by stippling. (In this and subsequent diagrams a standardized basic plan has been used. For simplicity only that segment of the posterior cerebral artery which forms part of the circle of Willis is shown, and the anterior communicating artery has been omitted. For explanation of reference letters see p. 205).

Histologically, the vessels which compose the rete have the characteristics of medium-sized, muscular arteries. The internal diameter, in paraffin sections of uninjected material, was found to range from about 70 to 230μ. There is a relatively thin adventitial coat, and this is covered by the endothelial cells which form the lining of the venous sinus in which the arteries of the rete lie. Occasional small nerve trunks are seen within the mesh formed by the arteries composing the rete.

Connexion of the rete with the circle of Willis (*arteria anastomotica*)

The vessels of the supero-medial and super-lateral surfaces of the rete re-form into two main groups of vessels which anastomose with one another and pass medially and backwards through the orbital fissure together with the ophthalmic division of the trigeminal nerve. After entering the cranium they pass through the cavernous sinus and unite to form a single, large and short artery which pierces the dura to join the circle of Willis at the site occupied by the internal carotid artery in those species in which this vessel is present. The arteries passing from the rete to the circle of Willis between the dural layers are larger in calibre than the vessels composing the body of the rete, and their number and pattern is variable. Taken together they form the 'arteria anastomotica' (figures, 10, 12, 13, plate 12; figure 15, plate 13.)

One of the posterior vessels of the arteria anastomotica receives the ramus anastomoticus (figures 12, 13). Pituitary and meningeal arteries arise from the arteria anastomotica, which also not infrequently gives origin to a branch communicating with the internal ethmoidal artery.

Arteries supplying the orbit

The vessels of the anterior concave surface of the rete give rise to various arteries which supply the orbit. The extent to which some of the orbital tissues receive their blood supply from the rete and from the maxillary artery respectively is variable. The extrinsic ocular muscles are largely supplied from the anterior surface of the rete, by a superior and an inferior group of vessels; the latter on one occasion took its origin from the medial side of the rete. The inferior group communicates with the internal ethmoidal and ciliary arteries and frequently gives origin to the zygomatic artery. The supra-orbital artery usually arises from the superior group.

The *ciliary artery* has a characteristic pattern which is readily recognizable (figures 12, 13). It takes its origin from the superior surface of the internal maxillary artery about midway along the course of the latter through the rete (figure 1). It is a large vessel and in its proximal portion is completely surrounded by the vessels of the rete, but it has no communication with any one of them. In its course within the rete the ciliary artery is tortuous, and on emerging from the rete it makes a spiral turn around the optic nerve. When it again reaches the lateral side of this nerve just behind the globe, it breaks up into long and short ciliary branches (figure 12). A small artery arising from the rete anastomoses with the ciliary artery (figure 1) and gives off other ciliary branches before joining the main vessel. The inferior group of vessels to the extrinsic ocular muscles also freely anastomose with the ciliary artery. An internal ophthalmic artery, connecting the circle of Willis with the ciliary artery (the arteria ophthalmica reported by Davis & Story 1943), has not been found in any specimen.

The *lacrimal artery* is usually a branch of the anterior deep temporal artery but sometimes has a different source of origin. Occasionally it is a branch of the external ethmoidal artery; in other cases it arises from the rete at its antero-superior border by several roots and is connected with the anterior deep temporal artery either at its root or in the early part of its course.

The *frontal artery* is commonly a branch of the external ethmoidal artery (figure 1), but occasionally it takes its origin from the rete.

Ethmoidal arteries

The *external ethmoidal artery* generally springs from the antero-superior edge of the rete, medial to the lacrimal and deep temporal arteries (figures 1, 13). It has several roots, and after passing above and medial to the muscle cone it reaches the medial wall of the orbit, gives off the frontal artery and almost immediately passes through the ethmoidal foramen to reach the olfactory fossa. Sometimes the lacrimal artery is a branch of the external ethmoidal artery.

The *internal ethmoidal artery* takes its origin by several roots from the anterior part of the medial and inferior surfaces of the rete (figures 1; 15, plate 13). These vessels of origin give the impression of forming a continuation of the rete at its medial antero-inferior angle. After passing beneath the optic nerve they unite to form a single trunk which enters the cranium through the optic foramen and runs across the base of the skull, deep to the dura, to anastomose in the mid-line with the corresponding vessel of the opposite side. A single vessel, the nasal meningeal artery (figures 1, 15), runs forward, generally in the mid-line, from the point of anastomosis and communicates with the external ethmoidal artery and the olfactory branch of the anterior cerebral artery by means of the ethmoidal arterial plexus. (In one cat the nasal meningeal artery joined the anterior branch of the anterior cerebral artery of one side). Although Davis & Story (1943) use the term 'ethmoidal rete' we do not consider this plexus as a true rete. From the ethmoidal plexus, vessels pass through the cribriform plate to supply the ethmoidal region of the nose and the sphenoidal sinus. Within the orbit the internal ethmoidal artery has communications with the inferior group of vessels to the extrinsic ocular muscles and with the ciliary artery.

Often a branch from the circle of Willis on either side communicates with each of the internal ethmoidal arteries before the latter join each other (figure 1). This is said to happen in the absence of an internal ophthalmic artery (Davis & Story 1943). The ophthalmic artery described by Davis & Story has, however, never been observed in this study, and when no communication with the circle of Willis was present, a vessel was found connecting the internal ethmoidal artery either with the medial side of the rete, or else with the arteria anastomotica just before its junction with the circle of Willis.

Arteries supplying the muscles of mastication

Some of the temporal arteries arise from the internal maxillary artery proximal to the rete, while other short vessels have their origin in the supero-lateral surface of the rete itself. One large vessel, the anterior deep temporal artery, has its origin near the base of the rete. It either arises from the maxillary artery alone, or it has one or more additional roots in the rete (figures 1, 13). The anterior deep temporal artery frequently gives rise to the lacrimal artery and occasionally to the external ethmoidal artery, and always anastomoses with the superficial temporal artery.

The arteries which supply the pterygoid muscles, the buccinator and the tensor palatinae arise from the inferior portion of the rete (figures 1, 13, 14) and have a variable degree of communication with the maxillary artery and with one another near their origin.

The vessel which connects the rete with the inferior dental artery supplies the anterior tympanic artery and another vessel which accompanies the lingual nerve.

The ramus anastomoticus

This artery is usually a branch of the internal maxillary artery, taking its origin almost opposite to the root of the inferior dental artery (figure 12). Occasionally it arises from the most proximal of the arteries which supply the rete or from the superior surface of the rete itself at its posterior extremity. The ramus anastomoticus passes through the foramen ovale and then divides into two, the smaller branch forming the middle meningeal artery, and the larger running forwards to join one of the more posterior vessels of the arteria anastomotica within the cavernous sinus (figure 13). The middle meningeal artery gives rise to a vessel which passes to the middle ear accompanying the superficial petrosal nerves. In one specimen the middle meningeal artery was larger than the continuation of the ramus anastomoticus.

The internal carotid artery

The remains of an internal carotid artery was found in dissected preparations as a fine strand of fibrous tissue, extending from the common carotid artery to the tympanic bulla. In no specimen, however, could the patency of the vessel be demonstrated by the use of an injection mass. This may be due to the fact that the youngest cat examined was about 1 month old.

The ascending pharyngeal artery

This artery generally arises from the occipital artery near its origin from the external carotid artery. After passing over the inferior surface of the tympanic bulla, it enters the cranium through the foramen lacerum medium (foramen lacerum of man) and courses through the cavernous sinus to join the arteria anastomotica at the point where this passes through the dura (figures 1, 15). It seems probable that the intracranial portion of the ascending pharyngeal artery is a persisting segment of the internal carotid artery.

The circle of Willis

The main vessels which are connected by the circle of Willis are the basilar artery, the superior cerebellar artery, the posterior cerebral artery, the ascending pharyngeal artery, the arteria anastomotica, and the middle and anterior cerebral arteries (figures 1, 15). The brain clearly derives the greater part of its blood supply from the maxillary artery through the rete and arteria anastomotica, but in addition a substantial contribution is provided by the basilar artery, which receives blood from the vertebral artery of each side (figure 10, plate 12). An occipito-vertebral anastomosis is present.

SHEEP, *Ovis aries*

(Figures 2; 16, 17, plate 13; 18 to 20, plate 14)

In the sheep, as in other artiodactyls, the carotid rete lies within the cranium, and for this reason we use the term intracranial rete to emphasize the difference of its situation from that of the extracranial carotid rete of the cat.

The carotid rete

The intracranial rete consists of a compact, oval-shaped, arterial plexus lying in the cavernous sinus at the base of the skull (figures 16, 17, 19). It is situated near to the mid-line, extends from the foramen ovale to the orbital fissure and communicates with the rete of the opposite side by a few anastomotic vessels of varying calibre which lie in the posterior part of the pituitary fossa (figure 17). The rete is closely related to the branches of the trigeminal nerve after these leave the trigeminal ganglion. The pattern of the vessels which compose the rete is essentially similar to that seen in the cat. The vessels are of relatively uniform calibre, intertwined and with frequent anastomoses (figure 17).

The rete has two main sources of blood supply, both of which are branches of the internal maxillary artery. In the near-term foetus a further source of supply is provided by the ascending pharyngeal artery (see below). The internal maxillary artery lies at a distance from the rete outside the cranium and gives off a single branch (the ramus anastomoticus), which breaks up into the lateral and posterior portion of the rete (figures 16, 17, 19), and a group of several short trunks (the arteria anastomotica) which join the rete anteriorly (figures 16, 17).

Histologically, the arteries of the sheep's rete are essentially similar to those which form the rete of the cat. They are vessels of medium size (the internal diameter, in paraffin sections of uninjected material, ranges from about 120 to 350μ) and have muscular walls. The adventitial layer tends to be a little thicker than it is in the cat, but is again covered by a layer of endothelial cells which separates the walls of the retial arteries from the venous blood of the cavernous sinus.

Connexion of the rete with the circle of Willis

The numerous small vessels of the rete re-form at the anterior part of its medial surface to make a single large arterial trunk which bends sharply upwards to penetrate the dura and join the circle of Willis. This is the internal carotid artery, which persists only at this level (figure 18).

The arteria anastomotica

The term 'arteria anastomotica' is used to designate the anterior group of vessels connecting the rete with the internal maxillary artery. (The reasons for applying this name to this group of arteries are given in the discussion, where the homologous nature of certain vessels is considered.) This group of vessels (arteria anastomotica) consists of two or three large trunks and several small vessels which pass through the orbital fissure to enter the cranium where they immediately break up to join the rete (figure 17). The maxillary division of the trigeminal nerve passes between major vessels of the arteria anastomotica near the floor of the orbit.

Arteries supplying the orbit

The orbit derives the greater part of its blood supply from a single vessel, the external ophthalmic artery. The latter arises from the arteria anastomotica (figure 2), and passes over and to the medial side of the orbital muscle cone. During this course it gives rise to a plexus of arteries, the orbital rete (figure 20). This is a less complex structure than the carotid rete, but the vessels which form the orbital rete are again of fairly uniform calibre and are plexiform in their arrangement. The numerous vessels of this rete are supplied directly from the external ophthalmic artery and empty into a single large vessel, the ciliary artery, which also receives a branch from the circle of Willis (the internal ophthalmic artery). Beyond the origin of the orbital rete, the external ophthalmic artery is continued as the external ethmoidal artery which gives rise to the frontal artery before leaving the orbit (figure 20).

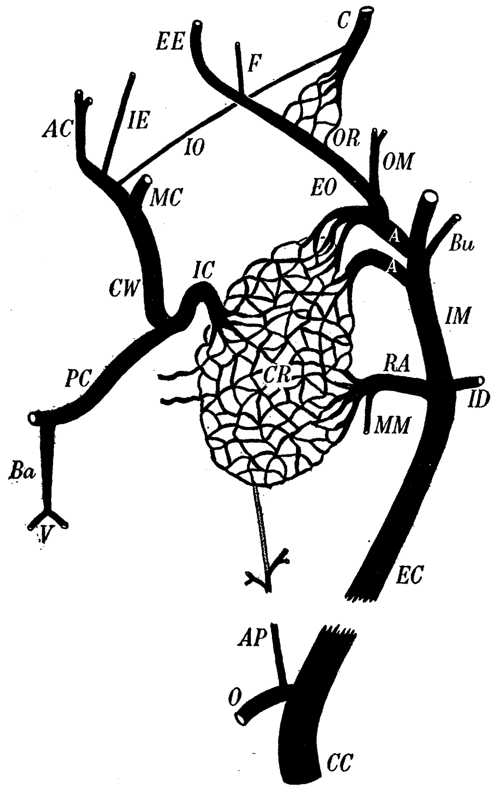


FIGURE 2. Sheep (*Ovis aries*). Schema of the carotid rete and its associated arteries. That part of the ascending pharyngeal artery which was present in the near-term foetus, but absent in the adult, is indicated by stippling. (For explanation of reference letters see p. 205.)

Ethmoidal arteries

As indicated above, the *external ethmoidal artery* forms the continuation of the external ophthalmic artery and leaves the orbit by the ethmoidal foramen. Within the cranium it anastomoses both with the internal ethmoidal artery and with a branch of the anterior cerebral artery by means of an ethmoidal plexus situated within the olfactory fossa.

The *internal ethmoidal artery* takes its origin from the circle of Willis (figure 2).

Arteries supplying the muscles of mastication

These vessels are not related to the carotid rete but for the most part are branches of the maxillary artery and the ramus anastomoticus. It is of interest that the mandibular division of the trigeminal nerve lies medial to the maxillary artery, whereas in the cat it is situated lateral to it.

The ramus anastomoticus

The ramus anastomoticus forms one of the major contributions to the carotid rete. It is a large vessel which arises from the internal maxillary artery nearly opposite to the origin of the inferior dental artery (figures 16, 17) and enters the cranium through the foramen ovale. Here it immediately breaks up to form the posterior part of the rete and also to supply some vessels to the meninges.

The internal carotid artery

The only portion of the internal carotid artery which was found to persist in the sheep was the short trunk which connected the carotid rete to the circle of Willis (figure 18). In no specimen, including near-term foetuses, did this vessel persist at a more proximal level, i.e. between the common carotid artery and the rete.

The ascending pharygeal artery

In the near-term foetus the ascending pharyngeal artery contributes part of the blood supply to the carotid rete (figures 2, 17). It arises from the occipital artery and enters the cranium through the foramen lacerum medium to join the inferior surface of the rete. Its extracranial course is thus similar to that found in the cat. In the adult sheep the ascending pharyngeal artery has no major communication with the carotid rete.

The circle of Willis

The circle of Willis in the sheep is similar to that of man (figures 2, 18). The basilar artery, however, appears to be a branch of the circle of Willis rather than an artery which supplies the circle, for it diminishes in calibre as it passes caudally along the brain stem (figures 16, 19), and has only insignificant communications with the vertebral and occipital arteries. Moreover, the angle of branching of the cerebellar and pontine arteries (acute caudally) suggests that the direction of flow in the basilar artery is away from and not towards the circle of Willis. This suggestion is confirmed by observations made on the living animal by means of rapid serial angiography. Thus it would appear that in the sheep virtually the whole of the cerebral blood supply is derived from the internal maxillary artery (i.e. from the external carotid system) through the carotid rete.

GOAT, *Capra hircus*

(Figures 3; 21, 22, plate 15; 23 to 25, plate 16)

In general, the vascular arrangements of the rete and its associated vessels in the goat closely resemble those of the sheep described above.

The carotid rete

The carotid rete is situated intracranially in the cavernous sinus as it is in the sheep (figures 21, 22). The pattern and calibre of the vessels forming the rete and the sources from which it receives its blood supply are essentially the same as those found in the sheep (figures 23 to 25). However, the vessels which connect the rete of each side with one another in the posterior part of the pituitary fossa are more numerous and plexiform (figures 21, 25).

Connexion of the rete with the circle of Willis

As in the sheep, an internal carotid artery, which is formed by the vessels leaving the rete, passes upwards through the dura to join the circle of Willis (figures 22, 23, 25).

The arteria anastomotica

The characteristic features of this vessel (figures 23, 24) and its anatomical relations resemble those found in the sheep.

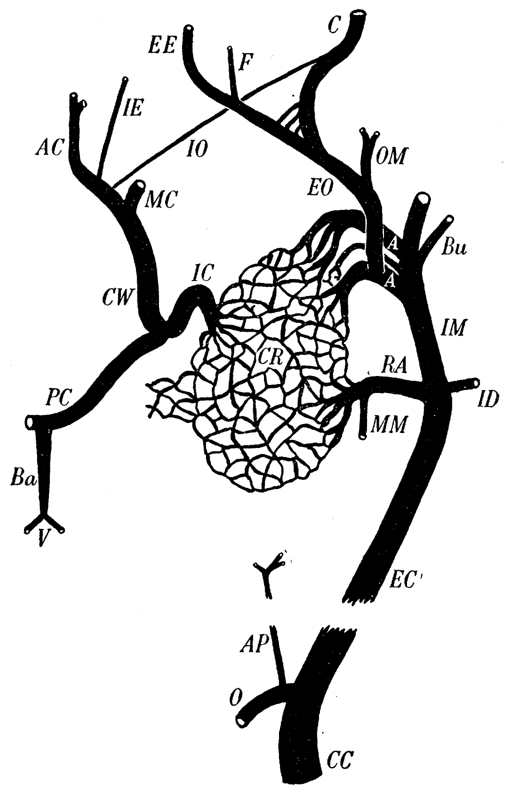


FIGURE 3. Goat (*Capra hircus*). Schema of the carotid rete and its associated arteries. (For explanation of reference letters see p. 205.)

Arteries supplying the orbit

The main vessel of supply to the orbit is the external ophthalmic artery. This artery arises either from the most proximal of the trunks forming the arteria anastomotica (figure 3) or from the internal maxillary artery itself close to the origin of the arteria anastomotica (figures 23, 24). It passes over the orbital cone to the medial side, where it divides into a ciliary artery and an external ethmoidal artery. Shortly after this bifurcation the latter vessels communicate with one another by a rete of simple structure (figure 3). These connecting vessels are the counterpart of the more highly developed orbital rete seen in the sheep and in the ox. The ciliary artery curves beneath the optic nerve to reach its lateral side and there gives rise to long and short ciliary branches.

An internal ophthalmic artery is present and forms a connexion between the circle of Willis and the ciliary artery. This vessel passes through the optic foramen to reach the orbit.

Ethmoidal arteries and arteries supplying the muscles of mastication

The origin and distribution of these two groups of vessels do not differ in any important respect from those found in the sheep.

The ramus anastomoticus

In general, the ramus anastomoticus of the goat is very similar to that of the sheep. The proximity of the respective roots of the ramus anastomoticus and of the inferior dental artery in the internal maxillary artery was emphasized by the finding that in one animal the inferior dental artery was found to take its origin from the proximal part of the ramus anastomoticus itself (figure 24).

The internal carotid artery

As in the sheep, no proximal portion of the internal carotid artery was found. The only persisting segment of this vessel was the short trunk which connected the rete with the circle of Willis (figures 23, 25).

The ascending pharyngeal artery

In the animals examined the ascending pharyngeal artery did not have any major communication with the carotid rete, but the meningeal branches of this artery communicated with meningeal branches springing from the rete and from the ramus anastomoticus. (No foetuses were available for study in this species, as was the case in the sheep.)

The circle of Willis

The arrangements of the circle of Willis and the basilar artery in the goat are similar to those seen in the sheep (figure 3). Again, the direction of blood flow in the basilar artery would appear to be away from, and not towards, the circle of Willis.

OX, *Bos taurus*

(Figures 4; 26 to 28, plate 17; 29, 30, plate 18)

Only one example of this species of animal was available for study; this was a calf of about 4 months old. Whereas the arrangements of the vessels related to the rete were found to be essentially the same in the sheep and in the goat, those seen in this specimen of the ox were in some respects markedly different.

The carotid rete

The carotid rete is again an intracranial rete lying in the cavernous sinus at the base of the skull. The arrangement of the vessels composing the rete is similar to that seen in the artiodactyls described above, but the shape of the structure so formed is somewhat different (figure 28). The main body of the rete of one side is joined to that of the other side at both the anterior and posterior ends by continuations of the retial vessels; thus a ring of retial arteries is formed which surrounds the hypophysis cerebri. Anteriorly there is a V-shaped extension of the retial arteries which is supplied by vessels from the anterior communicating portion of the two retia (figure 28). At its origin this extension lies beneath the optic chiasm and each arm of the V accompanies an optic nerve. The posterior communicating portion of the two retia receives the large serpentine arteries of the basi-sphenoidal plexus (figures 26, 28). In the specimen examined the calibre of the retial arteries was found to vary in different portions of the rete, the vessels being considerably smaller posteriorly than anteriorly. The rete derives 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 artery through a few small vessels (figure 4).

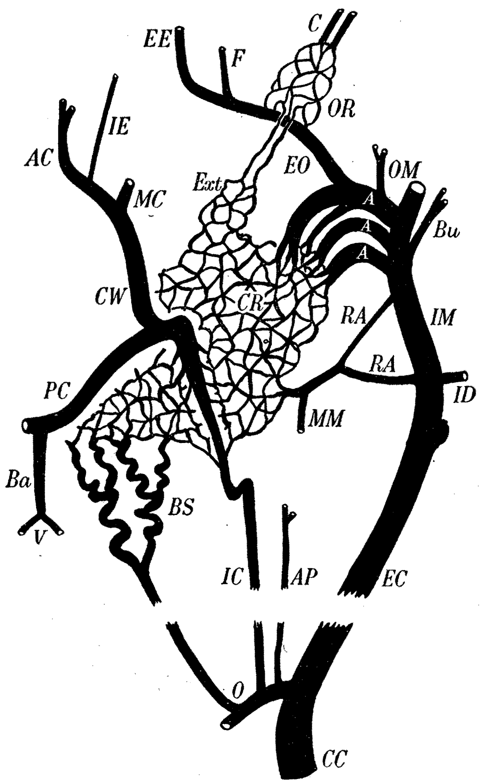


FIGURE 4. Ox (*Bos taurus*). Schema of the carotid rete and its associated arteries. Only one specimen was examined, and this was a young animal. (For explanation of reference letters see p. 205.)

Connexion of the rete with the circle of Willis

In this specimen the communication between the rete and the circle of Willis was provided by small offshoots from the rete which joined the distal portion of the internal carotid artery. (The unusual features of the internal carotid artery in this animal will be described below.)

The arteria anastomotica

The arteria anastomotica is formed by a group of branches of the internal maxillary artery which pass through the orbital fissure to join the anterior portion of the rete (figures 26 to 28). These arrangements are essentially the same as those seen in the sheep and goat, but the branches which compose the arteria anastomotica are more numerous (figure 26). These vessels pass between the bundles of the maxillary nerve.

Arteries supplying the orbit

As in the sheep and goat, the main artery which supplies the orbit is the external ophthalmic artery. This artery takes its origin from one of the most anterior trunks of the arteria anastomotica (figures 4, 27). During its course over the muscle cone it gives off numerous small branches which form the orbital rete (figure 30). This rete, which has numerous small communications with the anterior V-shaped extension of the carotid rete, is more highly developed than the orbital rete of the sheep and the goat, but is still much less complex than the carotid rete. The vessels of the orbital rete re-form to make two trunks, the ciliary arteries (figure 30). The external ophthalmic artery continues beyond the rete as the external ethmoidal artery, which gives off the frontal artery.

No internal ophthalmic artery was found in this preparation.

Ethmoidal arteries and arteries supplying the muscles of mastication

In the calf the arrangements of these two groups of vessels showed no important differences from those found in the sheep and goat.

The ramus anastomoticus

This vessel was found to have two roots in the maxillary artery (figure 27), and though relatively small in calibre its course and distribution were essentially the same as in the other artiodactyls described above.

The internal carotid artery

In the specimen examined a complete internal carotid artery was found to be present. 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 vessel showed the marked bend in the region of the tympanum which is characteristic of the internal carotid artery in certain other species (figures 26 to 28). As it approached the posterior part of the inferior surface of the carotid rete, the internal carotid artery, which up to this level was relatively small, was found to give off a few fine vessels to supply the rete and then to plunge into its midst (figure 26). During its course within the rete the internal carotid artery received several vessels from the body of the rete and steadily increased in calibre until finally, when it emerged again from the medial surface of the rete to join the circle of Willis, it was a large vessel (figures 4, 29).

The ascending pharyngeal artery

This artery, which had its origin in the proximal part of the occipital artery, did not communicate directly with the rete, and had only minor connexions with meningeal vessels related to the ramus anastomoticus.

The occipital artery

In this animal, the occipital artery was found to give a major contribution to the carotid rete. The occipital artery arose from the common carotid artery as a trunk of considerable size (figure 4). This trunk gave off the internal carotid and ascending pharyngeal arteries and then divided, the major branch passing on towards the cranium, which it entered between the atlas and the occipital bone. Within the skull on the upper surface of the basi-sphenoid the occipital artery of each side supplied a large arterial plexus which had, in addition, connexions with the vertebral arteries. This basi-sphenoidal arterial plexus communicated directly with the posterior part of the carotid rete of each side (figure 28).

The circle of Willis

Apart from the fact that the circle of Willis receives part of its blood supply from the internal carotid arteries and from the occipital arteries via the basi-sphenoidal plexus, the vessels related to the circle are essentially similar to those seen in the sheep and the goat. The basilar artery is again a relatively insignificant vessel, diminishing in calibre caudally (figure 29).

PIG, *Sus scrofa*

(Figures 5; 31, 32, plate 18; 33, plate 19)

In the pig the carotid rete is situated intracranially within the cavernous sinus, but it lies more posteriorly than in the other artiodactyls. When compared with the latter animals, however, certain marked differences are found in the vessels which supply the rete.

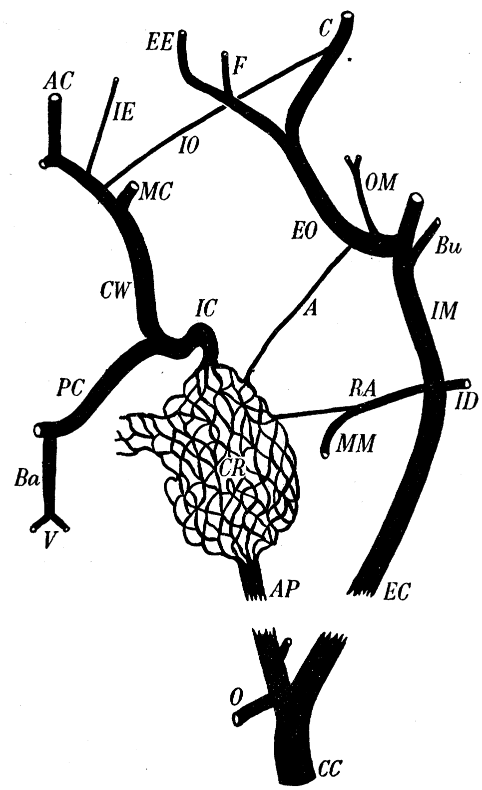


Figure 5. Pig (*Sus scrofa*). Schema of the carotid rete and its associated arteries. (For explanation of reference letters see p. 205.)

The carotid rete

The rete is oval in shape and consists of a closely knit plexus of small arteries which run predominantly in the sagittal plane (figure 32). The vessels of the rete of each side connect so freely with one another at their antero-medial borders across the floor and posterior part of the pituitary fossa that the two retia have the appearance of a single structure.

The rete derives almost its entire blood supply from the ascending pharyngeal artery (figures 31, 32, 33). It receives insignificant contributions from the internal maxillary artery via the arteria anastomotica, which is a very small vessel, and via the ramus anastomoticus, which in the distal part of its course is also a tenuous vessel (figures 5, 32, 33).

Connexion of the rete with the circle of Willis

At the anterior extremity of the rete the vessels of this network re-form into a single short trunk which pierces the dura and joins the circle of Willis (figure 33). This trunk is the only persistent portion of the internal carotid artery.

The arteria anastomotica

This is a tenuous vessel which arises from the external ophthalmic artery and joins the rete at its anterior border (figures 32, 33).

Arteries supplying the orbit

Most of the arteries supplying the orbit arise from the external ophthalmic artery, which in this animal takes its origin from the internal maxillary artery (figure 33). There is no orbital rete in the pig.

An internal ophthalmic artery is present. This forms a connexion between the circle of Willis and the ciliary artery, and also communicates with the internal ophthalmic artery of the opposite side.

Ethmoidal arteries and arteries supplying the muscles of mastication

The arrangements of both these groups of vessels are the same as those seen in the other artiodactyls.

The ramus anastomoticus

In the other artiodactyls, the ramus anastomoticus is a large vessel which connects the internal maxillary artery with the carotid rete and gives off only small branches to supply the meninges of the middle cranial fossa. In the pig, however, the main vessel passes to the meninges and the distal part of the ramus anastomoticus is represented by only a very small branch which passes to the rete (figures 5, 33).

The internal carotid artery

The only persisting portion of the internal carotid artery which was found even in the new-born pig was the short trunk which connects the carotid rete with the circle of Willis (figure 33).

The ascending pharyngeal artery

The ascending pharyngeal artery is a large vessel which shortly after arising from the common carotid artery gives off the occipital artery (figures, 32, 33). It enters the cranium through the foramen lacerum medium and then immediately breaks up into vessels which form the rete.

The circle of Willis

The only unusual feature of the circle of Willis in the pig is the junction of the right and left anterior cerebral arteries to form a single anterior cerebral artery (figure 5). The basilar artery and the vertebral arteries are noticeably larger than they are in the other artiodactyls. The degree of anastomosis between the occipital and vertebral arteries is considerable. The major contribution to the circle of Willis would appear to be derived from the ascending pharyngeal artery through the carotid rete (figures 31, 32).

DOG, *Canis familiaris*

(Figures 6; 35, plate 19)

Most of our findings agree with the description given by Jewell (1952). There is no carotid rete in the dog, though a few vessels are present which can be considered as a counterpart of the well-developed intracranial rete which was present in the artiodactyls examined (figure 6).

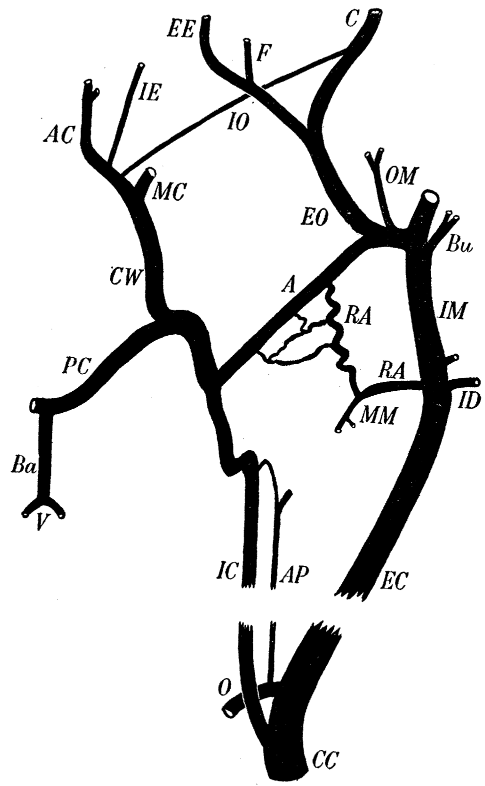


FIGURE 6. Dog (*Canis familiaris*). Schema of the vessels homologous with the carotid rete and associated arteries illustrated in figures 1 to 5. (For explanation of reference letters see p. 205.)

The internal maxillary artery

The internal maxillary artery, after passing deep to the ramus of the mandible, runs deep to the mandibular nerve and across the pterygoid muscles to reach the orbit. During this course it gives rise to arteries which supply the muscles of mastication and to the ramus anastomoticus and the external ophthalmic artery.

The arteria anastomotica

The arteria anastomotica takes its origin from the external ophthalmic artery soon after the latter has arisen from the internal maxillary artery at the apex of the orbit (figure 35).

From this origin the arteria anastomotica enters the skull through the orbital fissure and runs backwards to join the internal carotid artery at the posterior end of the cavernous sinus (figure 35). Soon after entering this sinus the arteria anastomotica receives the ramus anastomoticus itself as well as a few small branches of this vessel.

The ramus anastomoticus

This artery arises from the maxillary artery opposite the origin of the inferior dental artery and passes through the foramen ovale to enter the cranium. Soon after entering the skull the ramus anastomoticus gives off the middle meningeal artery and then runs forwards through the cavernous sinus to communicate with the arteria anastomotica both directly and by a few small vessels (figures 6, 35). These communications between the ramus anastomoticus and the arteria anastomotica have been considered as an internal rete of primitive or vestigial form by Tandler (1899) and Ask-Upmark (1935). The middle meningeal artery may be larger or smaller than the continuation of the ramus anastomoticus beyond the point of origin of the former vessel. From the middle meningeal artery a small branch accompanies the petrosal nerves to the middle ear.

Arteries supplying the orbit

The orbital tissues derive the greater part of their blood supply from the external ophthalmic artery. This artery, after giving off the arteria anastomotica, soon divides into several branches including the ciliary, lacrimal, and extrinsic ocular muscular arteries and the external ethmoidal arteries (figure 6).

The internal ophthalmic artery is a branch of the circle of Willis which enters the orbit through the optic foramen and anastomoses with the ciliary artery.

Ethmoidal arteries

The *external ethmoidal artery* runs across the apex of the orbit from the lateral to the medial side to reach the ethmoid foramen, and just before passing through the latter into the cranium it gives off the frontal artery. In the olfactory fossa it anastomoses with the *internal ethmoidal artery* which arises from the circle of Willis (figure 35) and also with vessels from the olfactory branch of the anterior cerebral artery before distributing vessels to the nose.

The internal carotid artery

The internal carotid artery is a relatively large vessel (figure 35). It arises from the common carotid artery and, after entering the cranium, receives the arteria anastomotica within the cavernous sinus before joining the circle of Willis, becoming larger in calibre distal to the point of junction.

The ascending pharyngeal artery

The ascending pharyngeal artery takes its origin from the occipital artery and largely supplies the pharynx. Small vessels provide communications between this artery and the arteries supplying the meninges of the middle fossa. The ascending pharyngeal artery communicates also with the internal carotid artery via small branches to the middle ear.

The circle of Willis

The pattern and distribution of the vessels which form or are associated with the circle of Willis are similar to those seen in man (figure 35). The main arteries which supply the circle of Willis are the internal carotid arteries and the vertebral arteries (via the basilar artery) while, in addition, a substantial contribution is received from the external carotid system via the arteria anastomotica and the ramus anastomoticus. An occipito-vertebral anastomosis is present.

RABBIT, *Oryctolagus cuniculus*

(Figures 7; 34, plate 19)

The rabbit does not have a carotid rete, and no counterpart of this structure can be recognized.

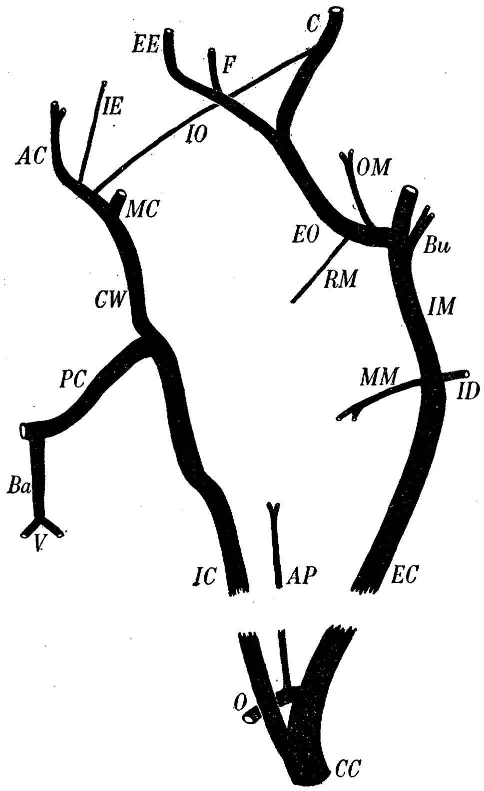


FIGURE 7. Rabbit (*Oryctolagus cuniculus*). Schema of the vessels homologous with those arteries which in certain species (figures 1 to 5) are associated with a carotid rete. (For explanation of reference letters see p. 205.)

The internal maxillary artery

The internal maxillary artery has a course similar to that seen in the dog. Most of the branches which it gives off correspond to those seen in that animal, but the artery which in its origin and early course is similar to the ramus anastomoticus of the dog is, in the rabbit, distributed only to the meninges of the middle fossa and is known as the middle meningeal artery (figure 7).

Arteries supplying the orbit

The external ophthalmic artery, which arises from the internal maxillary artery, has an orbital distribution essentially the same as that in the dog. There is, however, one major difference between the external ophthalmic arteries of the dog and the rabbit, in that in the rabbit there is no direct communication between the trunk of this vessel and the internal carotid artery corresponding to the arteria anastomotica of the dog (figure 7). One small branch of the external ophthalmic artery runs backwards through the orbital fissure, but this vessel supplies only the meninges and is called the recurrent meningeal artery. Its branches anastomose with those of the middle meningeal artery.

An internal ophthalmic artery arises from the circle of Willis and joins the ciliary artery after the latter has entered the orbit through the optic foramen.

Ethmoidal arteries

The account of these vessels given in the description of the dog applies equally well to those found in the rabbit.

The internal carotid artery

This artery arises either from the common carotid artery or from a short trunk common to it and to the occipital artery (figure 34). Its course is similar to that of the dog, but it receives no vessel which corresponds to the arteria anastomotica.

The ascending pharyngeal artery and the circle of Willis

The arrangements of these vessels are in each case similar to those found in the dog (figures 7, 34). In the absence of a ramus anastomoticus and an arteria anastomotica, the circle of Willis derives its blood supply almost exclusively from the internal carotid arteries and from the vertebral arteries (via the basilar artery). An occipito-vertebral anastomosis is present.

RAT, *Rattus norvegicus*

(Figures 8; 36, plate 19)

The rat has no carotid rete and the external carotid artery does not give rise to an internal maxillary artery but is continued as the inferior dental artery. The region which in the other species studied is supplied by the internal maxillary artery is in the rat supplied almost entirely by the stapedial artery (figure 8).

The stapedial artery

The stapedial artery arises from the internal carotid artery (figures 8, 36), passes through the middle ear and between the crura of the stapes to reach the Glaserian fissure where it comes to lie immediately beneath the dura. Here it gives off the middle meningeal artery and then passes forward along a groove on the outer aspect of the petrous bone to enter the pterygoid region, which it traverses to reach the orbit. At the apex of the orbit the artery divides into a supra-orbital and an infra-orbital division (figure 8).

The supra-orbital division of the stapedial artery gives off three main groups of vessels: (*a*) the external ethmoidal artery, which crosses the muscular cone of the eyeball to reach the medial wall of the orbit, where a frontal branch arises before the main trunk of the vessel passes into the cranial cavity to reach the olfactory fossa; (*b*) the ciliary artery, which takes a spiral course around the optic nerve before dividing into the long and short ciliary branches; (*c*) muscular branches to the extrinsic ocular muscles and a lacrimal artery.

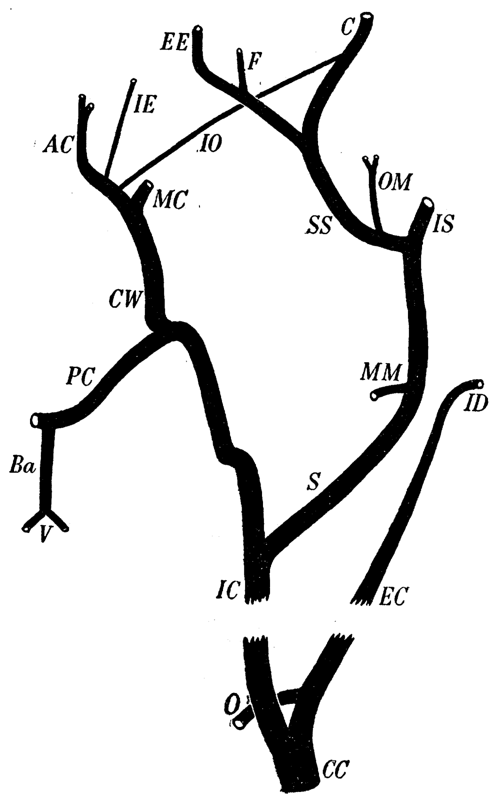


FIGURE 8. Rat (*Rattus norvegicus*). Schema of the vessels homologous with those arteries which in certain species (figures 1 to 5) are associated with a carotid rete. (For explanation of reference letters see p. 205.)

The infra-orbital division of the stapedial artery continues along the floor of the orbit and supplies some branches to the muscles of the orbit, before breaking up into branches which supply the face, the nose and the palate.

The internal ethmoidal artery arises from the circle of Willis.

The internal carotid artery

The internal carotid artery arises either from the common carotid artery or from the occipital artery near to its root. It enters the cranium through the alisphenoid canal before joining the circle of Willis.

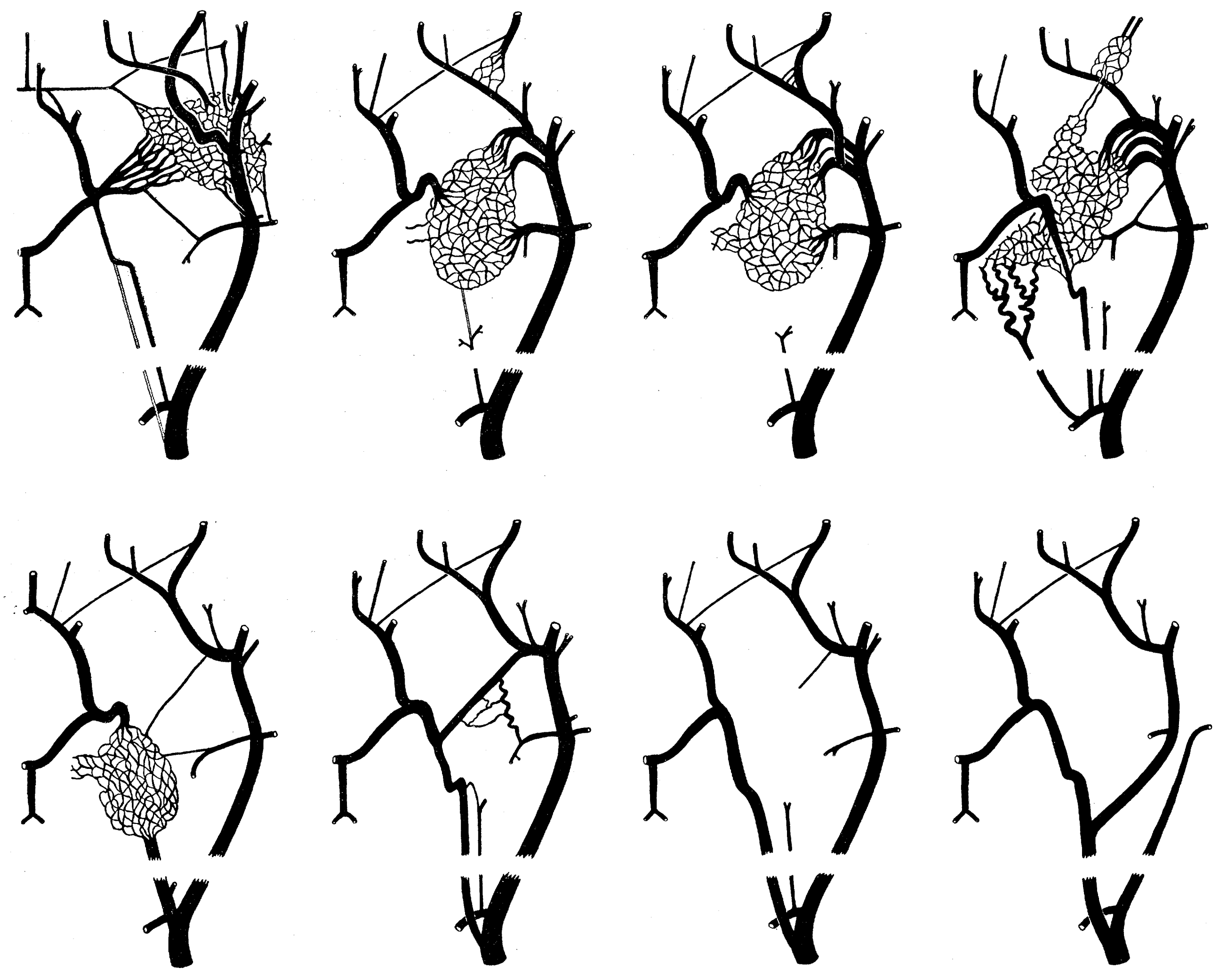
The circle of Willis

The circle of Willis receives its blood supply from the same sources as in man, namely, the internal carotid arteries and the basilar artery, the latter vessel being supplied by the vertebral arteries which receive a small contribution from the occipital arteries (figures 8, 36).

Discussion

In the following pages our observations on the major arteries of the head, including the carotid rete, when present, will be considered from the comparative anatomical point of view. It will be of assistance to the reader to refer from time to time to figure 9, where the schemata of the arteries of the different species are brought together.

a. Felis domestica *b. Ovis aries* *c. Capra hircus* *d. Bos taurus*



e. Sus scrofa *f. Canis familiaris* *g. Oryctolagus cuniculus* *h. Rattus norvegicus*

Figure 9. Schemata illustrated in figures 1 to 8, brought together to facilitate a comparative study. Note the basic pattern of the vessels and its variations.

The carotid rete

In the species examined in this investigation the presence of a well-developed carotid rete was associated with the non-persistence of an internal carotid artery or with a degenerating internal carotid artery. In man and in the rabbit, where the internal carotid artery is present in adult life, no carotid rete exists, but in the dog, which has a relatively large internal carotid artery, a rudimentary rete can be identified. In the goat, sheep and pig no trace of an internal carotid artery was found proximal to the rete, notwithstanding the fact that the specimens included foetal (near-term) sheep and some new-born pigs. The casts of the vessels of the cat showed in no case an internal carotid artery, but a fibrous cord running from the common carotid artery to the tympanic bulla was observed in dissected specimens. Davis & Story (1943) state that this degenerating vessel has a lumen for only the first two weeks of post-natal life. The only specimen of *Bos taurus* which we examined was a calf of about four months old and this showed a complete internal carotid artery, but Tandler (1899) found that in adult life this vessel no longer remained.

Although the carotid rete was found to be an essentially similar structure in the various types of animal, namely, a compact plexus of intertwined arterial vessels, the retia of different species showed certain differences in their characteristic features. One of the most important of these was the different situation of the rete in the cat as compared with that found in the other animals in which a similar structure was present. In the sheep, goat, pig and dog, the carotid rete is situated intracranially, lying in the cavernous sinus. In the cat, however, the rete is situated extracranially near the apex of the orbit. Davis & Story (1943) refer to a small plexus of vessels comprising an 'internal rete' as well as an 'external rete', but we have not seen an 'internal rete' of the type described. However, the group of freely anastomosing vessels, which in this species form the arteria anastomotica and pass through the orbital fissure into the skull to connect the extracranial rete with the circle of Willis, may perhaps be a simple type of intracranial carotid rete. It is presumably these vessels which Ask-Upmark (1935) regarded as a rudimentary carotid rete in the cat, but it is hard to evaluate his findings because he appears to have overlooked the much more striking extracranial carotid rete in this animal. It was his view that an extracranial carotid rete was extremely unusual and obviously present only in certain Lemuridae, where it was situated at the beginning of the internal carotid artery in its cervical portion.

In all species in which it is present the carotid rete communicates with the circle of Willis by means of a short trunk of large calibre which is formed by vessels leaving the rete. In the cat, this trunk, which is occasionally double, is the distal part of the arteria anastomotica, but in the sheep, goat and pig, the connecting trunk is the only persisting portion of the internal carotid artery, the segment proximal to the rete having degenerated. Evidence in support of the identity of the vessel in these artiodactyls was provided by the calf, in which it was found that a similar trunk joining the rete to the circle of Willis was continuous throughout the body of the rete with a still persisting but relatively narrow proximal portion of the internal carotid artery. It was, in fact, the distal portion of a complete internal carotid artery, which had increased in calibre during its passage through the carotid rete as a result of receiving vessels from this structure (figure 9*d*).

The main vessels which may supply the carotid rete are the internal maxillary artery (usually via the ramus anastomoticus and the arteria anastomotica), the ascending pharyngeal artery, and the occipital artery. The internal maxillary artery provides the greatest contribution in the cat, sheep, goat and ox, but in the pig the major vessel supplying the rete is the ascending pharyngeal artery; the latter vessel is also of some importance in the cat and in the mature foetal lamb. The occipital artery plays a significant part in the blood supply of the rete only in the ox. When the rete is intracranial, the internal maxillary artery is connected to it by the ramus anastomoticus and the arteria anastomotica. The relative contributions of these two connexions are comparable in the sheep and in the goat, but in the ox the arteria anastomotica is a much greater contributor than the ramus anastomoticus, and in the pig both vessels are relatively insignificant. The rudimentary rete of the dog is also related to the ramus anastomoticus and the arteria anastomotica (figure 9*f*). In the cat, where the rete is extracranial and surrounds the internal maxillary artery, blood from the latter artery passes to the rete by numerous short afferent arteries. The ramus anastomoticus and the arteria anastomotica contribute nothing to this extracranial rete, but they join one another intracranially within the cavernous sinus, the site at which the intracranial rete of the artiodactyls is present (figure 9*a*).

In the species which we have examined the carotid rete, when it replaces an absent or degenerating internal carotid artery, has in all cases been well developed. It has, however, been reported by others, who have studied a wider range of species, that the degree of development of this structure varies considerably (Ask-Upmark 1935; Tandler 1899; Davis & Story 1943). The pattern formed by the vessels of the rete itself, and in the case of the intracranial rete the degree of communication across the mid-line with the rete of the opposite side, shows some variations from species to species.

Orbital and ethmoidal groups of arteries

The external ophthalmic artery

The simplest arrangement of this artery was seen in the rabbit. In this animal the external ophthalmic artery takes its origin from the internal maxillary artery soon after the latter enters the orbit. It divides into several branches, the chief of which are the anterior ethmoidal, the ciliary, the lacrimal and the recurrent meningeal arteries. In the pig and in the dog, the external ophthalmic artery arises from the internal maxillary artery at a level similar to that in the rabbit, but an arteria anastomotica is present and connects the external ophthalmic artery with the rete. In the sheep, goat and calf the external ophthalmic artery may arise from one of the group of vessels which form the arteria anastomotica, or it may take its origin directly from the internal maxillary artery near the roots of the arteria anastomotica. In either case, it is a less conspicuous vessel than the arteria anastomotica. The cat, rat and man have no external ophthalmic artery as such. In the rat the appropriate territory is supplied by the supra-orbital division of the stapedial artery, in the cat by vessels arising from the rete, and in man by an ophthalmic artery.

The internal ophthalmic artery

The internal ophthalmic artery was present in all the animals examined except the cat and the ox. This vessel arises from the circle of Willis and runs through the optic foramen into the orbit where it joins the ciliary artery. An internal ophthalmic artery was found in some cats by Davis & Story (1943), but when it was absent a vessel from the circle of Willis joined the internal ethmoidal artery. The latter arrangement was a constant finding in this investigation.

In man an ophthalmic artery, which arises from the internal carotid artery before the latter vessel joins the circle of Willis, supplies the orbito-ethmoidal region.

The external ethmoidal artery

In most of the animals examined the external ethmoidal artery was found to be a branch of the external ophthalmic artery. In the cat it arises from the extracranial rete, and in the rat from the supra-orbital division of the stapedial artery, but in all species its course and distribution are essentially the same. This artery is fundamentally the same as that found in man, where it is a branch of the ophthalmic artery.

The internal ethmoidal artery

In the species examined the internal ethmoidal artery is usually a branch of the circle of Willis, but in the cat it arises from the rete and joins the corresponding vessel of the opposite side in the mid-line.

The orbital rete

This interesting structure lies between the external ethmoidal artery and the ciliary artery in the sheep and in the ox; it is more highly developed in the latter species. The orbital rete is supplied by several vessels arising from the external ophthalmic artery; distally the vessels of this rete reform to constitute the ciliary artery. The goat has no true orbital rete, but a rudimentary form of this structure can be identified.

Homologies of the vessels

In describing the arteries supplying the head we have used a standardized terminology throughout. This terminology, which differs slightly from that used by other authors, has been found helpful in this comparative study, for even though the degree of development of a given vessel is variable, a common term which indicates an individual vessel in one animal or a group of vessels in another makes for a clearer understanding of the basic pattern of the vessels.

Homologies can be recognized in the different animals by studying the following features: the course of the vessels through bony foramina or the soft tissues, their relationship to nerves and their areas of distribution. In this study, all these criteria have been used. The trigeminal nerve and the bony foramina of the base of the skull are particularly useful guides in that they indicate the course of the arteries supplying blood to specific regions at a primitive stage. The foramen ovale is traversed in all the species studied by the mandibular division of the trigeminal nerve, and the artery which accompanies this nerve, although having a different name in some species, is a homologous vessel. This vessel, which is known as the middle meningeal artery in the rabbit and in man, is the counterpart of the vessel termed the ramus anastomoticus in the cat, dog, sheep, goat, pig and ox. The homologous nature of these vessels is emphasized by the fact that in the cat, dog and pig a middle meningeal artery is given off by the ramus anastomoticus, and this is sometimes larger than the continuation of the ramus anastomoticus. Further, in the sheep, goat and ox, the dura of the middle fossa is supplied by the ramus anastomoticus. The middle meningeal artery also gives off a branch to the middle ear (the petrosal artery) which accompanies the petrosal nerves. The ramus anastomoticus of the artiodactyls seems to have been overlooked by Tandler (1899), and Lawrence & Rewell (1948) did not describe this vessel in their account of the giraffe.

The orbital fissure is traversed by the ophthalmic division of the trigeminal nerve, and the vessel or group of vessels which accompany this nerve has been named either the arteria anastomotica when it has a direct communication with the internal carotid system (cat, sheep, goat, ox, pig, dog), or a recurrent meningeal artery when it is small and ends in the meninges (rabbit, man). A certain obvious difference in the arteria anastomotica of different species should be appreciated. In the artiodactyls the arteria anastomotica forms some of the afferent vessels to an intracranial rete; in the cat it forms the efferent vessels from an extracranial rete; and in the dog it is a single vessel which connects the external ophthalmic artery with the internal carotid artery, the rudimentary rete lying between the arteria anastomotica and the ramus anastomoticus. In all these species, however, the arteria anastomotica communicates with the ramus anastomoticus, either directly as in the cat or dog, or through the intracranial rete of the artiodactyls. In view of this connexion, it is significant that the recurrent meningeal artery and the middle meningeal artery of the rabbit and man, which are homologous with the arteria anastomotica and the ramus anastomoticus respectively, communicate with each other through fine anastomotic vessels.

In some species (pig, dog, rabbit) the arteria anastomotica or its homologue appears to be a branch of the external ophthalmic artery, whereas in other species (sheep, goat, ox) the latter vessel seems to be a branch of the former. This suggests that the common trunk of these two arteries, which arises from the internal maxillary artery at approximately the same level in all species, is a homologous vessel. In the cat the site of this common trunk is occupied by the carotid rete, and thus no one vessel can be identified as an external ophthalmic artery; the tissues which in other species are supplied by the latter vessel receive their blood supply from several vessels which arise from the carotid rete. It may be that the main stem of the external ophthalmic artery has been replaced by the rete, and that consequently the peripheral orbital and ethmoidal branches frequently have their roots in this structure. In the rat the so-called supra-orbital division of the stapedial artery arises from the stapedial artery at the apex of the orbit and has a distribution similar to that of the external ophthalmic artery of other animals (figure 9). In fact, as will be shown later, it is probably a true external ophthalmic artery.

The site of origin of the peripheral vessels supplying the orbito-ethmoidal region was found to vary frequently in the cat, and also, though much less commonly, in the other species. In the latter the variations seen consisted merely of a shift of the origin of the branches along the main trunk of the external ophthalmic artery. In the cat, however, possibly due to the presence of a rete at this site, the origin of the vessels which correspond to the external ophthalmic artery was found frequently to be transferred to adjacent vessels. The great variability in the vascular arrangements of this system in the cat suggests that a definitive pattern has not yet been established in this animal.

An interesting feature of the cranial vessels of the cat is the formation of a single nasal meningeal artery by the junction of the internal ethmoidal arteries of either side in the mid-line. The internal ethmoidal arteries of the cat are different in their origin and course from the arteries of the same name in the other species studied. In this animal an apparently secondary connexion of the internal ethmoidal arteries with the circle of Willis is present. It is probable that this secondary connexion with the circle of Willis is the homologue of the internal ethmoidal artery of the other species, and that the nasal meningeal artery of the cat is produced by a fusion of these homologous vessels. In this respect it is worth noting that the nasal meningeal artery has a peripheral distribution similar to that of the internal ethmoidal arteries usually seen in mammals. The portion of the internal ethmoidal artery of the cat proximal to its connexion with the circle of Willis is possibly a modified internal ophthalmic artery, for it passes through the optic foramen.

When the cranial arteries of the different species (excluding the rat) are compared a basic pattern is apparent (see figure 9). The main vessels are the internal carotid artery, the external carotid artery, the ascending pharyngeal artery, the ramus anastomoticus, the arteria anastomotica and the external ophthalmic artery. The situation of the carotid rete in relation to this basic pattern is different in the cat and in the artiodactyls, but the difference may be cursorily explained as a shift along the line of the arteria anastomotica.

The fact that there is a basic pattern of the major vessels suggests that a more primitive vessel plays an important part in the formation of this vascular system. If the pattern in the rat, as described in this paper, and that seen in the hedgehog and in the mole (Tandler 1899) are studied, it is evident that the stapedial artery is still important in the adult of these species (figure 9*h*). It seems probable, therefore, that the variations which are seen in the basic arrangements of different species are due to modifications of the stapedial artery at an earlier stage.

The stapedial artery

Tandler's (1902) embryological studies of the rat have shown that the stapedial artery (2nd arch artery) takes over the branches of the primitive mandibular artery (1st arch artery) and so gives origin to the supra-orbital, infra-orbital and mandibular arteries. When the external carotid artery has developed it annexes the mandibular branch, and the latter then loses its connexion with the stapedial artery. In the hedgehog the external carotid artery ends in the superficial temporal artery, and in the mole the stapedial artery takes over the superficial temporal artery (Tandler 1899). However, in the rabbit and man (Padget 1948; Evans 1912) the external carotid artery takes over the whole of the region previously supplied by the stapedial artery.

In the primitive state the branches of the first branchial arch artery accompany the divisions of the trigeminal nerve. These peripheral branches would not alter if only the main stem of the primitive mandibular artery were replaced by the stapedial artery. The supra-orbital division of the stapedial artery would then have an extensive intracranial course from the petrous bone to the orbit; this intracranial course of the supra-orbital division is seen in *Arctomys* (Tandler 1899).

The relationsip of the ramus anastomoticus to the mandibular nerve in all the animals studied, the fact that it lies opposite or nearly opposite to the inferior dental artery (in the goat, the inferior dental artery has been seen to arise from the ramus anastomoticus), and further the fact that the ramus anastomoticus gives off the middle meningeal artery, all suggest that this ramus or its homologue and the inferior dental artery are remnants of the mandibular branch of the stapedial artery.

As has been suggested above, the supra-orbital division of the stapedial artery in the rat probably corresponds to the external ophthalmic artery of other species. However, its peripheral distribution is that of a true supra-orbital division of the stapedial artery and in this animal the intracranial portion has been lost while the supra-orbital division has acquired a secondary communication with the infra-orbital division as the latter vessel enters the orbit.

Fuchs' (1905) embryological studies in the rabbit showed that the supra-orbital division of the stapedial artery was annexed by the internal maxillary artery to form an external ophthalmic artery, and that the intracranial portion of the stapedial artery persisted as the recurrent meningeal branch of the external ophthalmic artery.

The arteria anastomotica, whether a single artery or a group of arteries, may be regarded as a modified supra-orbital division of the stapedial artery, both because of its course through the orbital fissure in company with the ophthalmic division of the trigeminal nerve, and because of its relation to the external ophthalmic artery.

A suggestion that the internal maxillary artery of man is the persistent part of the infra-orbital division of the stapedial artery was made by Evans (1912); he considered that the middle meningeal artery represented the remains of the common maxillo-mandibular stem of the stapedial artery which had been present at an earlier stage in the rat. Padget (1948) suggested that a further vestigial remnant of the stapedial artery was represented in man by the carotico-tympanic arteries.

Both on comparative anatomical and embryological grounds, therefore, it would appear that the arteria anastomotica, the ramus anastomoticus, and the internal maxillary artery, or their homologues, are the persistent remains of a primitive stapedial artery. It may be that the petrosal artery is the remains of part of the stem of the stapedial artery.

It has been suggested by Jewell (1952) that the internal ophthalmic artery of the dog should be considered as the counterpart of the ophthalmic artery of man. However, our comparative studies and those of other workers indicate that it is not the internal ophthalmic artery but the external ophthalmic artery which in its peripheral distribution has taken over the regions supplied by the primitive ophthalmic artery and by the supra-orbital artery. In man, on the other hand, although the ophthalmic artery has a similar peripheral distribution, its site of origin in the internal carotid system is not the same as that of the true internal ophthalmic artery, which arises from the circle of Willis. It may be that the primitive ophthalmic artery persists as the internal ophthalmic artery of the adult. Padget's (1948) work shows that embryologically the ophthalmic artery of man is a later development than the internal ophthalmic artery and that the former in its peripheral distribution replaces the external ophthalmic artery. The spiral turn of the ciliary artery in the species examined is readily understood if the origin from the internal maxillary artery is regarded as a secondary development.

In the earlier stages of development of man the internal maxillary artery lies medial to the mandibular nerve, but later a secondary vessel is formed lateral to the nerve and this finally becomes the main artery. The lateral relation of the internal maxillary artery to the mandibular nerve is seen in the artiodactyls, but in the cat, although there is a smaller vessel lateral to the nerve (the vessel arises from the inferior dental artery), the main artery lies medial to the nerve.

The fact that the stapedial artery has no connexion with the internal carotid artery at a level corresponding to the position of the intracranial rete indicates that the development of the rete must occur at a relatively late stage. Tandler (1906) showed that the rete in the pig was not a modification of an early capillary plexus but was a secondary development. As Ask-Upmark (1935) suggested, the site of development of the intracranial rete may be along the line of the first arch artery.

The circle of Willis

From this study it would appear that the variations which occur in the pattern of the cranial arteries of the different species are associated with the degree of development or degeneration of the internal carotid artery, which in a primitive stage is the most important vessel supplying the brain. In all the species studied the brain is supplied from the circle of Willis and its associated vessels, and consequently the calibre of the vessels which supply the circle of Willis provides an indication of their importance in relation to the circulation of the brain.

The circle of Willis may derive its blood supply from one or more of five sources, namely, the internal carotid artery, the external carotid arterial system, the ascending pharyngeal artery, the vertebral artery and the occipital artery. The persistence or degeneration of the internal carotid artery appears to be the major factor in determining the degree of the contribution provided by the other vessels (see figure 9 and table 1).

The simplest arrangement of vessels supplying the circle of Willis is that seen in man, the rabbit and the rat. In these species, blood is carried to the circle of Willis only by the internal carotid artery and the vertebral artery (through the basilar artery) of each side. The occipital artery has a minor communication with the vertebral artery.

TABLE 1. THE SOURCES OF BLOOD SUPPLY TO THE CIRCLE OF WILLIS

species	internal carotid artery	external carotid system via arteria anastomotica and ramus anastomoticus	ascending pharyngeal artery	vertebral artery	occipital artery
Cat (*Felis domestica*) carotid rete present	(−)	+ + +	+	+	(+)
Sheep (*Ovis aries*) carotid rete present	.	+ + +	(−)	.	.
Goat (*Capra hircus*) carotid rete present	.	+ + +	.	.	.
Ox* (*Bos taurus*) carotid rete present	+	+ + +	.	.	+ +
Pig (*Sus scrofa*) carotid rete present	.	(+)	+ + +	+	(+)
Dog (*Canis familiaris*) carotid rete rudimentary	+ +	+ +	.	+	(+)
Rabbit (*Oryctolagus cuniculus*) carotid rete absent	+ +	.	.	+	(+)
Rat (*Rattus norvegicus*) carotid rete absent	+ +	.	.	+	(+)
Man (*Homo sapiens*) carotid rete absent	+ + +	.	.	+	(+)

+, + +, + + + degrees of contribution to circle of Willis.
(+) minor contribution only.
(−) vessel does not persist in adult life.
* Only one specimen examined. This was a calf about 4 months old.

The arrangement is similar in the dog, but in this animal there is an additional substantial supply from the external carotid system via the arteria anastomotica and the ramus anastomoticus.

A somewhat more complex arrangement is present in the goat and sheep. This complexity is associated with the presence of a well-developed carotid rete (situated intracranially), which is connected on the one hand to the external carotid system by means of the ramus anastomoticus and the arteria anastomotica, and on the other to the circle of Willis by a short trunk which is the only persisting portion of the internal carotid artery. In these species the vertebral vessels are very small at their point of communication with the basilar artery, and it would appear that the direction of flow in the basilar artery is away from the circle of Willis. A caudal direction of the flow has in fact been observed in the sheep in angiograms of the living animal, but in both species this direction of flow is suggested by the fact that the calibre of the basilar artery diminishes caudally, by the angle at which the branches of the artery are given off, and by observations made during decerebration. For this reason, although an occipito-vertebral anastomosis is present, the occipital artery probably carries no blood to the circle of Willis in these species.

The calf had essentially the same arrangements as the sheep and goat as regards the basilar and vertebral arteries and the vessels which connect the circle of Willis with the external carotid system. In addition, however, a major contribution was provided by the occipital artery via the basi-sphenoidal arterial plexus, and a complete internal carotid artery was present. Tandler (1899) found that the internal carotid artery proximal to the rete was absent in the adult of the species.

A different arrangement is found in the cat. In this animal the circle of Willis gains the major portion of its blood supply from the external carotid system via the carotid rete, which in this animal is situated extracranially and is connected to the circle of Willis by vessels which constitute the arteria anastomotica; some blood is also derived from the same source via the ramus anastomoticus. Smaller contributions to the circle of Willis are provided by the ascending pharyngeal artery and by the vertebral artery (via the basilar artery) and also by a relatively unimportant branch of the occipital artery through an occipito-vertebral anastomosis.

The pig is strikingly different from the other animals studied, in that the circle of Willis derives its blood supply almost entirely from the ascending pharyngeal artery via the intracranial carotid rete. The arteria anastomotica and the ramus anastomoticus were found to be insignificant vessels, and thus the contribution to the circle of Willis provided by the internal maxillary artery would appear to be negligible. The vertebral and occipital arteries provide a fairly substantial contribution to the circle of Willis (through the basilar artery).

The significance of the carotid rete

Two features of the carotid rete are of especial interest, first, its high degree of development in those species of animal in which the internal carotid artery has degenerated, or is undergoing degeneration, and secondly, its situation along the path of the major vessel or vessels which supply blood to the brain. It would seem that in those species in which it is present the carotid rete is of some haemodynamic significance in relation to the cerebral circulation. The fact that the rete, whether situated intracranially or extracranially, lies within a venous lake is another feature of interest, which probably has a physiological significance. The reason why some species have a carotid rete while others do not is not at all obvious, and the fact that even in those species in which a rete is present the vessels which supply it are not the same (e.g. the cat, the sheep, and the pig) makes the problem still more complex. Not the least of the peculiarities which has to be explained is the presence of a carotid rete in species so diverse in their habits as Felidae and Artiodactyla. Much more information is required from comparative anatomical and physiological studies before a satisfactory explanation for the existence of the rete is forthcoming. In the meanwhile, the carotid rete is clearly a structure whose existence and possible influence should not be overlooked when problems of the cerebral circulation are being considered in animals in which it is present.

We should like to express our gratitude to Mr R. Beesley for technical assistance.

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Descriptions of plates 12 to 19

List of reference letters (used also in figures 1 to 8)

A	arteria anastomotica
AC	anterior cerebral artery
AP	ascending pharyngeal artery
AT	anterior deep temporal artery
Ba	basilar artery
BS	basi-sphenoidal arterial plexus
Bu	buccinator artery
C	ciliary artery
CC	common carotid artery
CR	carotid rete
CW	circle of Willis
EC	external carotid artery
EE	external ethmoidal artery
EM	external maxillary artery
EO	external ophthalmic artery
Ext	V-shaped anterior extension of carotid retia
F	frontal artery
IC	internal carotid artery
ID	inferior dental artery
IE	internal ethmoidal artery
IM	internal maxillary artery
IO	internal ophthalmic artery
IOr	infra-orbital artery
IS	infra-orbital division of stapedial artery
La	lacrimal artery
LC	long ciliary branches
Li	lingual artery
MC	middle cerebral artery
MM	middle meningeal artery
NM	nasal meningeal artery
O	occipital artery
OM	arteries of extrinsic ocular muscles
OR	orbital rete
P	pterygoid artery
PC	posterior communicating artery and proximal part of posterior cerebral artery
RA	ramus anastomoticus
RM	recurrent meningeal artery
S	stapedial artery
SS	supra-orbital division of stapedial artery
ST	superficial temporal artery
V	vertebral artery

Note. All figures (except lateral radiographs) are mounted so that the rostral or anterior end of the specimen is above, and the caudal or posterior end below.

Plate 12

Figure 10. *Felis domestica.* Radiograph of head of cat in ventro-dorsal projection. The arteries had been injected with a suspension of bismuth carbonate. Note the position of the extracranial carotid rete which is wrapped around the internal maxillary artery, and is connected to the circle of Willis by a leash of vessels which in this species represents the arteria anastomotica. ($\frac{7}{8}$ natural size.)

Figure 11. Radiograph of one half of same specimen as in figure 10 (divided sagittally) in lateral projection to show the position of the rete. Note the small branch of the inferior dental artery which joins the inferior part of the rete. ($\frac{7}{8}$ natural size.)

Figure 12. Cat. Neoprene cast showing general view of right carotid rete and related vessels (supero-lateral aspect). In this species the carotid rete is situated extracranially, lying at the back of the orbit immediately beneath the base of the skull. (Magn. $\times 2{\cdot}4$.)

Figure 13. Cat. Neoprene cast of right carotid rete seen from the supero-lateral aspect and showing pattern of vessels composing it. The rete is wrapped around the internal maxillary artery and is supplied by small branches from it; only the most proximal of these is visible. The ramus anastomoticus gives off a small middle meningeal artery, and joins one of the group of vessels which connects the rete with the circle of Willis; in this species the latter group of vessels forms the arteria anastomotica. The marked bend in the ciliary artery is characteristic. This vessel arises from the internal maxillary artery within the rete but has no connexions with the vessels composing the rete (see figure 1). Note the numerous vessels which leave the anterior part of the rete. (Magn. $\times 5{\cdot}5$.)

PLATE 13

FIGURE 14. Cat. Neoprene cast of antero-lateral angle of right carotid rete, viewed from in front and below. Note the tunnel which encloses the maxillary nerve. (Magn. ×5·8.)

FIGURE 15. Cat. Neoprene cast of left carotid rete and related vessels, seen from below. Note that the internal ethmoidal artery, which takes its origin by several roots from the rete, anastomoses with the contralateral vessel to form a single trunk, the nasal meningeal artery, which passes forward in the mid-line. The ascending pharyngeal artery and the arteria anastomotica join each other just before entering the circle of Willis.

FIGURE 16. *Ovis aries*. Dissected preparation of head of sheep foetus (near-term) the arteries of which had been injected with neoprene latex. In this species the carotid rete is situated intracranially within the cavernous sinus and near to the mid-line. The photograph shows the right and left carotid retia viewed from below, after removal of the base of the skull. For a clearer view of the vessels see figure 17. (Magn. ×1·6.)

FIGURE 17. Same specimen as in figure 16 after maceration of the tissue, again seen from below. This cast shows the manner in which the carotid rete is supplied from the internal maxillary artery via the ramus anastomoticus and by the group of vessels which forms the arteria anastomotica. In this specimen a further contribution is provided by the ascending pharyngeal artery, but the connexion of this vessel with the rete does not persist into adult life. The vessel which is seen connecting the two retia across the mid-line lies in the posterior part of the pituitary fossa.

PLATE 14

FIGURE 18. Sheep (near-term foetus). Neoprene latex cast of circle of Willis viewed from above. In this species, only the terminal segment of the internal carotid artery persists and this short trunk connects the carotid rete (not visible here) with the circle of Willis. (Magn. ×3·2.)

FIGURE 19. Sheep (near-term foetus). Radiograph of head in ventro-dorsal projection after an arterial injection of bismuth carbonate. Compare with figure 10 and note the difference in the situation of this, an intracranial, carotid rete. (Natural size.)

FIGURE 20. Sheep (near-term foetus). Neoprene latex cast showing the plexus of arteries which form the orbital rete. This rete is supplied by the external ophthalmic artery and empties into the ciliary artery. (Magn. ×5·0.)

PLATE 15

FIGURE 21. *Capra hircus*. Radiograph of head of young goat in ventro-dorsal projection. The arterial system had been injected with a suspension of bismuth carbonate. Note that the situation of the carotid rete in this species is similar to that in the sheep (figure 19), but there is a greater degree of communication between the two retia across the mid-line. (Natural size.)

FIGURE 22. Radiograph of one-half of same specimen as in figure 21 (divided sagittally) in lateral projection. (Natural size.)

PLATE 16

FIGURE 23. Goat. Neoprene latex cast of left carotid rete seen from lateral aspect. To show how the vessels of the rete reform into a single trunk which then joins the circle of Willis. This short trunk is the only persisting portion of the internal carotid artery. The vessels which supply the rete from the internal maxillary artery, the ramus anastomoticus and the arteria anastomotica, are also seen. (Magn. ×2·3.)

FIGURE 24. Goat. Neoprene latex cast of right carotid rete viewed from infero-medial aspect. The supply of the rete by the arteria anastomotica and the ramus anastomoticus is well seen. The vessels of the rete form a connexion between these two arteries within the cavernous sinus.

Note that, in this specimen, the inferior dental artery arises from the root of the ramus anastomoticus. (Magn. × 2·2.)

FIGURE 25. Goat. Neoprene latex cast of right and left carotid retia, viewed from below. Note the vessels which connect the posterior ends of the two retia across the mid-line. These vessels lie in the posterior part of the pituitary fossa. (Magn. × 2·1.)

PLATE 17

FIGURE 26. *Bos taurus*. Neoprene latex cast of the right carotid rete of a calf, seen from below. This is another example of an intracranial carotid rete. In this animal the arteria anastomotica is represented by several large trunks. The ramus anastomoticus and the basi-sphenoidal arterial plexus (which receives blood from the occipital arteries) also supply the rete. The internal carotid artery is seen approaching the rete, to which it contributes a few small vessels. It then passes through the midst of the rete and joins the circle of Willis. (Magn. × 2·7.)

FIGURE 27. Same specimen as in figure 26 viewed from lateral aspect. Note the small calibre of the ramus anastomoticus; its origin from the internal maxillary artery is by a double root. (Magn. × 2·1.)

FIGURE 28. Calf. Neoprene latex cast of right and left carotid retia and associated vessels, viewed from below. Note the free communication between the two retia across the mid-line, both anteriorly and posteriorly. The ring of vessels thus formed surrounds the hypophysis cerebri. The basi-sphenoidal arterial plexus can be seen joining the retia posteriorly. Anteriorly there is an extension of the two retia which is normally V-shaped but has been spread out in displaying the specimen. (Magn. × 1·4.)

PLATE 18

FIGURE 29. Calf. Neoprene latex cast of circle of Willis seen from above. Note the small calibre of the basilar artery. (Magn. × 2·1.)

FIGURE 30. Calf. Neoprene latex cast showing right orbital rete and ciliary arteries. The vessels of this rete spring from the external ophthalmic artery and join together to form two ciliary arteries. The latter break up into serpentine vessels which give rise to the long and short ciliary branches (seen above). (Magn. × 1·8.)

FIGURE 31. *Sus scrofa*. Radiograph of head of young pig in ventro-dorsal projection. The arteries had been injected with bismuth carbonate. In this species also the carotid rete is situated intracranially, but the vessel from which it derives its main blood supply is the ascending pharyngeal artery. The circle of Willis is well seen. (Natural size.)

FIGURE 32. Young pig. Neoprene cast of the right and left carotid retia and related vessels, seen from below. Compare the shape of these retia and the pattern of their vessels with those seen in the retia of the sheep (figure 17), goat (figure 25) and ox (figure 28). Note the large calibre of the ascending pharyngeal artery and the tenuous arteria anastomotica. The ramus anastomoticus is also a small vessel and is better seen in figure 33. The single trunk formed by the junction of the two anterior cerebral arteries (see figure 5) is not visible here. (Magn. × 2·0.)

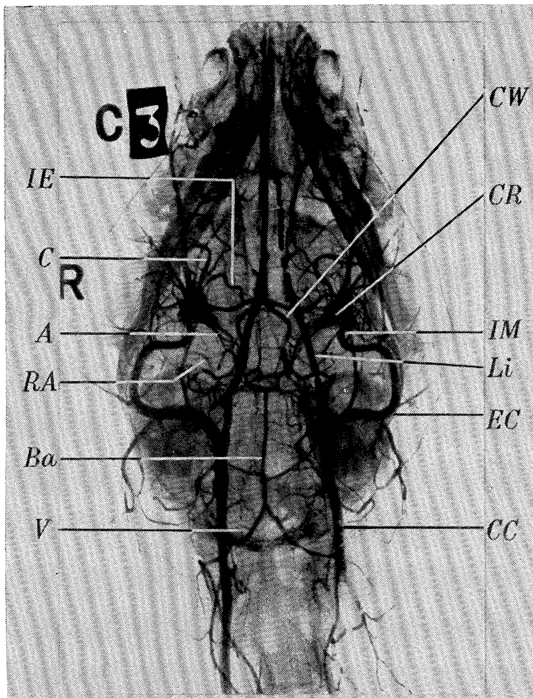
PLATE 19

FIGURE 33. Young pig. Neoprene cast of the right carotid arterial system seen from the lateral aspect. Compare the calibre of the ascending pharyngeal artery with that of the external carotid artery. Note how the vessels springing from the anterior end of the rete join to form the terminal part of the internal carotid artery. The origin of the tenuous arteria anastomotica from the external ophthalmic artery can be seen. Note the small calibre of the ramus anastomoticus beyond the origin of the relatively large middle meningeal artery. (Magn. × 2·5.)

FIGURE 34. *Oryctolagus cuniculus.* Radiograph of head of rabbit in ventro-dorsal projection after an arterial injection of bismuth carbonate (lower jaw removed). There is no carotid rete in this species. The circle of Willis is supplied by the internal carotid arteries and by the vertebral arteries (via the basilar artery). (Natural size.)

FIGURE 35. *Canis familiaris.* Neoprene latex cast of the right and left carotid arterial system of a dog seen from below. In this species there is no carotid rete, though there are a few small vessels in the cavernous sinus which may be considered as a counterpart of this structure (see figure 6). The internal carotid artery is a vessel of large calibre and is joined at the posterior end of the cavernous sinus by the arteria anastomotica. The latter vessel, which arises from the root of the external ophthalmic artery, receives the ramus anastomoticus midway along its course. (Magn. $\times$ 2·0.)

FIGURE 36. *Rattus norvegicus.* Radiograph of head of rat in ventro-dorsal projection after arterial injection of bismuth carbonate. There is no carotid rete in this species, and the territory which in other species is supplied by the internal maxillary artery is supplied in the rat by the stapedial artery. The circle of Willis receives its blood supply from the internal carotid arteries and from the vertebral arteries (via the basilar artery). (Magn. $\times$ 1·6.)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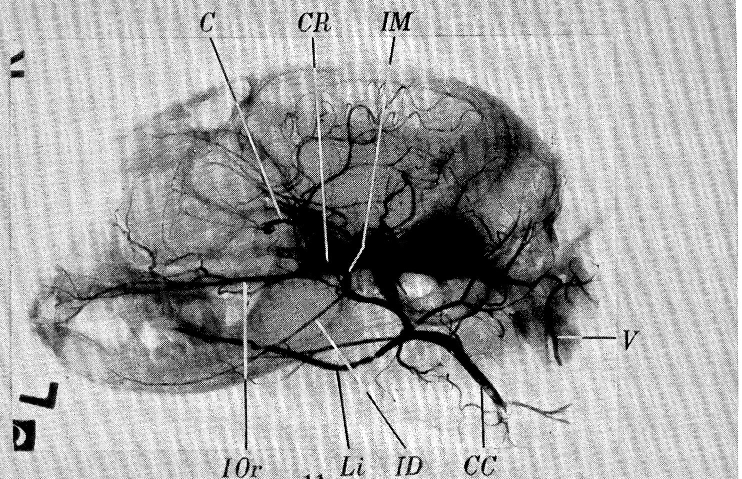
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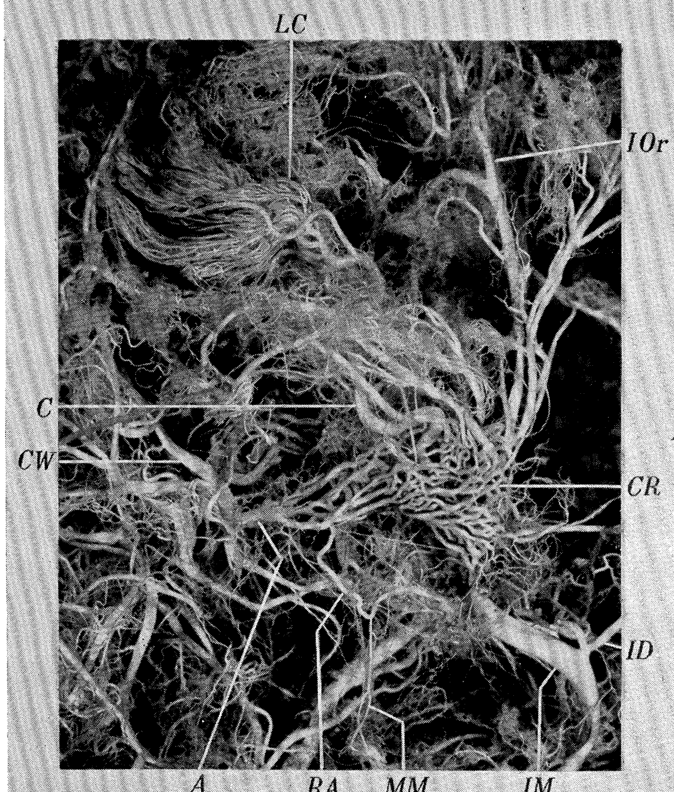
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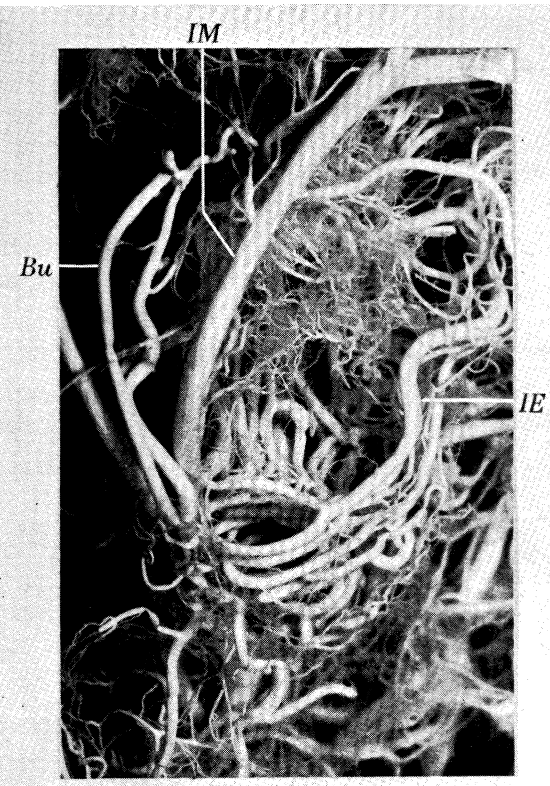
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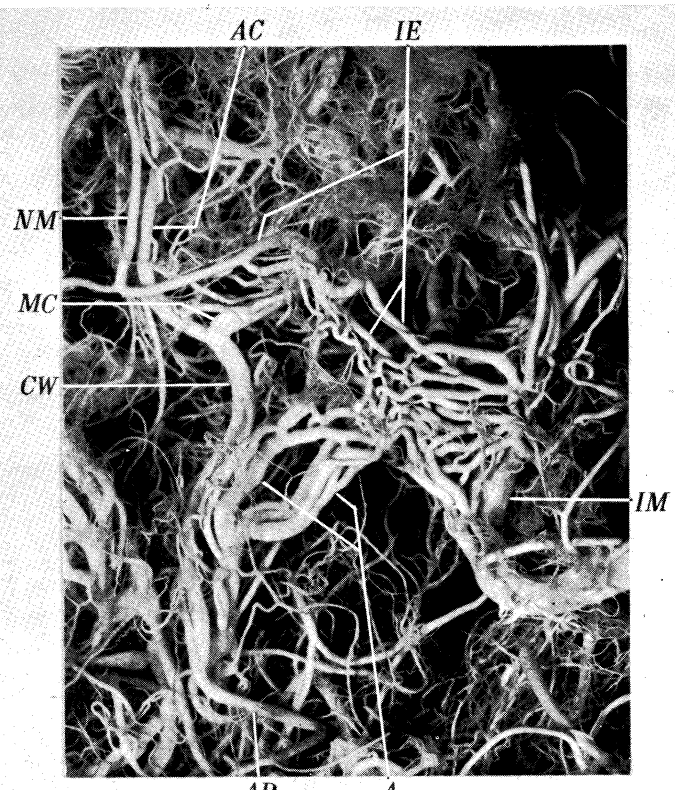
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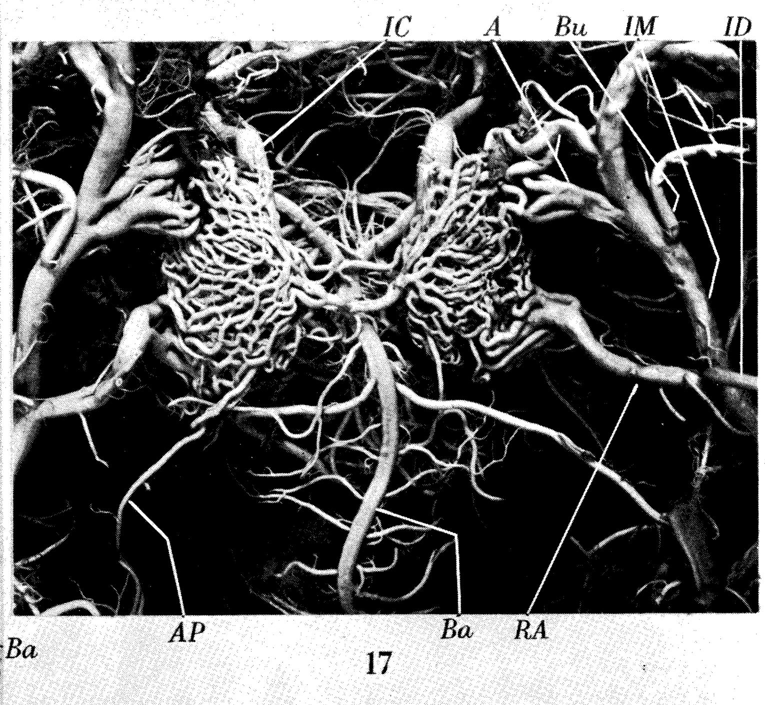
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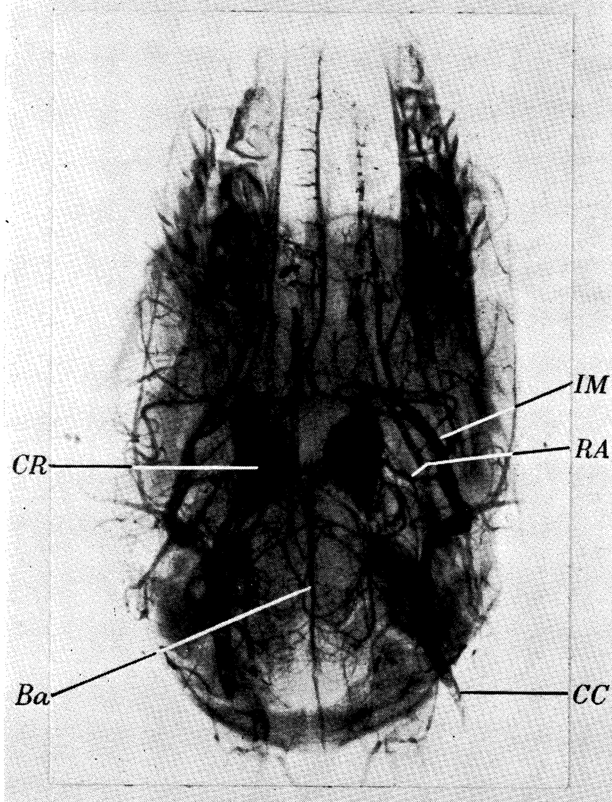

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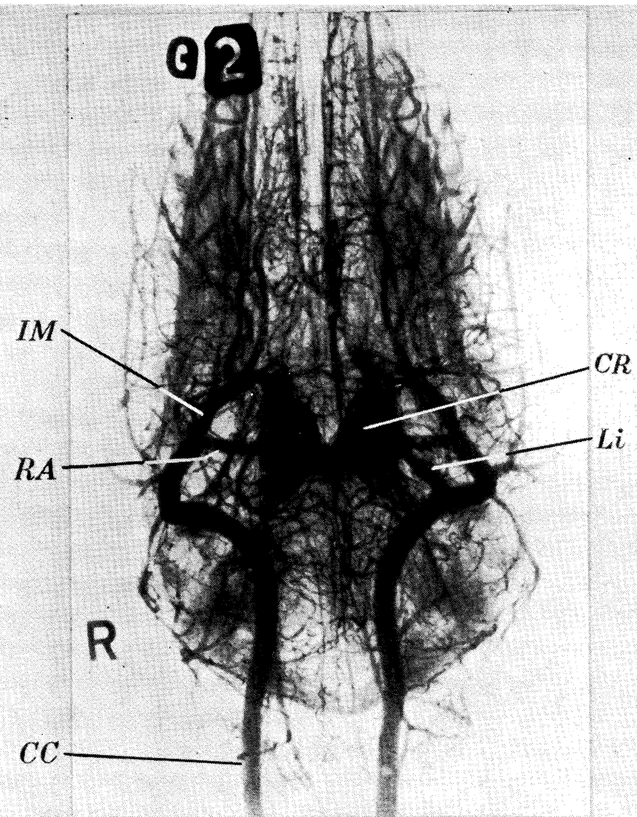

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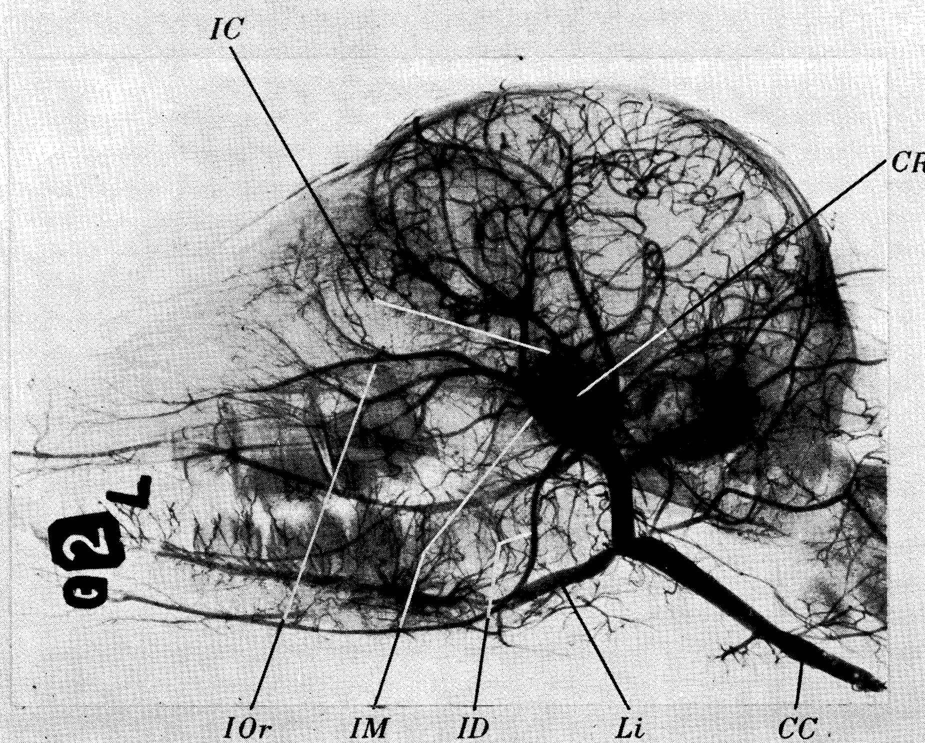

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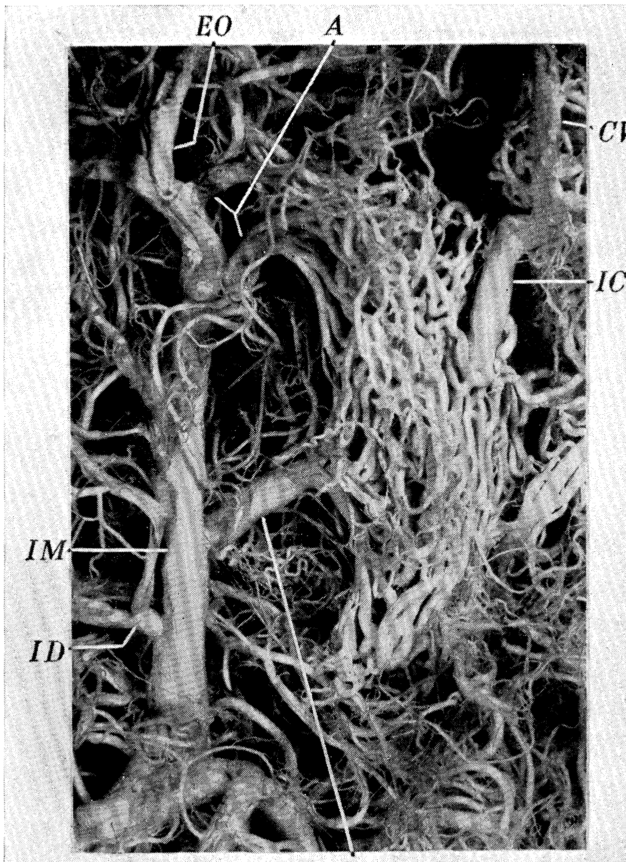

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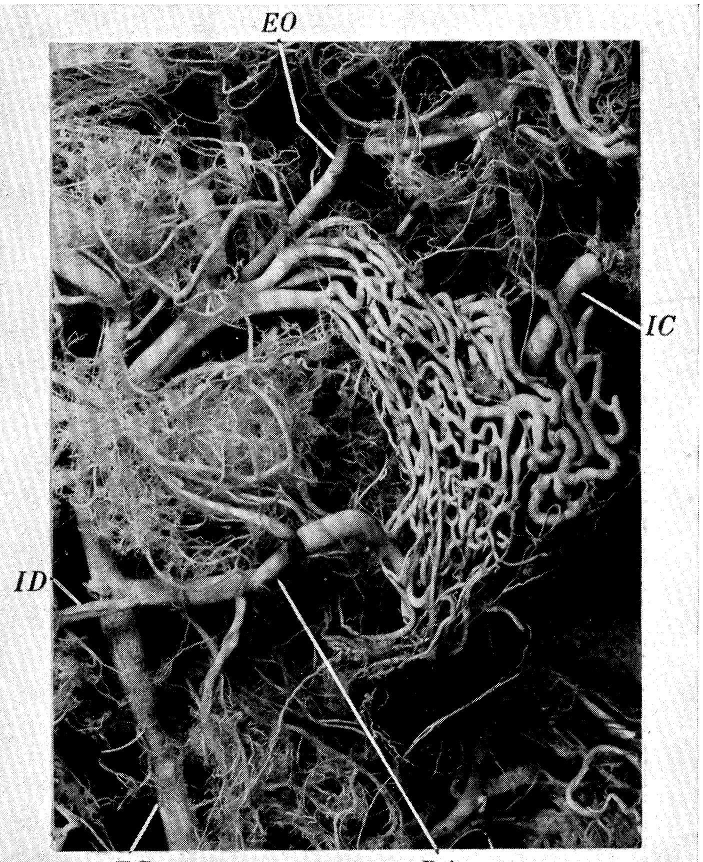

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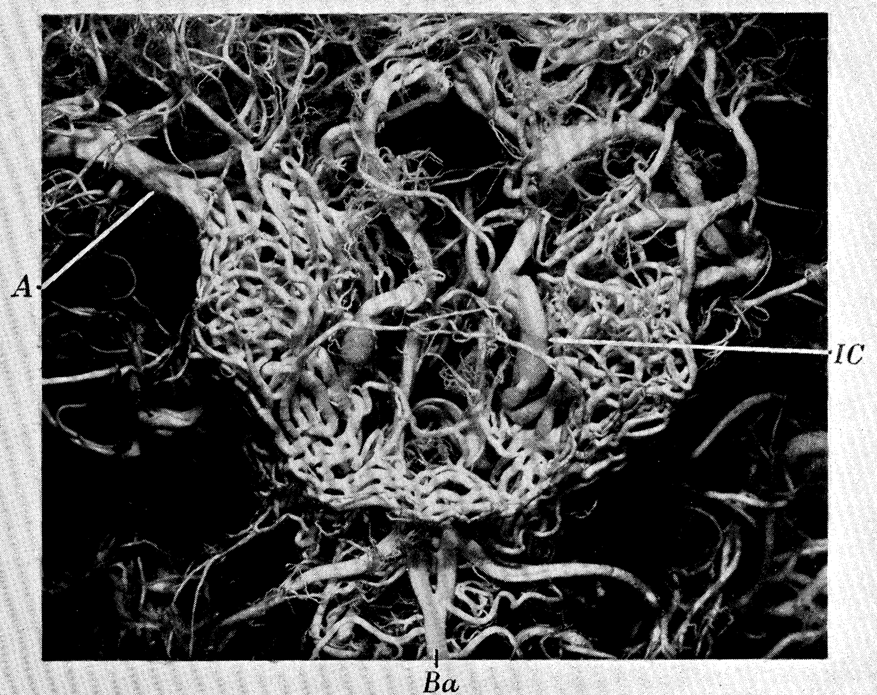

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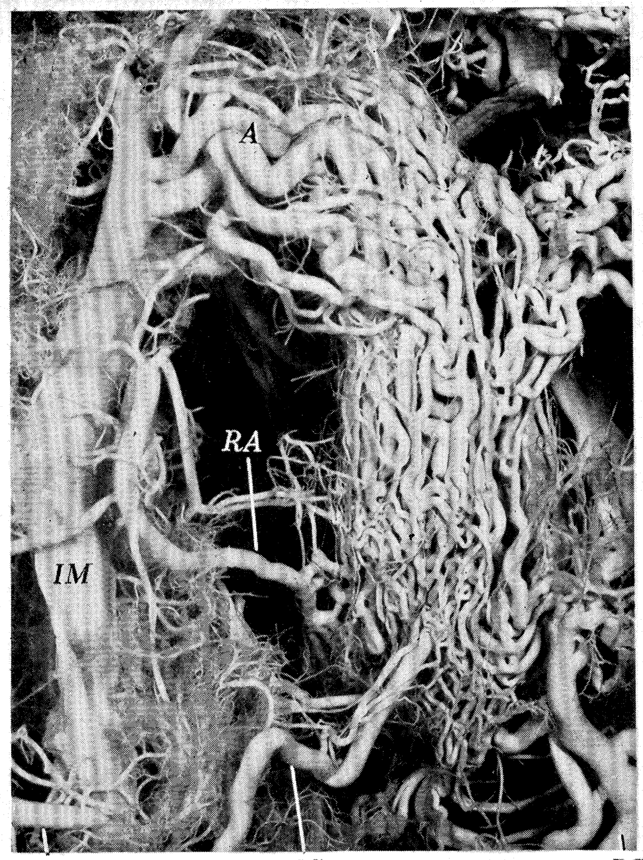

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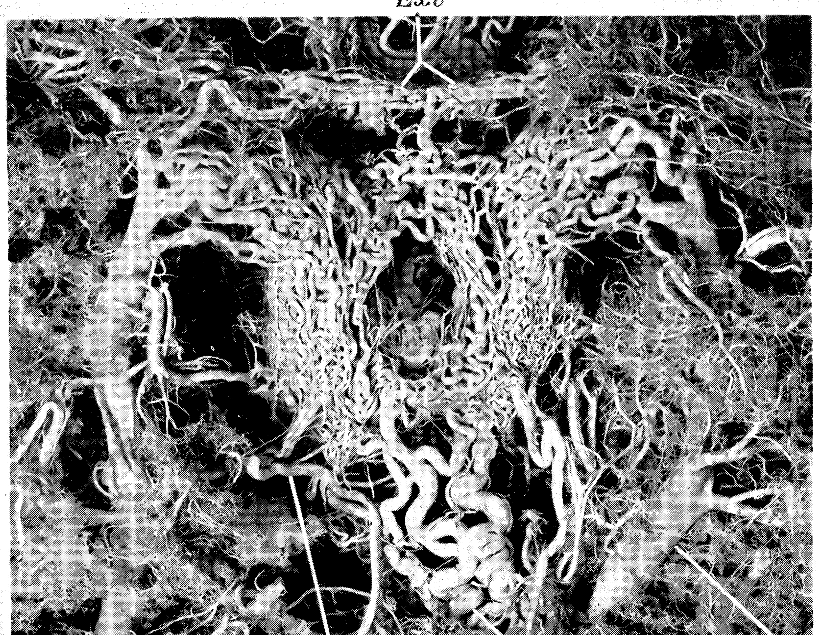

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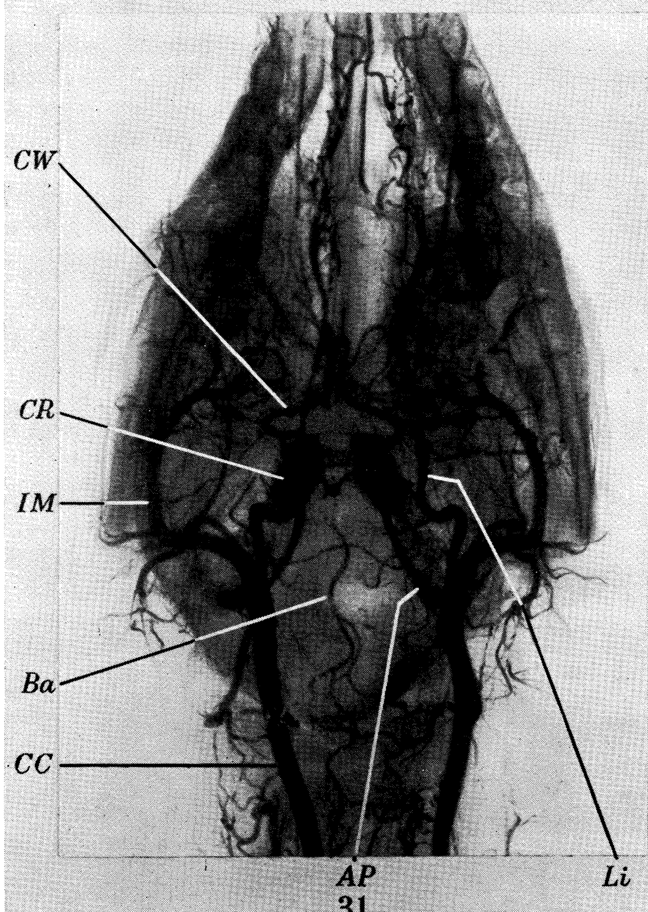

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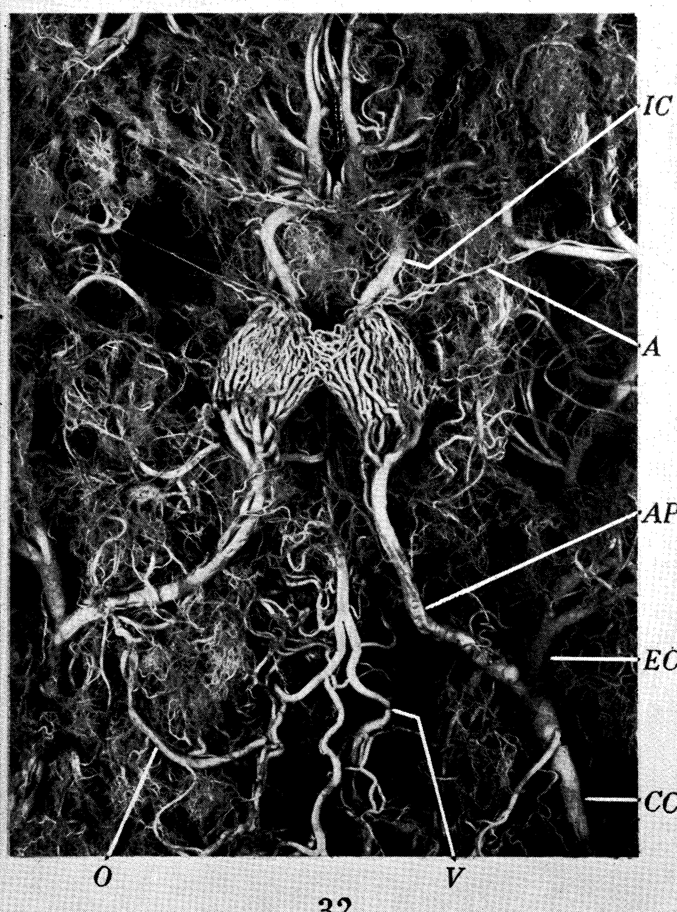

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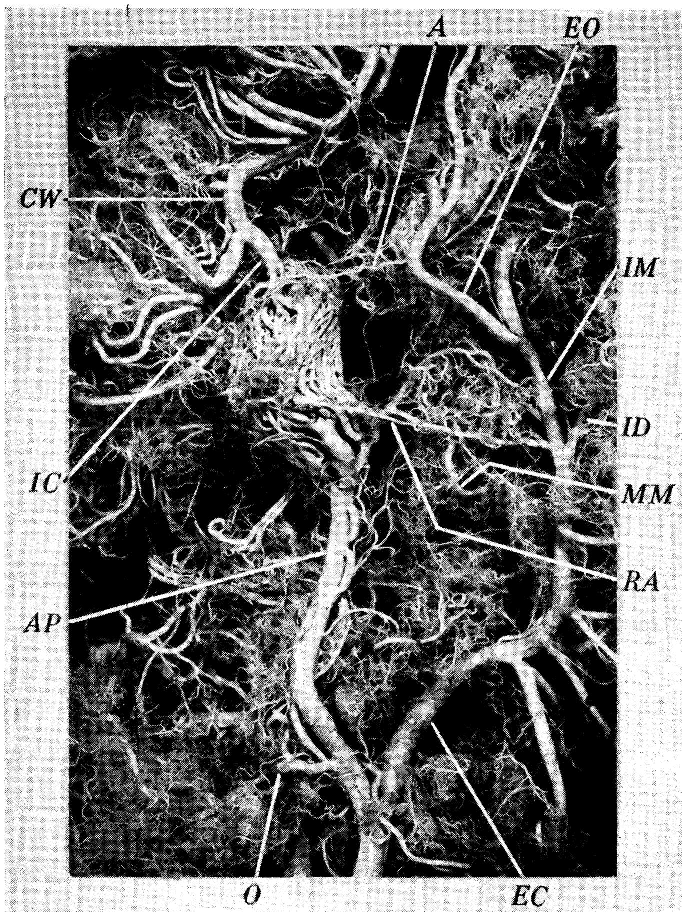
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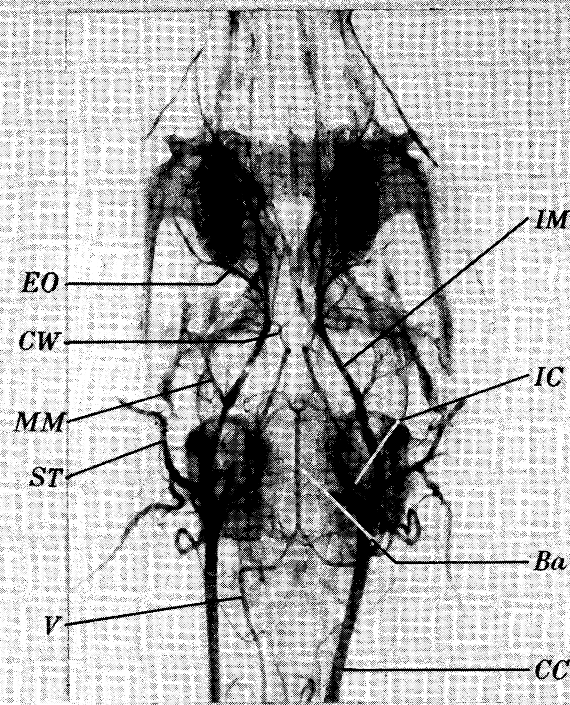
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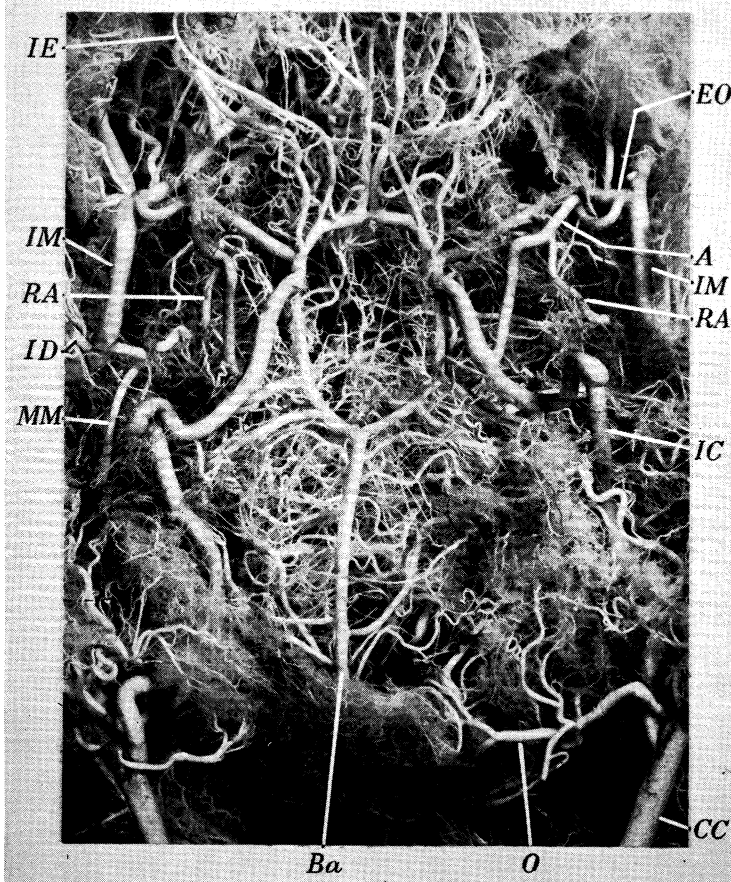
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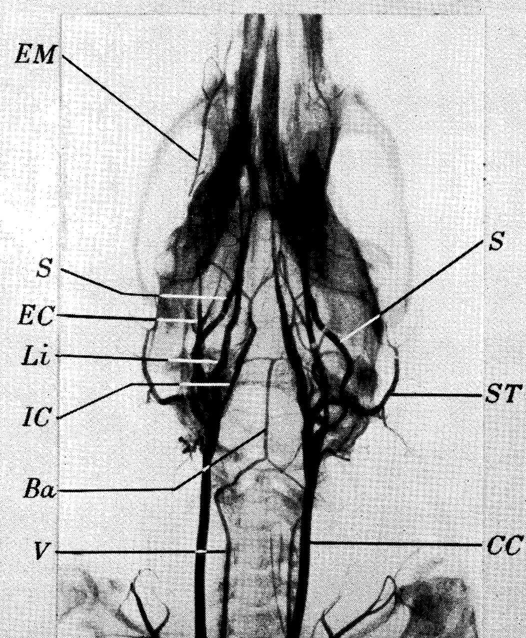
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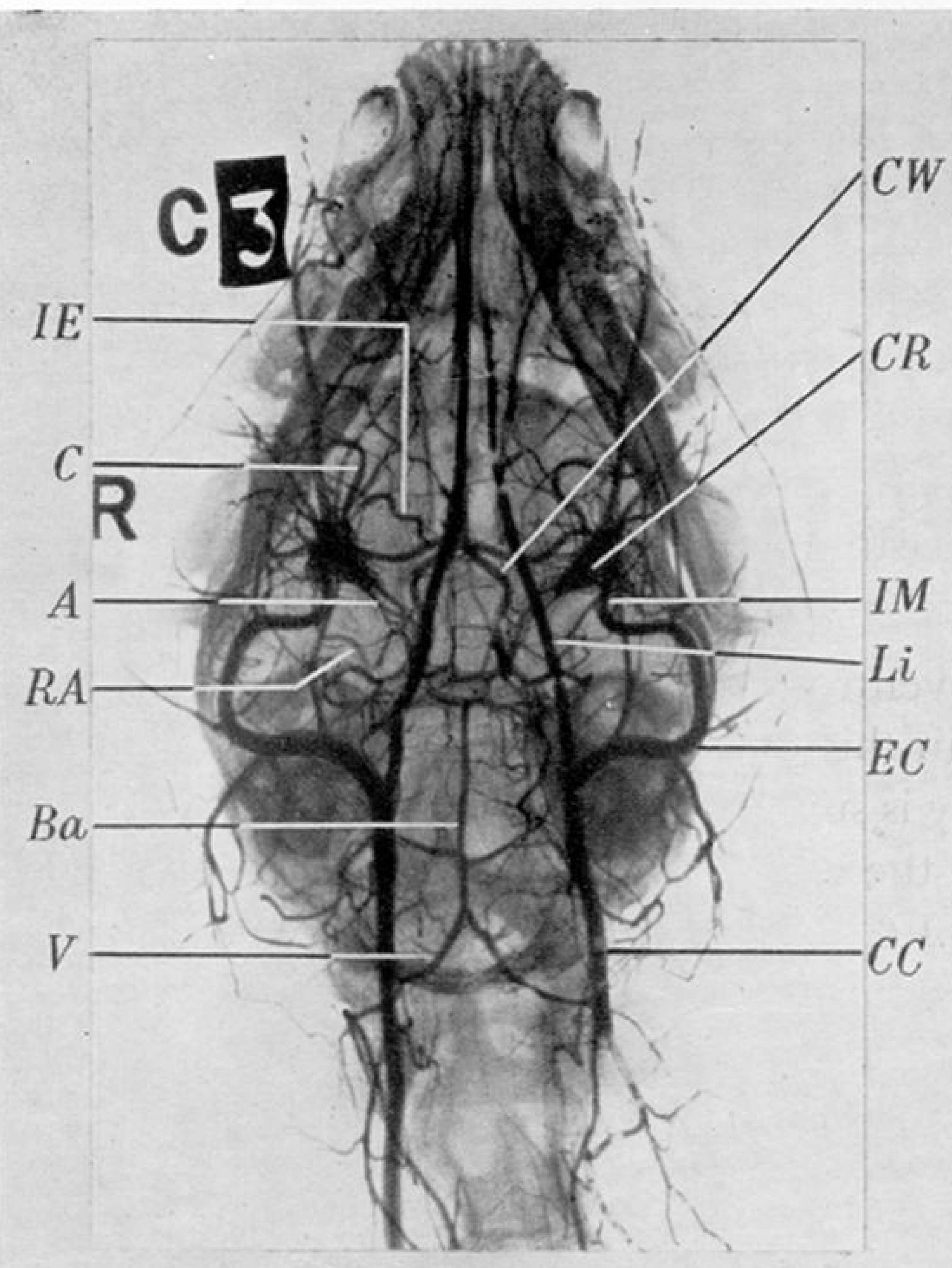

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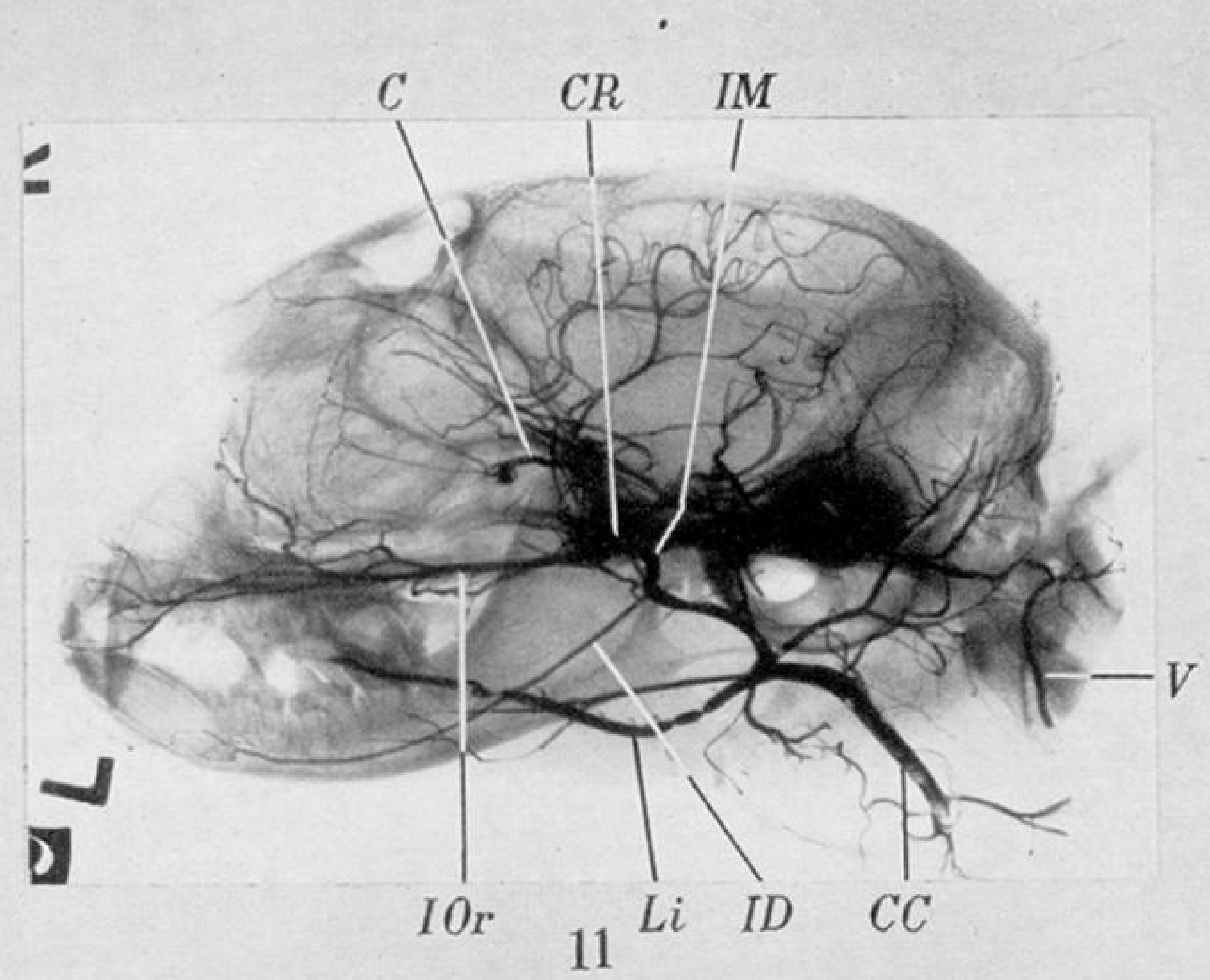

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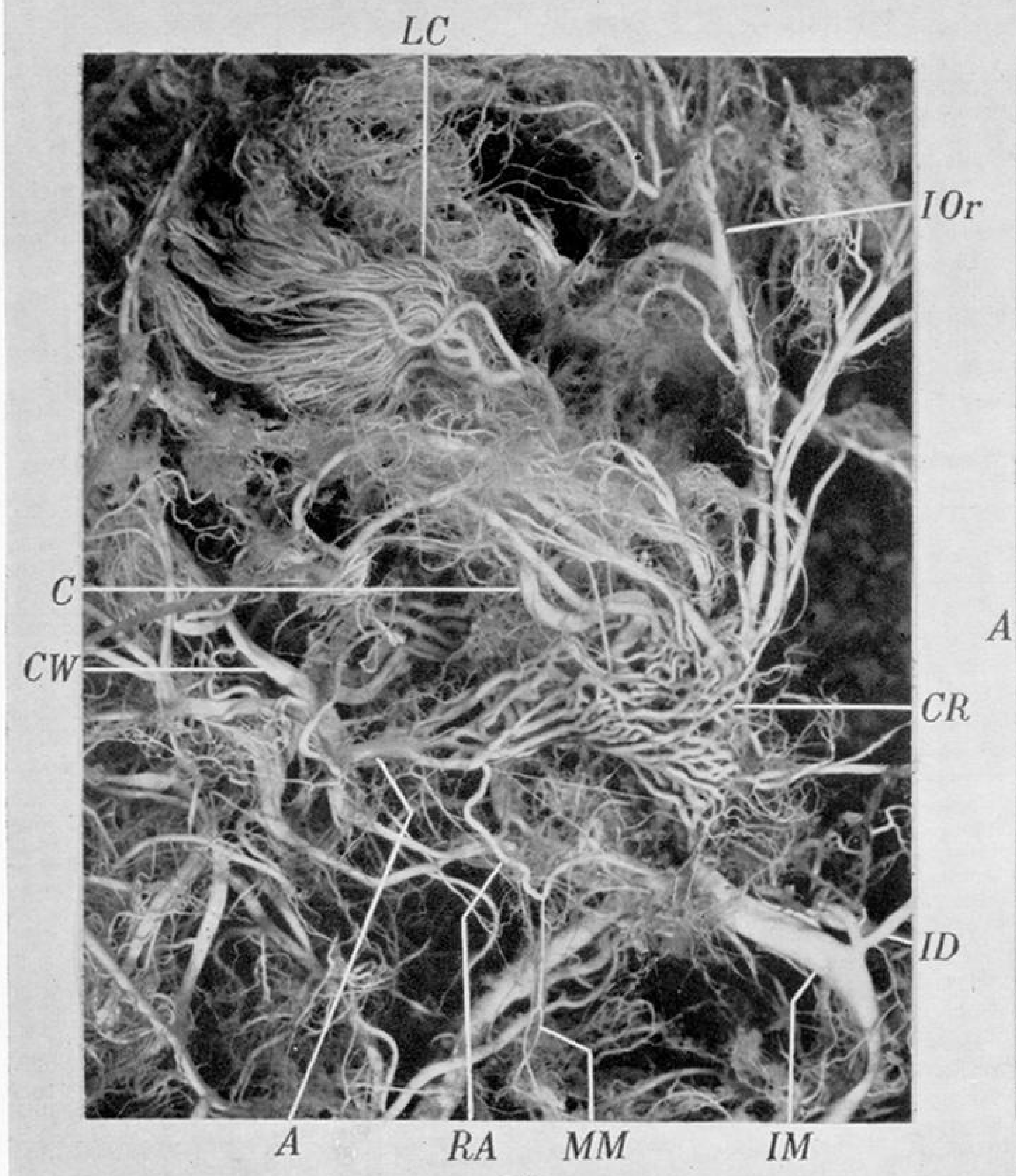

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PLATE 12

FIGURE 10. *Felis domestica.* Radiograph of head of cat in ventro-dorsal projection. The arteries had been injected with a suspension of bismuth carbonate. Note the position of the extracranial carotid rete which is wrapped around the internal maxillary artery, and is connected to the circle of Willis by a leash of vessels which in this species represents the arteria anastomotica. ($\frac{7}{8}$ natural size.)

FIGURE 11. Radiograph of one half of same specimen as in figure 10 (divided sagittally) in lateral projection to show the position of the rete. Note the small branch of the inferior dental artery which joins the inferior part of the rete. ($\frac{7}{8}$ natural size.)

FIGURE 12. Cat. Neoprene cast showing general view of right carotid rete and related vessels (supero-lateral aspect). In this species the carotid rete is situated extracranially, lying at the back of the orbit immediately beneath the base of the skull. (Magn. $\times$ 2·4.)

FIGURE 13. Cat. Neoprene cast of right carotid rete seen from the supero-lateral aspect and showing pattern of vessels composing it. The rete is wrapped around the internal maxillary artery and is supplied by small branches from it; only the most proximal of these is visible. The ramus anastomoticus gives off a small middle meningeal artery, and joins one of the group of vessels which connects the rete with the circle of Willis; in this species the latter group of vessels forms the arteria anastomotica. The marked bend in the ciliary artery is characteristic. This vessel arises from the internal maxillary artery within the rete but has no connexions with the vessels composing the rete (see figure 1). Note the numerous vessels which leave the anterior part of the rete. (Magn. $\times$ 5·5.)

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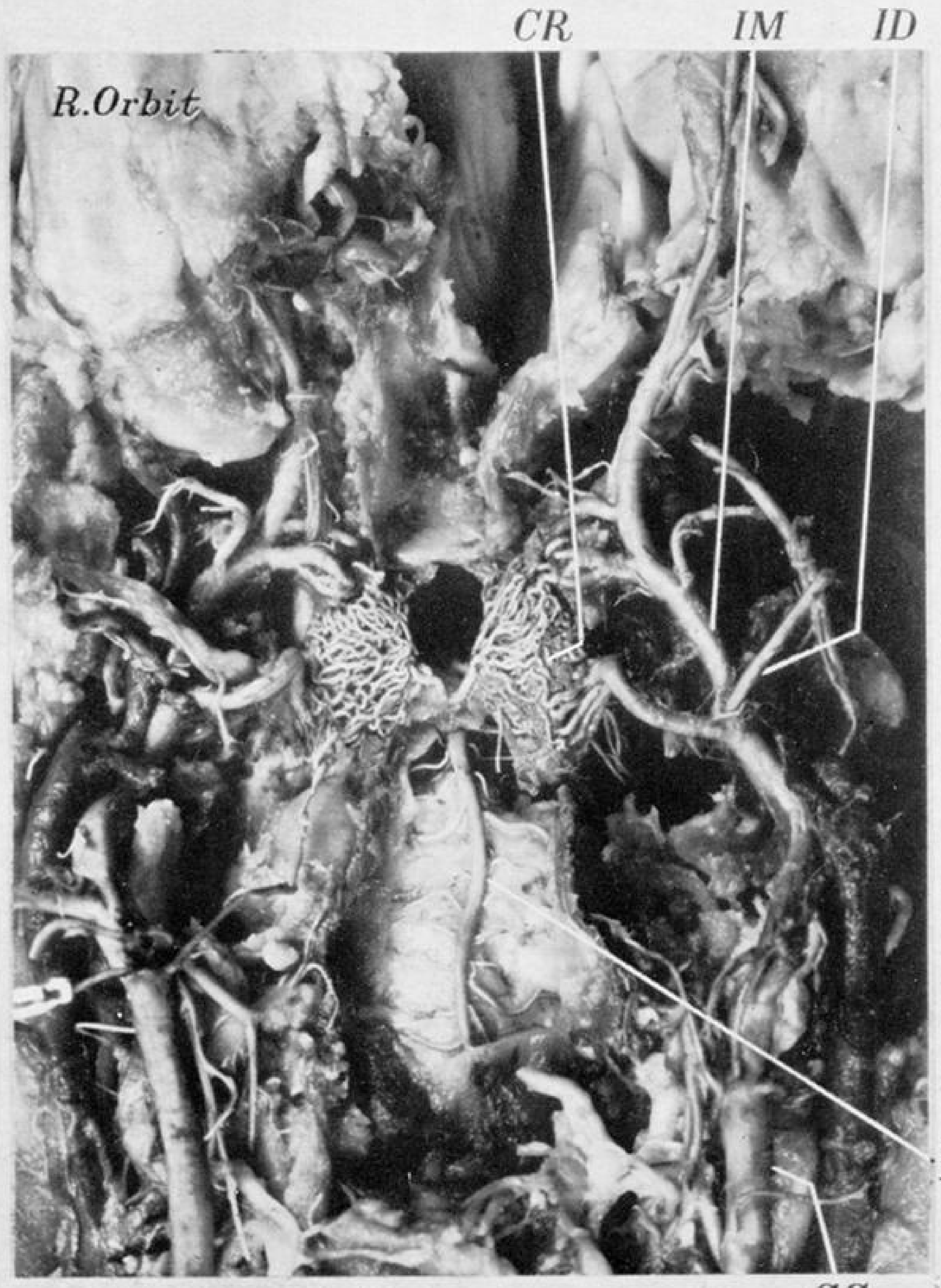

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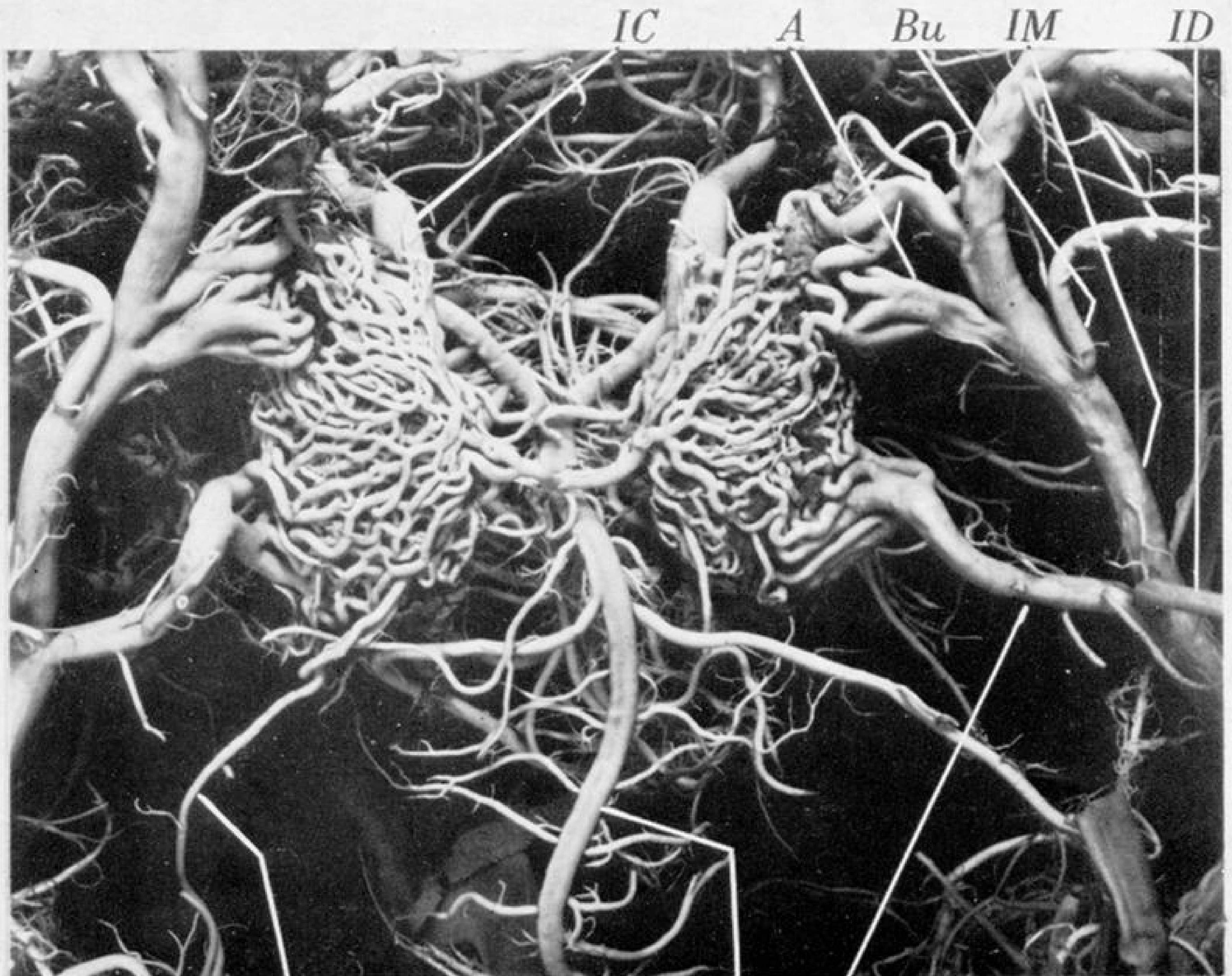

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PLATE 13

FIGURE 14. Cat. Neoprene cast of antero-lateral angle of right carotid rete, viewed from in front and below. Note the tunnel which encloses the maxillary nerve. (Magn. ×5·8.)

FIGURE 15. Cat. Neoprene cast of left carotid rete and related vessels, seen from below. Note that the internal ethmoidal artery, which takes its origin by several roots from the rete, anastomoses with the contralateral vessel to form a single trunk, the nasal meningeal artery, which passes forward in the mid-line. The ascending pharyngeal artery and the arteria anastomotica join each other just before entering the circle of Willis.

FIGURE 16. *Ovis aries*. Dissected preparation of head of sheep foetus (near-term) the arteries of which had been injected with neoprene latex. In this species the carotid rete is situated intracranially within the cavernous sinus and near to the mid-line. The photograph shows the right and left carotid retia viewed from below, after removal of the base of the skull. For a clearer view of the vessels see figure 17. (Magn. ×1·6.)

FIGURE 17. Same specimen as in figure 16 after maceration of the tissue, again seen from below. This cast shows the manner in which the carotid rete is supplied from the internal maxillary artery via the ramus anastomoticus and by the group of vessels which forms the arteria anastomotica. In this specimen a further contribution is provided by the ascending pharyngeal artery, but the connexion of this vessel with the rete does not persist into adult life. The vessel which is seen connecting the two retia across the mid-line lies in the posterior part of the pituitary fossa.

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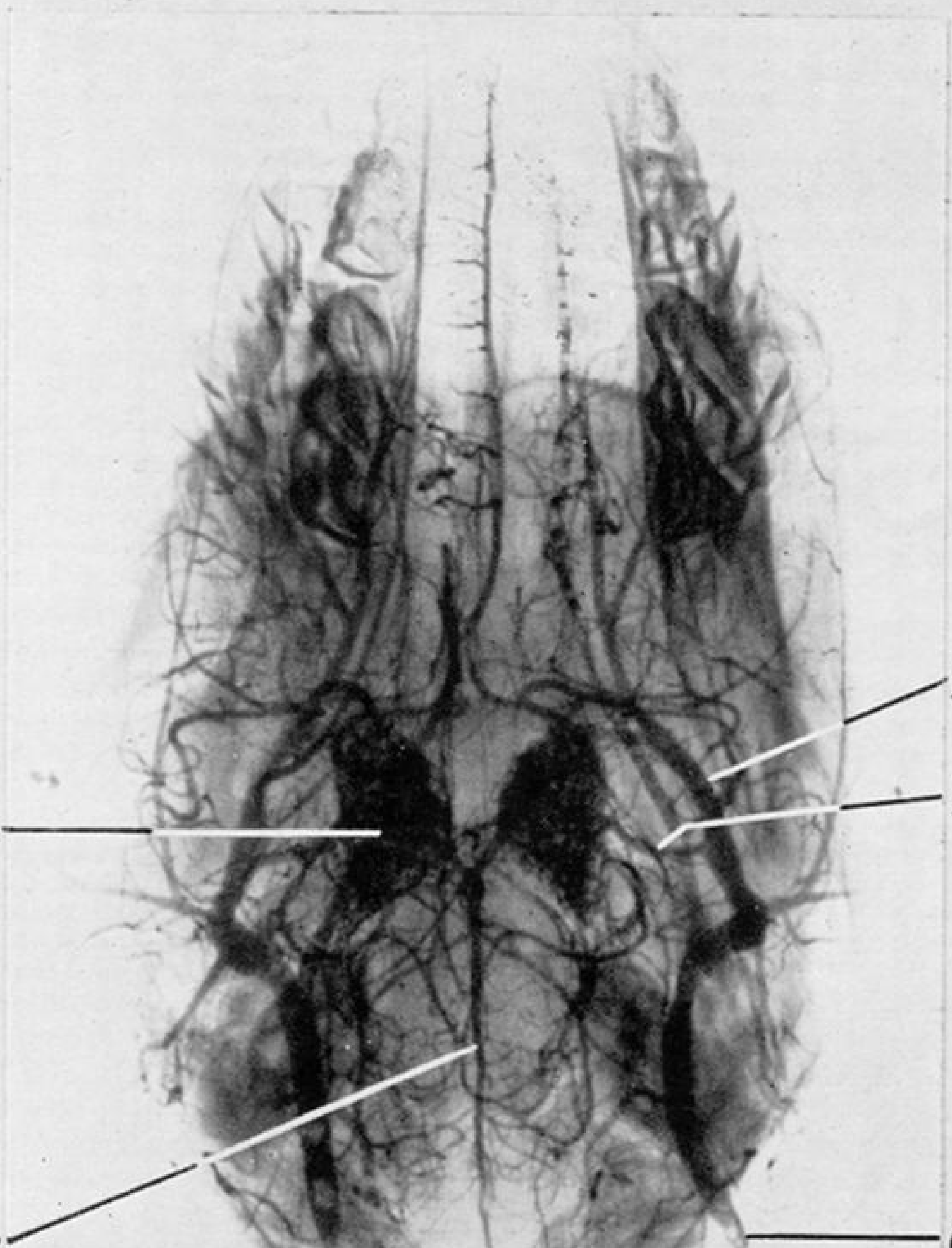

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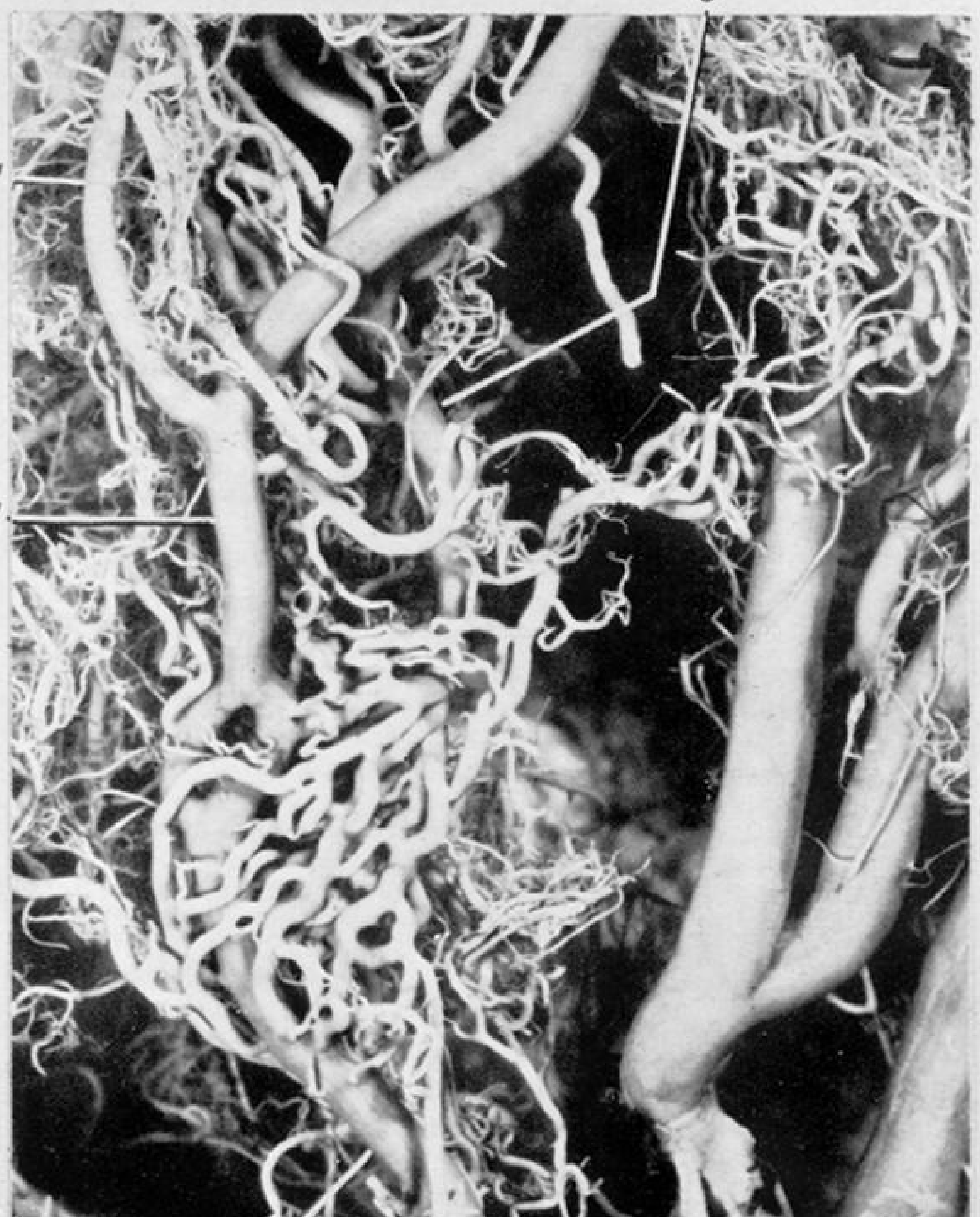

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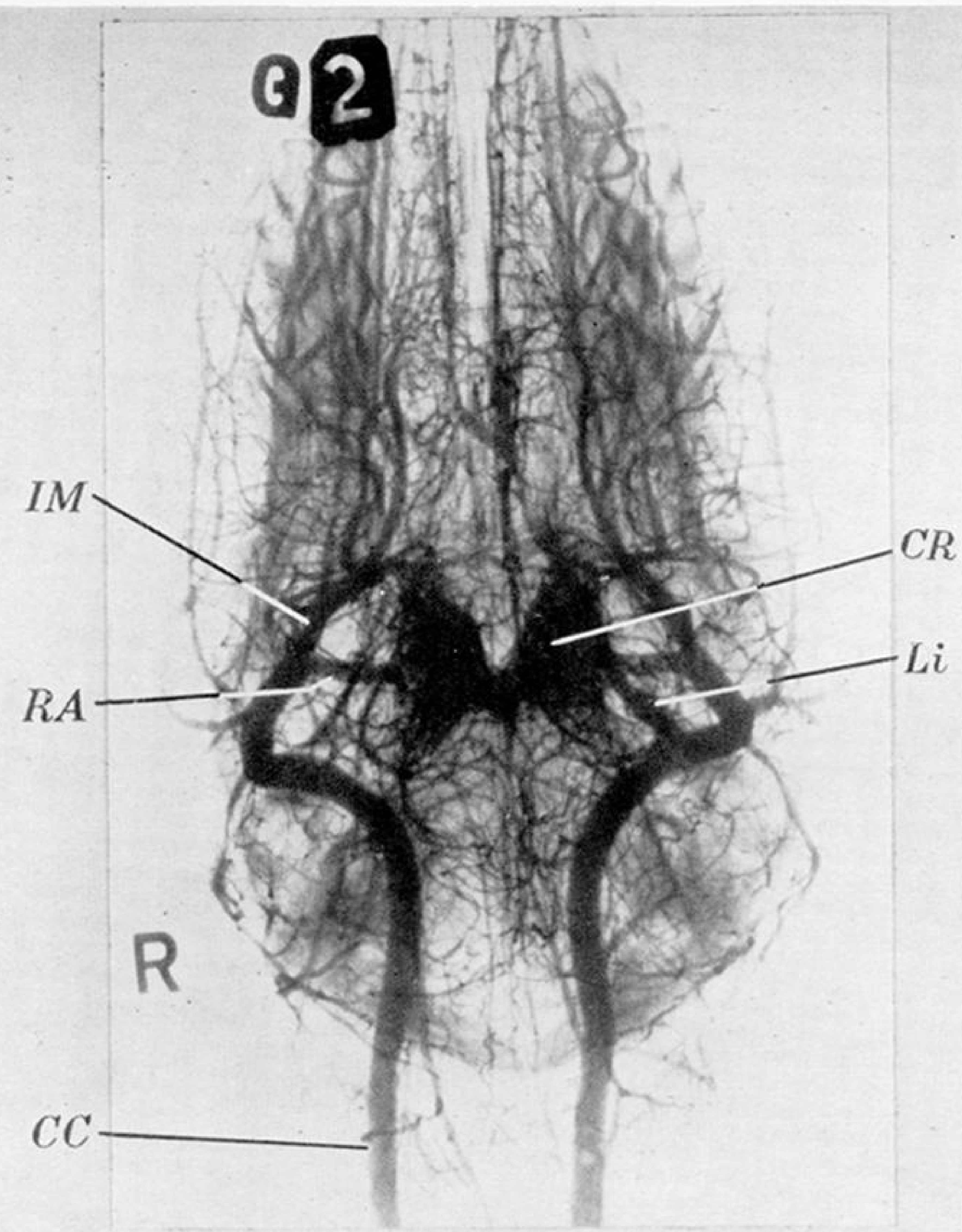
PLATE 14

FIGURE 18. Sheep (near-term foetus). Neoprene latex cast of circle of Willis viewed from above. In this species, only the terminal segment of the internal carotid artery persists and this short trunk connects the carotid rete (not visible here) with the circle of Willis. (Magn. × 3·2.)

FIGURE 19. Sheep (near-term foetus). Radiograph of head in ventro-dorsal projection after an arterial injection of bismuth carbonate. Compare with figure 10 and note the difference in the situation of this, an intracranial, carotid rete. (Natural size.)

FIGURE 20. Sheep (near-term foetus). Neoprene latex cast showing the plexus of arteries which form the orbital rete. This rete is supplied by the external ophthalmic artery and empties into the ciliary artery. (Magn. × 5·0.)



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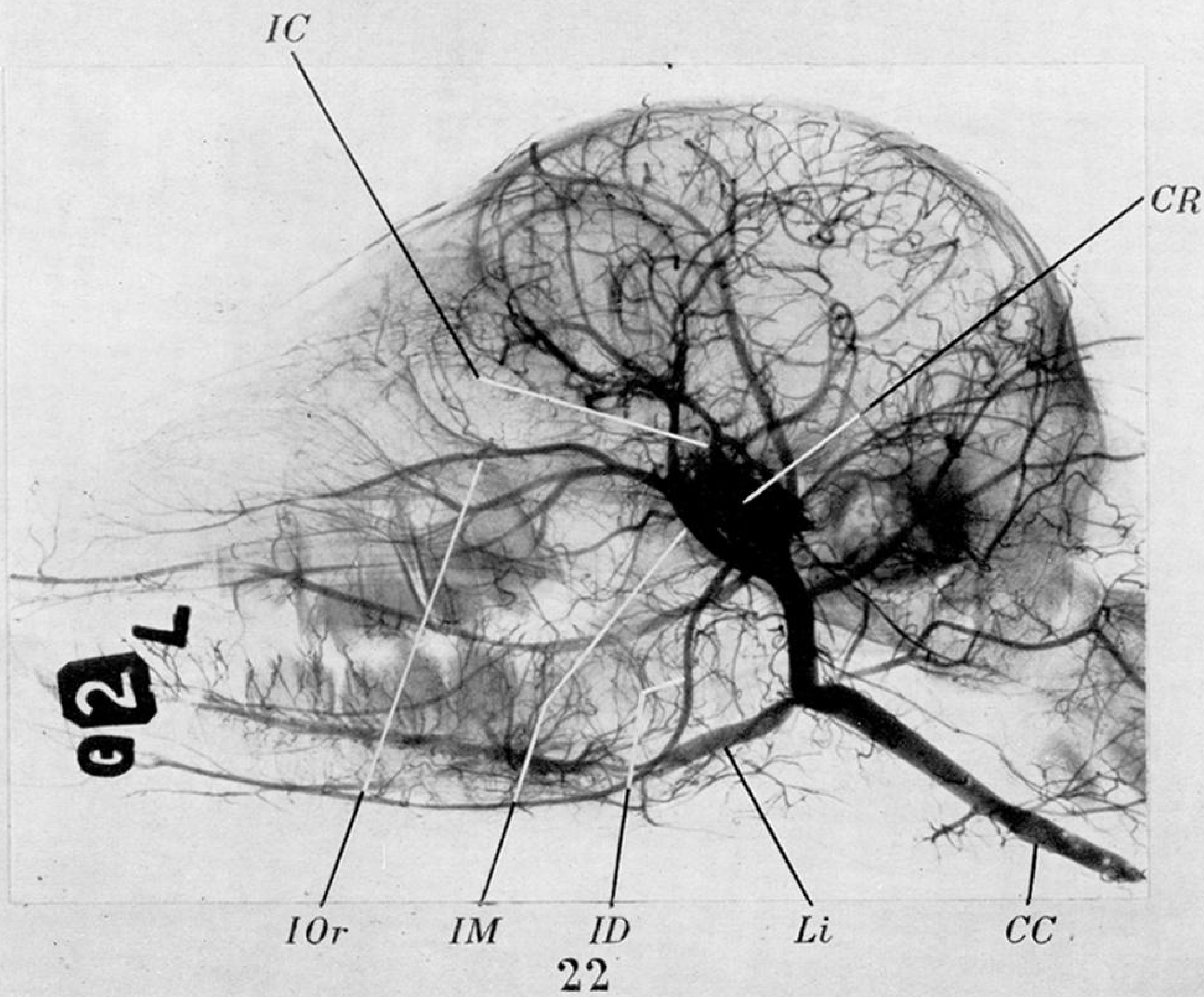

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PLATE 15

FIGURE 21. *Capra hircus*. Radiograph of head of young goat in ventro-dorsal projection. The arterial system had been injected with a suspension of bismuth carbonate. Note that the situation of the carotid rete in this species is similar to that in the sheep (figure 19), but there is a greater degree of communication between the two retia across the mid-line. (Natural size.)

FIGURE 22. Radiograph of one-half of same specimen as in figure 21 (divided sagittally) in lateral projection. (Natural size.)

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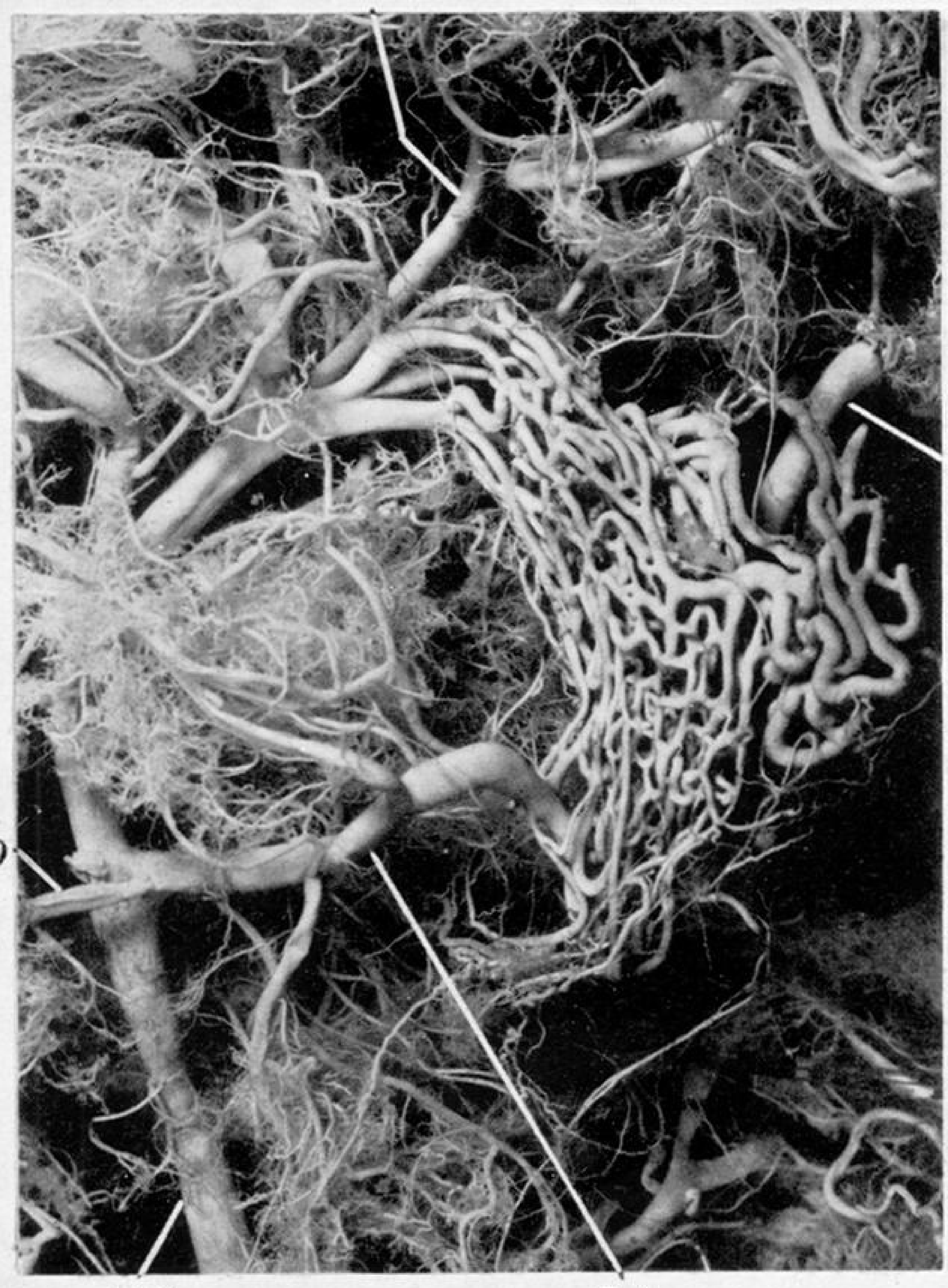

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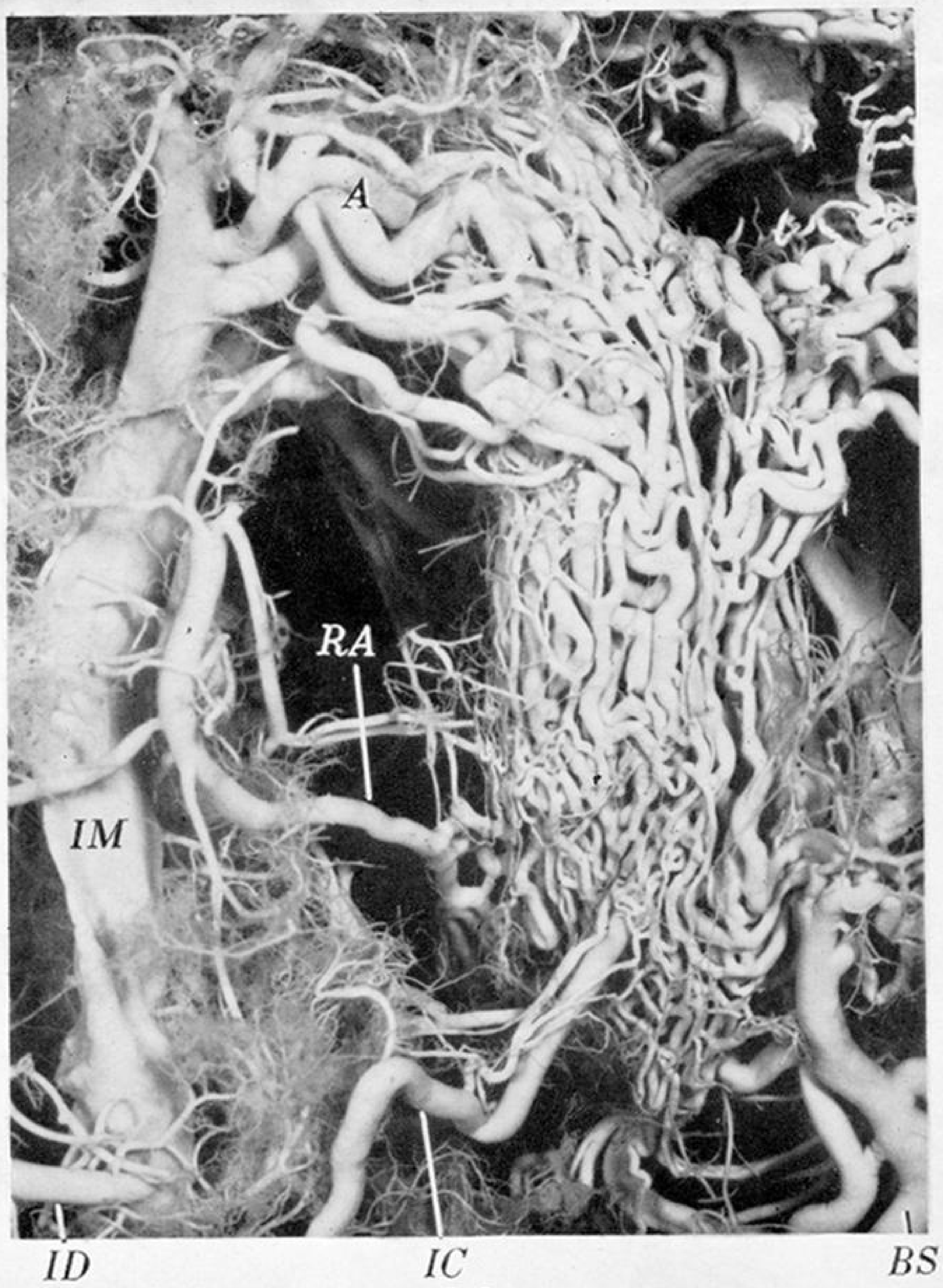
PLATE 16

FIGURE 23. Goat. Neoprene latex cast of left carotid rete seen from lateral aspect. To show how the vessels of the rete reform into a single trunk which then joins the circle of Willis. This short trunk is the only persisting portion of the internal carotid artery. The vessels which supply the rete from the internal maxillary artery, the ramus anastomoticus and the arteria anastomotica, are also seen. (Magn. × 2·3.)

FIGURE 24. Goat. Neoprene latex cast of right carotid rete viewed from infero-medial aspect. The supply of the rete by the arteria anastomotica and the ramus anastomoticus is well seen. The vessels of the rete form a connexion between these two arteries within the cavernous sinus. Note that, in this specimen, the inferior dental artery arises from the root of the ramus anastomoticus. (Magn. × 2·2.)

FIGURE 25. Goat. Neoprene latex cast of right and left carotid retia, viewed from below. Note the vessels which connect the posterior ends of the two retia across the mid-line. These vessels lie in the posterior part of the pituitary fossa. (Magn. × 2·1.)



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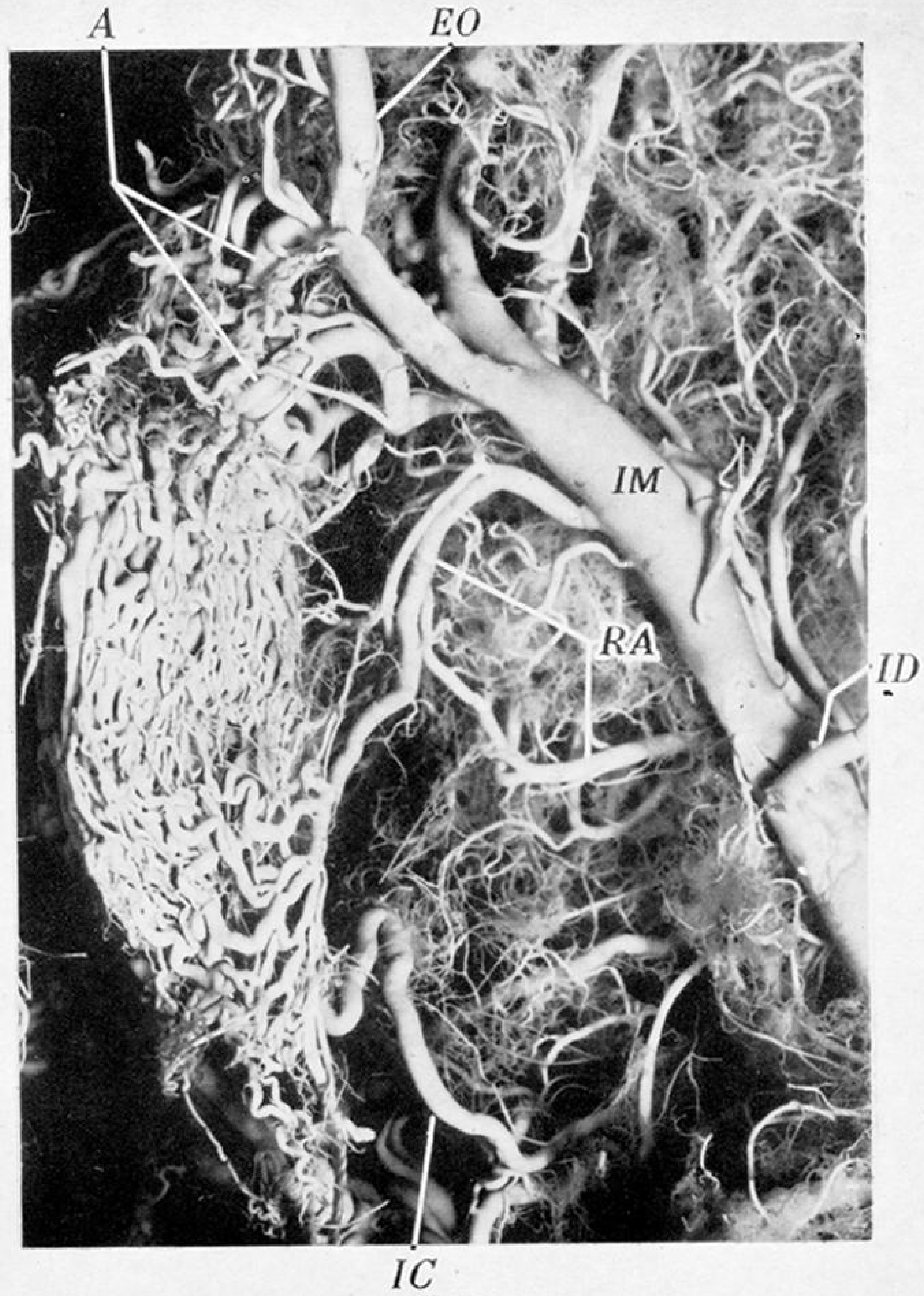

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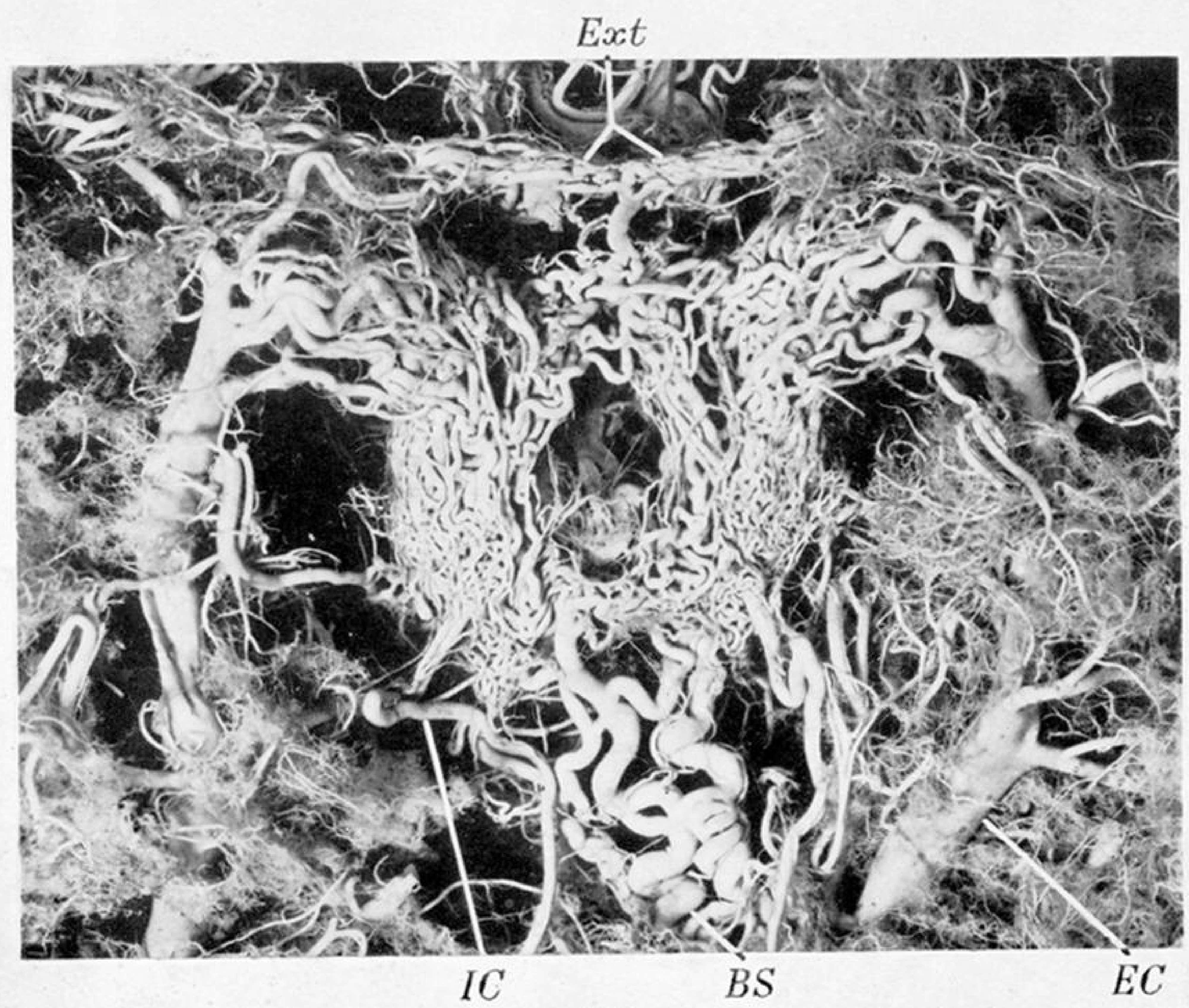

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PLATE 17

FIGURE 26. *Bos taurus*. Neoprene latex cast of the right carotid rete of a calf, seen from below. This is another example of an intracranial carotid rete. In this animal the arteria anastomotica is represented by several large trunks. The ramus anastomoticus and the basi-sphenoidal arterial plexus (which receives blood from the occipital arteries) also supply the rete. The internal carotid artery is seen approaching the rete, to which it contributes a few small vessels. It then passes through the midst of the rete and joins the circle of Willis. (Magn. ×2·7.)

FIGURE 27. Same specimen as in figure 26 viewed from lateral aspect. Note the small calibre of the ramus anastomoticus; its origin from the internal maxillary artery is by a double root. (Magn. ×2·1.)

FIGURE 28. Calf. Neoprene latex cast of right and left carotid retia and associated vessels, viewed from below. Note the free communication between the two retia across the mid-line, both anteriorly and posteriorly. The ring of vessels thus formed surrounds the hypophysis cerebri. The basi-sphenoidal arterial plexus can be seen joining the retia posteriorly. Anteriorly there is an extension of the two retia which is normally V-shaped but has been spread out in displaying the specimen. (Magn. ×1·4.)

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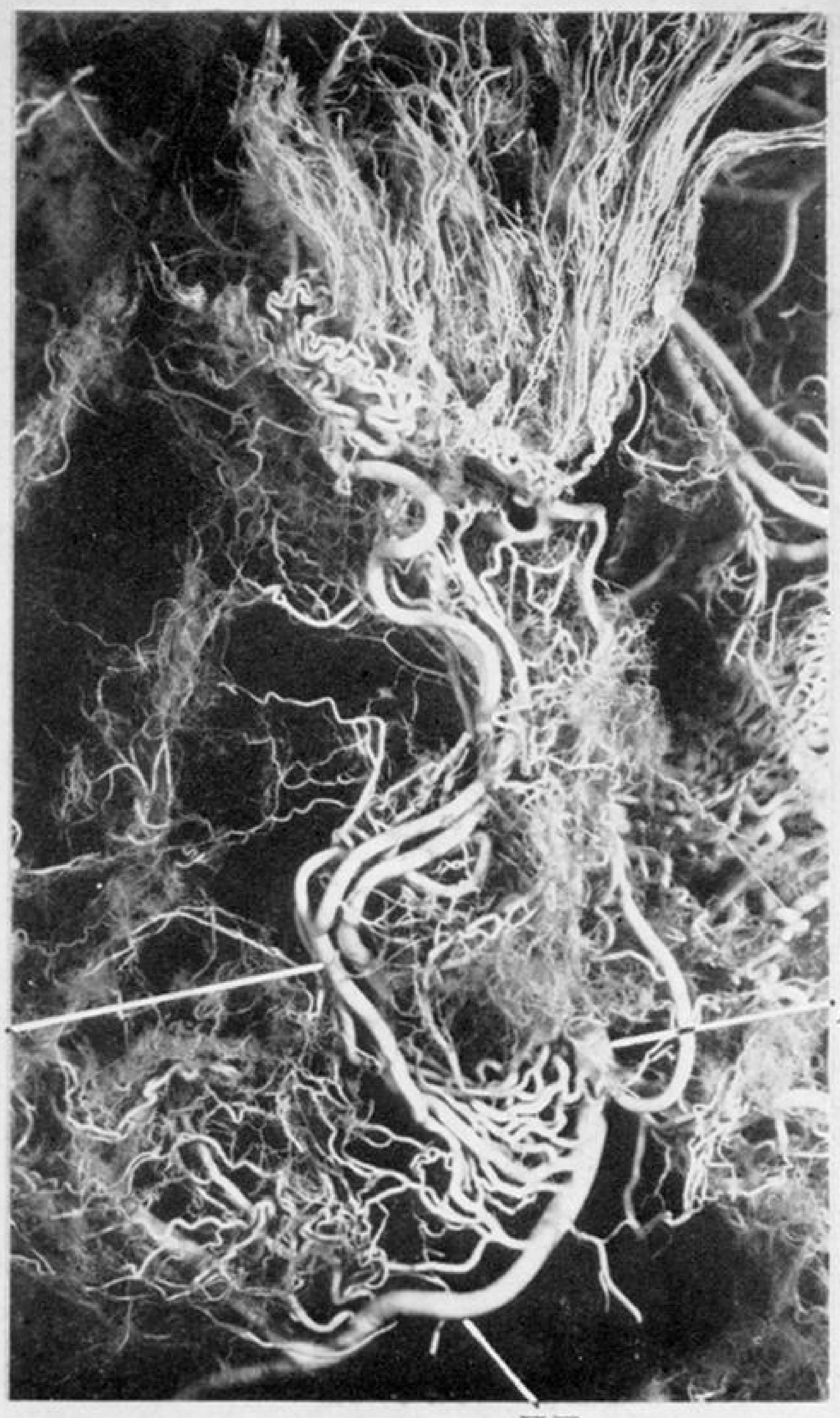

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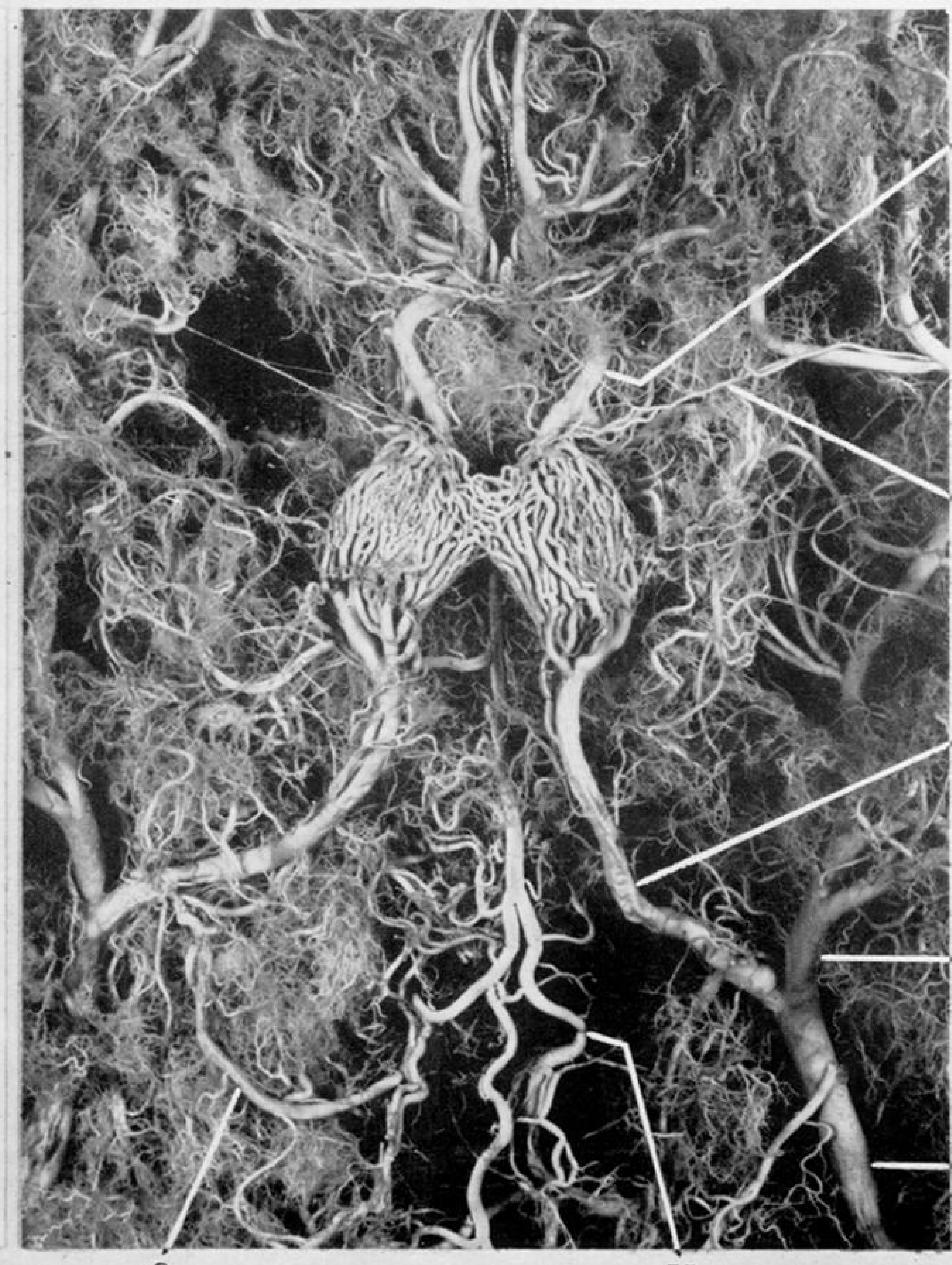

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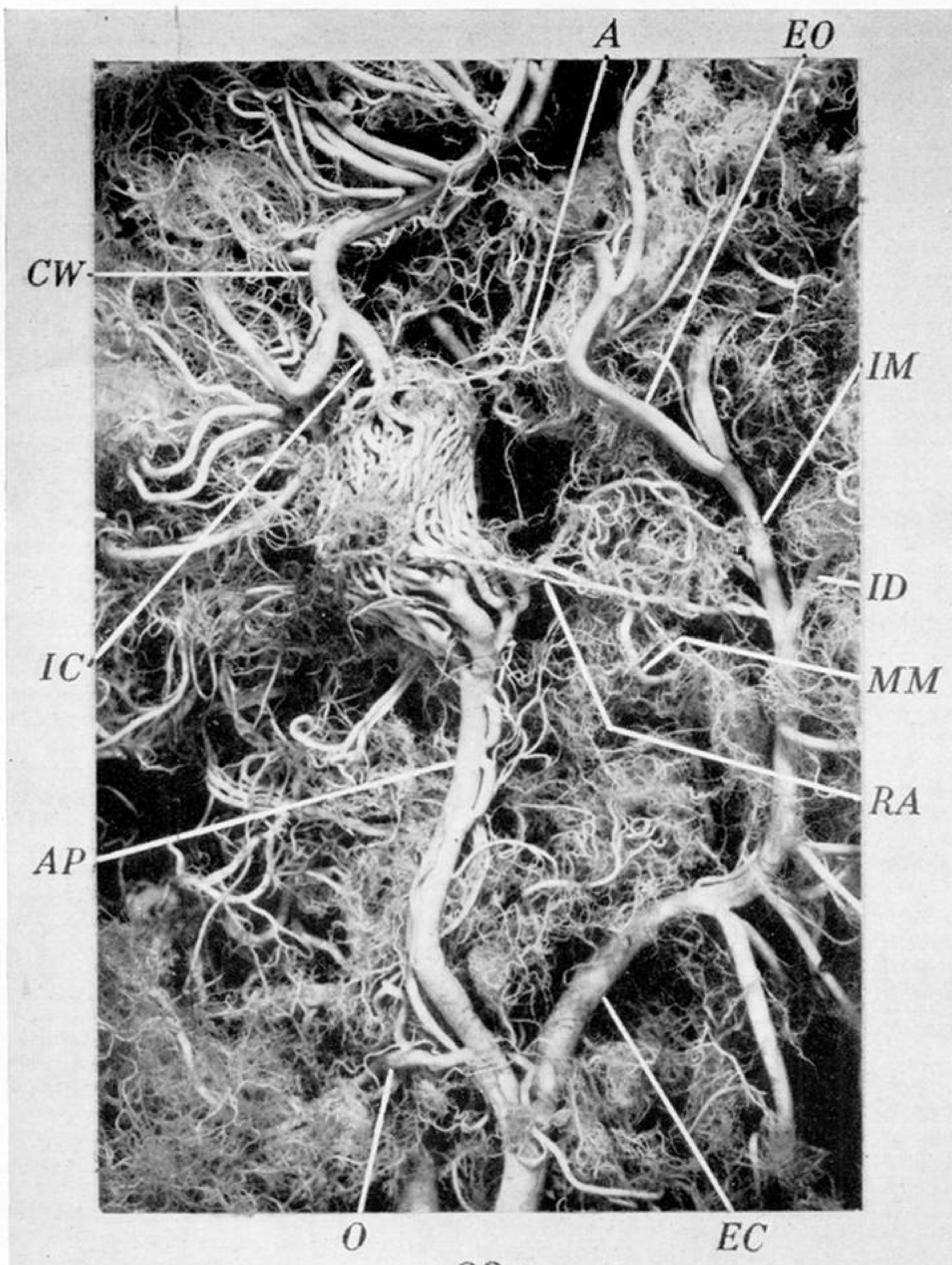
PLATE 18

FIGURE 29. Calf. Neoprene latex cast of circle of Willis seen from above. Note the small calibre of the basilar artery. (Magn. × 2·1.)

FIGURE 30. Calf. Neoprene latex cast showing right orbital rete and ciliary arteries. The vessels of this rete spring from the external ophthalmic artery and join together to form two ciliary arteries. The latter break up into serpentine vessels which give rise to the long and short ciliary branches (seen above). (Magn. × 1·8.)

FIGURE 31. *Sus scrofa*. Radiograph of head of young pig in ventro-dorsal projection. The arteries had been injected with bismuth carbonate. In this species also the carotid rete is situated intracranially, but the vessel from which it derives its main blood supply is the ascending pharyngeal artery. The circle of Willis is well seen. (Natural size.)

FIGURE 32. Young pig. Neoprene cast of the right and left carotid retia and related vessels, seen from below. Compare the shape of these retia and the pattern of their vessels with those seen in the retia of the sheep (figure 17), goat (figure 25) and ox (figure 28). Note the large calibre of the ascending pharyngeal artery and the tenuous arteria anastomotica. The ramus anastomoticus is also a small vessel and is better seen in figure 33. The single trunk formed by the junction of the two anterior cerebral arteries (see figure 5) is not visible here. (Magn. × 2·0.)



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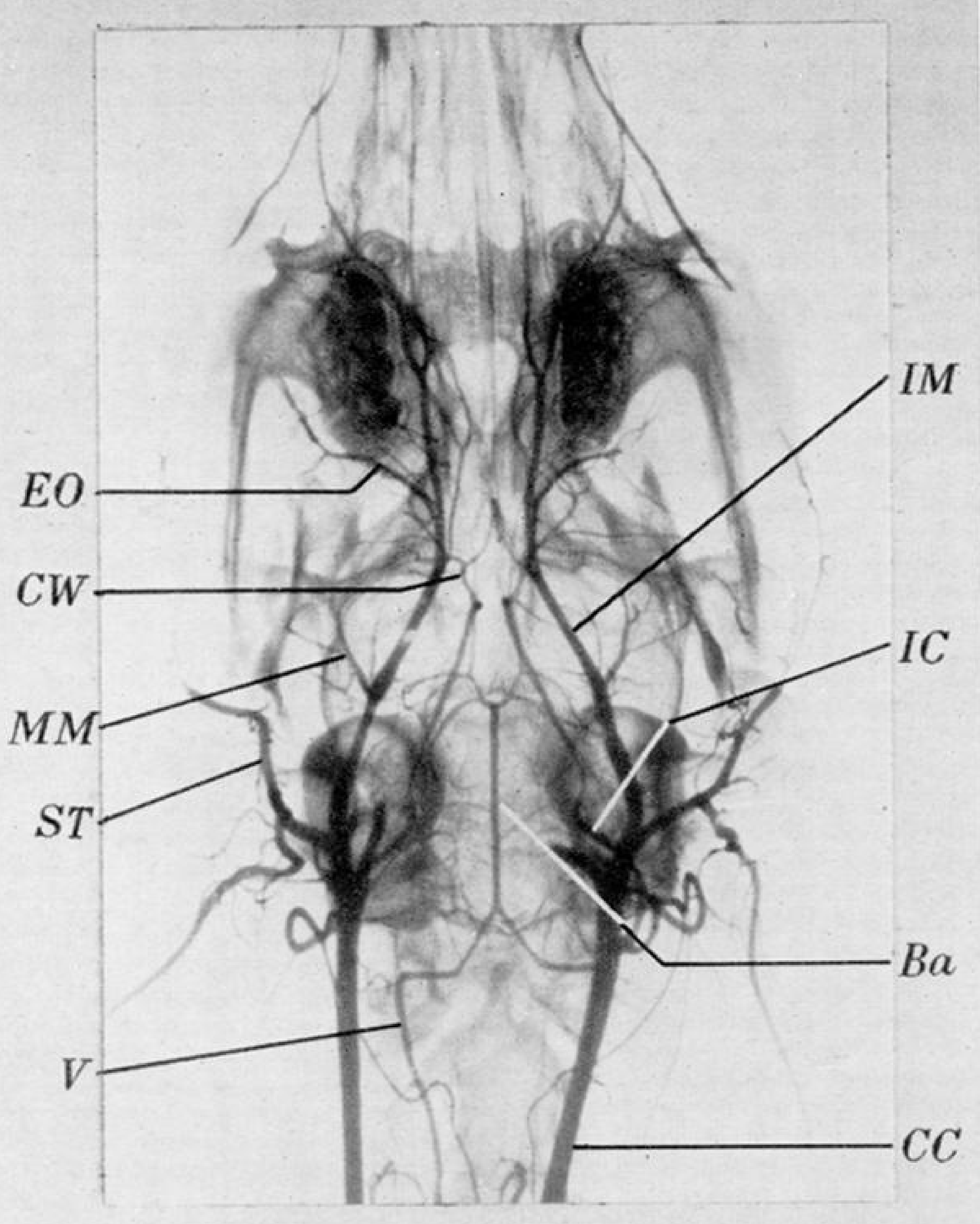

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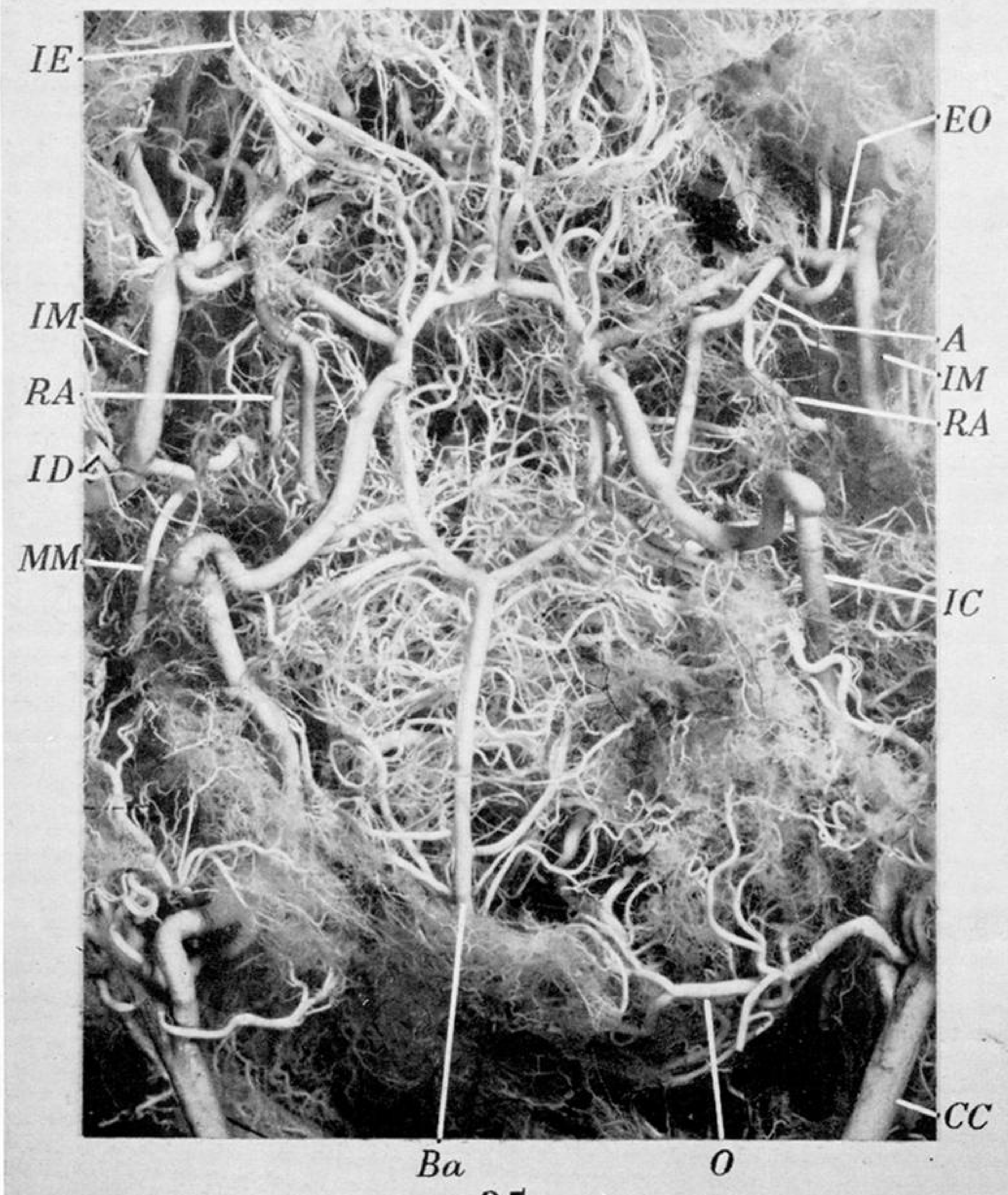

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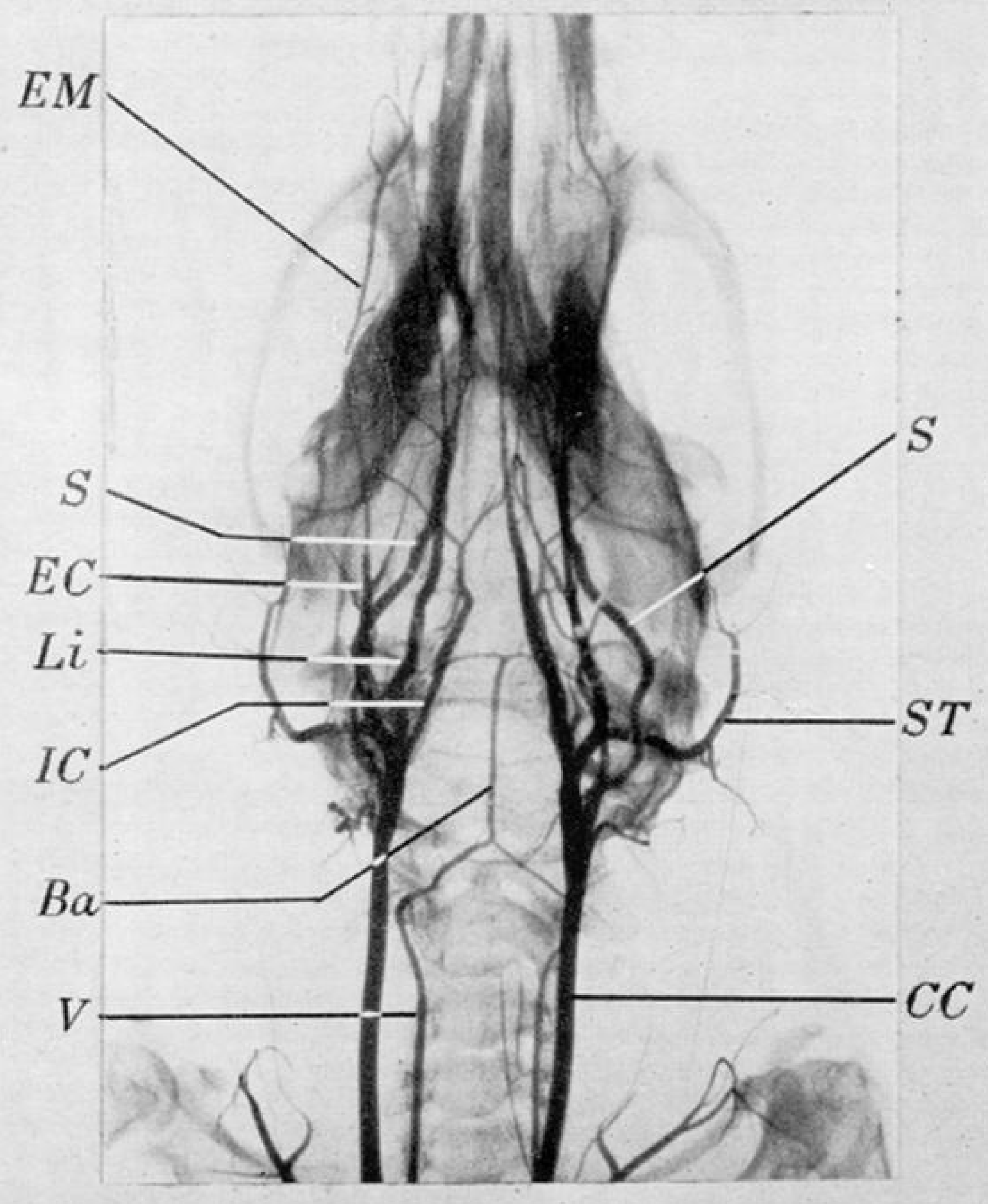

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Plate 19

Figure 33. Young pig. Neoprene cast of the right carotid arterial system seen from the lateral aspect. Compare the calibre of the ascending pharyngeal artery with that of the external carotid artery. Note how the vessels springing from the anterior end of the rete join to form the terminal part of the internal carotid artery. The origin of the tenuous arteria anastomotica from the external ophthalmic artery can be seen. Note the small calibre of the ramus anastomoticus beyond the origin of the relatively large middle meningeal artery. (Magn. × 2·5.)

Figure 34. *Oryctolagus cuniculus*. Radiograph of head of rabbit in ventro-dorsal projection after an arterial injection of bismuth carbonate (lower jaw removed). There is no carotid rete in this species. The circle of Willis is supplied by the internal carotid arteries and by the vertebral arteries (via the basilar artery). (Natural size.)

Figure 35. *Canis familiaris*. Neoprene latex cast of the right and left carotid arterial system of a dog seen from below. In this species there is no carotid rete, though there are a few small vessels in the cavernous sinus which may be considered as a counterpart of this structure (see figure 6). The internal carotid artery is a vessel of large calibre and is joined at the posterior end of the cavernous sinus by the arteria anastomotica. The latter vessel, which arises from the root of the external ophthalmic artery, receives the ramus anastomoticus midway along its course. (Magn. × 2·0.)

Figure 36. *Rattus norvegicus*. Radiograph of head of rat in ventro-dorsal projection after arterial injection of bismuth carbonate. There is no carotid rete in this species, and the territory which in other species is supplied by the internal maxillary artery is supplied in the rat by the stapedial artery. The circle of Willis receives its blood supply from the internal carotid arteries and from the vertebral arteries (via the basilar artery). (Magn. × 1·6.)